Ecosystem Services of Palmiet Wetlands: The Role of Ecosystem Composition and Function

Ecosysteemdiensten van Palmiet-Moerassen: De Rol van Ecosysteem Compositie en Functie

Ekosisteemdienste van Palmiet Vleilande: Die Rol van Ekosisteem Samestelling en Funksie

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Photographs:
Front cover: Theewaterskloof palmiet wetland with brightly-coloured fynbos on the hills in the foreground and background.
Back cover: Photograph taken from the centre of the Theewaterskloof palmiet wetland in a palmiet community with *Psoralea* sp emerging from the shrub layer.

“By the time it came to the edge of the Forest, the stream had grown up, so that it was almost a river, and, being grown-up, it did not run and jump and sparkle along as it used to do when it was younger, but moved more slowly. For it knew now where it was going, and it said to itself, “There is no hurry. We shall get there some day.” But all the little streams higher up in the Forest went this way and that, quickly, eagerly, having so much to find out before it was too late.”

-A. A. Milne (The House at Pooh Corner)

Declaration

By submitting this thesis electronically, I declare that the entirety of the work contained therein is my own, original work, that I am the sole author thereof (save to the extent explicitly otherwise stated), that reproduction and publication thereof by the University of Antwerp or Stellenbosch University will not infringe any third party rights and that I have not previously in its entirety or in part submitted it for obtaining any qualification.

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In the words of a wise musician:

Soli Deo Gloria

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Summary

Ecosystems are the critical infrastructure that provides society with multiple essential services. A change from one land-use to another (e.g. wetlands to agriculture) may result in trade-offs, or synergies, between different ecosystem services. As land globally becomes increasingly limited, there is greater emphasis being placed on whether ecosystems are being used optimally, in terms of their potential to provide services. Therefore a strong theoretical and empirical understanding of how ecosystems are structured, how they function and how this links to the delivery of ecosystem services is crucial in order to optimize benefits to society. Of all ecosystems, wetlands are considered to be one of the richest in terms of services provided, yet the complexity of wetland ecology has resulted in them being the least studied. South African wetlands are not well understood and many of these wetlands are in decline.

This dissertation focusses on palmiet wetlands in the Cape Floristic Region of South Africa and has four main aims: (1) to research scientifically sound measures to quantify ecosystem services (Chapter 2), (2) to map the current and historical spatial distribution of palmiet wetlands in South Africa (Chapter 3), (3) to learn about how these wetlands function to bring about the provision of ecosystem services by investigating the link between these ecosystem services, ecosystem functioning and functional diversity of wetlands at a landscape scale (Chapters 4, 5, 6, 8, 9), and (4) to test whether wetland functional groups are spectrally distinct, which may have useful applications for hyperspectral mapping of wetland ecosystem services (Chapter 7).

The main findings can be summarised in seven points. (1) Ecosystem services are not yet being adequately quantified (Chapter 2). (2) Palmiet wetlands have decreased by 31% since the 1940's (Chapter 3). (3) Channel erosion in palmiet wetlands has caused a change in water and soil quality and a shift in plant communities (Chapter 4). (4) Relative groundwater depth and soil pH explain patchiness in palmiet wetlands to some extent (Chapter 5). (5) Abiotic variables and various community weighted means were key in underpinning wetland ecosystem properties in palmiet wetlands (Chapter 6). (6) Functional groups, and even species, in palmiet wetlands appear to be spectrally distinct (Chapter 7). (7) Palmiet wetlands provide valuable ecosystem services to society, particularly the sequestration of carbon, water purification and flood attenuation (Chapters 8, 9). In conclusion, these findings highlight the uniqueness and value of palmiet wetlands, making a case for their conservation and restoration.

Samenvatting

De maatschappij is afhankelijk van ecosystemen voor tal van essentiële diensten. Een verandering in landgebruik (bijvoorbeeld moeras naar landbouw) kan leiden tot trade-offs of win-win situaties tussen verschillende ecosysteemdiensten. Door het wereldwijd schaarser worden van land wordt er meer nadruk gelegd op het optimaal benutten van ecosystemen in termen van ecosysteemdiensten. Een grondige theoretische en empirische kennis van hoe ecosystemen zijn gestructureerd, hoe ze functioneren en hoe dit leidt tot ecosysteemdiensten is cruciaal om deze voordelen voor de mens te optimaliseren. Moerasecosystemen worden als één van de rijkste ecosystemen in termen van ecosysteemdiensten beschouwd. Hun complexiteit heeft er echter toe geleid dat het één van de minst bestudeerde ecosystemen zijn. De kennis van Zuid-Afrikaanse moerassen in het bijzonder is beperkt waardoor ze sterk achteruitgaan.

Deze thesis focust op palmiet moerassen in de Floraregio van de Kaap van Zuid-Afrika en heeft 4 centrale doelen: (1) wetenschappelijk gefundeerde methodes voor het berekenen van ecosysteemdiensten bestuderen (Hoofdstuk 2), (2) de historische en huidige ruimtelijke verspreiding van palmiet moerassen in Zuid-Afrika in kaart brengen (Hoofdstuk 3), (3) inzicht krijgen in hoe deze moerassen functioneren en hoe dit leidt tot ecosysteemdiensten door de link tussen ecosysteemdiensten, ecosysteemfunctioneren en functionele diversiteit van moerassen op landschapsschaal te bestuderen (Hoofdstukken 4, 5, 6, 8 en 9), en (4) na te gaan of functionele groepen van moerassen spectraal verschillen, met als toepassing het hyperspectraal karteren van moerasecosysteemdiensten (Hoofdstuk 7).

De belangrijkste bevindingen kunnen samengevat worden in 7 punten. (1) Ecosysteemdiensten worden momenteel nog niet op een adequate manier gekwantificeerd (Hoofdstuk 2). (2) Palmiet moerassen zijn met 31% achteruitgegaan sinds 1940 (Hoofdstuk 3). (3) Oevererosie in palmiet moerassen heeft geleid tot een verandering in water- en bodemkwaliteit en in plantsamenstelling (Hoofdstuk 4). (4) Relatieve grondwaterdiepte en bodem pH verklaren voor een stuk de fragmentatie van palmiet moerassen (Hoofdstuk 5). (5) Abiotische variabelen en verschillende gemeenschapsgewogen gemiddeldes zijn sleutelelementen die de ecosysteemkenmerken van palmiet moerassen typeren (Hoofdstuk 6). Functionele groepen, en zelfs soorten, van palmiet moerassen blijken spectraal verschillend te zijn (Hoofdstuk 7). (7) Palmiet moerassen voorzien in belangrijke ecosysteemdiensten voor de maatschappij, met name koolstofopslag, waterzuivering en overstromingsbeperking (Hoofdstukken 8, 9). Deze bevindingen benadrukken de eigenheid en de waarde van palmiet moerassen en onderstrepen het belang van hun bescherming en herstel.

Opsomming

Ekosisteme is die kritiese infrastrukture wat die samelewing voorsien van verskeie noodsaaklike dienste. `n Verandering van een landgebruik na `n ander (bv. van vleilande tot landbou) kan lei tot kompromieë, of interaksies, tussen verskilende ekosisteemdienste. Soos wat land wêreldwyd toenemend skaarser word, word daar groter klem geplaas op die vraag of ekosisteme optimaal gebruik word in terme van hul potensiaal om dienste te lewer. Dus, `n grondige teoretiese en empiriese begrip van die strukturering van ekosisteme, hul funksionering en hoe dit verband hou met die lewering van ekosisteemdienste is noodsaaklik om die voordele vir die samelewing te optimaliseer. Van alle ekosisteme word vleilande beskou as van die rykste in terme van dienste wat verskaf word, maar die kompleksiteit van vleiland-ekologie het tot gevolg dat hulle die minste bestudeer word. Voldoende begrip van Suid-Afrikaanse vleilande ontbreek en heelwat van hierdie vleilande is aan die agteruitgang.

Hierdie proefskrif fokus op die palmiet-vleilande in die Kaapse Floristiese Streek van Suid-Afrika en het vier hoofdoelstellings: (1) om wetenskaplike gefundeerde maatreëls te ondersoek vir die kwantifisering van ekosisteemdienste (Hoofstuk 2), (2) om die huidige en historiese ruimtelike verspreiding van palmiet-vleilande te kaarteer (Hoofstuk 3), (3) om te leer oor hoe hierdie vleilande funksioneer om die verskaffing van ekosisteemdienste te bewerkstellig deur die verband tussen hierdie ekosisteemdienste, die funksionering van die ekosisteem en funksionele diversiteit van vleilande op `n landskapskaal te ondersoek (Hoofstukke 4, 5, 6, 8 en 9), en (4) om te toets of funksionele groepe van vleilande spektraal verskillend is, wat om die beurt nuttige toepassings vir hiperspektrale kartering van vleiland-ekosisteemdienste kan hê (Hoofstuk 7).

Die belangrikste bevindings kan in sewe punte opgesom word. (1) Ekosisteemdienste word nog nie voldoende gekwantifiseer nie (Hoofstuk 2). (2) Palmiet-vleilande het sedert die 1940's met 31% afgeneem. (3) Kanaal erosie in palmiet-vleilande het `n verandering in water- en grondkwaliteit en `n verskuiwing in plantgemeenskappe veroorsaak (Hoofstuk 4). (4) Relatiewe grondwaterdiepte en grond pH verduidelik, tot `n sekere mate, fragmentasie in palmiet-vleilande (Hoofstuk 5). (5) Abiotiese veranderlikes en verskeie gemeenskapsgewigte middele was die sleutel tot die ondersteuning van vleiland-ekosisteemeienskappe in palmiet-vleilande (Hoofstuk 6). (6) Funksionele groepe, en selfs spesies, in palmiet-vleilande, blyk spektraal verskillend te wees (Hoofstuk 7). (7) Palmiet-vleilande bied waardevolle ekosisteemdienste aan die samelewing, veral die sekwestrasie van koolstof, watersuiwering en vloeddemping (Hoofstukke 8 en 9). Ten slotte word `n saak gemaak vir die bewaar en herstel van palmiet-vleilande deur die beklemtoning van die bevindings aangaande die uniekheid en waarde van palmiet-vleilande.

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1

Introduction

The pristine Goukou palmiet wetland fills a valley-bottom near Riversdale in the Western Cape of South Africa. In the foreground fynbos is pictured on the hillslope, while in the distance agriculture (light yellow) and alien tree invasion (mostly Black Wattle) can be seen adjacent to the wetland (dark green).

1.1 Introduction

Ecosystems are the critical infrastructure that provide society with multiple essential services (MEA, 2005). A change from one land-use to another (e.g. natural vegetation to agriculture) may result in trade-offs, or synergies between different ecosystem services (Bennett et al., 2009; Smith et al., 2013). As land globally becomes an increasingly limited resource, greater emphasis is being placed on the optimal use of ecosystems, in terms of their potential to provide services (Van der Biest et al., 2014). Therefore a strong theoretical and empirical understanding of how ecosystems are structured, how they function and how this links to the delivery of ecosystem services is crucial to optimize benefits to society. Additionally robust measurements of both the stocks and flows of ecosystem services are required for decision makers (Crossman et al., 2012).

Biodiversity, one of the most important components of ecosystems, is in global decline (Blignaut and Aronson, 2008; Chapin et al., 2000; Daily, 1997; de Groot, 1992). Despite its importance, there is limited understanding of the links between biodiversity, ecosystem function, and ecosystem services. Chapin et al. (2000), in their review on the consequences of changing biodiversity, note a strong coupling of species diversity, ecosystem function and societal cost or benefit; and they call for further research to elucidate this connection. More recently, Nagendra et al. (2013) emphasise that despite much work being done on the connection between biodiversity and ecosystem function, the processes by which biodiversity affects ecosystems, remain insufficiently understood. Even less is understood about the relationship between ecosystem function and the provision of ecosystem services (Nagendra et al., 2013).

Functional traits, traits of organisms with demonstrable links to their function, correlate more strongly with ecosystem function than number of species *per se* (Díaz and Cabido, 2001). Therefore measuring and analyzing the functional traits of biotic components making up ecosystems could provide insight into ecosystem functioning, and possibly improve understanding of delivery of ecosystem services (Díaz and Cabido, 2001). Functional traits of plants have received particular attention, although interactions of plants with organisms of other trophic levels may also play a role in ecosystem functioning (Díaz et al., 2007; Lavorel et al., 2013). The study of traits of other key trophic groups, such as: microbes, soil macro and micro fauna, and fungi, requires specialist knowledge and are often expensive to quantify. As plant functional traits are often easy to quantify spatially, they are a useful tool to investigate the effects of biotic components of an ecosystem on ecosystem functioning (Díaz et al., 2007). In a recent study, Lavorel et al. (2011) attempt to use plant functional traits in combination with land-use and abiotic data to understand and map ecosystem service delivery. The need for a spatially explicit understanding of ecosystem service provision and spatial data on plan functional traits presents an opportunity for the use of remote sensing based methods (Lavorel et al., 2011; Ustin and Gamon, 2010). This is because spectral signatures of leaf chemistry or various other plant functional traits are able to act as surrogates for ecosystem properties or services (Lavorel et al., 2011).

Wetlands are considered to be one of the richest types of ecosystems in terms of ecosystem service supply, and yet the complexity of wetland ecology has resulted in them being the least studied system in ecosystem service science (de Bello et al., 2010). South African wetland studies are even scarcer, as little is known about the different types of wetlands, their distribution and functioning, and how wetland function in turn relates to ecosystem service provision (Sieben 2012; although see: SANBI 2009). South African wetlands and associated river systems are in a critical state, with over 65% reported to be damaged, and 50% estimated to have been destroyed (Nel et al., 2007). Increasing concern over South African wetland degradation has stimulated national–scale conservation and restoration efforts (e.g. Working for Water (Hobbs, 2004; van Wilgen et al., 1998)) and justifies urgent attention to research aimed at understanding the functioning and value of these wetlands. Palmiet wetlands are a unique type of South African wetland occurring throughout the Cape Floristic Region, one of the world's biodiversity hotspots (Myers et al., 2000). Palmiet wetlands are unchannelled valley-bottom peatlands, and as such provide many important ecosystem services to society (Rebelo, 2012), particularly water regulation, water purification and climate regulation (Moor et al., 2017). Nevertheless, there is very little known about these wetlands in terms of their composition and function, and they are extremely threatened (Rebelo, 2012).

1.2 Research Purpose

This dissertation aims to develop an understanding of the composition and functioning of South African palmiet wetland systems and how these relate to ecosystem services provided by these wetlands. Secondly it aims to further the theoretical understanding of the links between functional diversity and ecosystem function at several different scales (regional and landscape scales), using a combination of fieldwork, mapping and remote sensing techniques. The motivation for this research is to contribute to knowledge that can inform conservation and restoration efforts, and possibly to even inform policy and land-use planning. There are four main objectives of this dissertation, which form the basis of one synthesis chapter and eight data chapters.

The objectives are as follows:

1. Research robust (scientifically sound) methods/indicators to measure ecosystem services (**Chapter 2**).
2. Map the current and historical spatial distribution of palmiet wetlands in South Africa (**Chapter 3**).
3. Gain knowledge on how wetlands function to bring about the provision of ecosystem services by investigating the link between these ecosystem services, ecosystem functioning and functional diversity of wetlands at a landscape scale in South Africa (**Chapters 4, 5, 6, 8, 9**).
4. Test whether functional groups are spectrally distinct, the first step in investigating whether a hyperspectral remote sensing technique could be a possibility for ecosystem service hotspot mapping (**Chapter 7**).

1.3 Research Statement

The value that wetlands provide to society in terms of the provision of ecosystem services is not fully appreciated, largely because its value has neither been adequately quantified nor properly understood. The overall aim of this dissertation is thus of an exploratory nature and aims to answer the following question:

What is the role of functional diversity in ecosystem function and how do these both relate to ecosystem services provided by South African palmiet wetlands?

1.4 Definition of Key Terms and Concepts

The key concepts used in this study: ecosystem services, ecosystem function and ecosystem properties are often confused in the field of ecosystem service science. When attempting to measure an ecosystem service (e.g. climate regulation), an ecosystem function might be measured instead (e.g. carbon sequestration). It is therefore essential to define these key concepts, as well as some others used throughout this dissertation:

Ecosystem properties (or structure) refers to the abiotic and biotic components of an ecosystem, the "biophysical architecture" (TEEB, 2013).

Ecosystem function (or processes) refers to intrinsic ecosystem processes whereby ecosystem properties interact in time and space (MEA, 2005). Examples include nutrient cycling, decomposition and carbon sequestration. It was beyond the scope of this study to quantify ecosystem processes in the field, and therefore proxies were used.

Ecosystem services are the benefits that society derive from ecosystems (MEA, 2005), and may be divided into three main categories: provisioning, regulating and cultural ecosystem services (Haines-Young and Potschin, 2013), though there is much contention over the classification of ecosystem services, and even the name (*c.f.* 'natures benefits'). In this dissertation, ecosystem services are defined as the final services that are provided to society, and intermediate (supporting) ecosystem services are considered as ecosystem functions (e.g. nutrient cycling is not considered an ecosystem services, but part of ecosystem function that provides the service: soil quality).

An ecosystem service hotspot is defined as an area that provides a large proportion of a particular ecosystem service (Egoh et al., 2009). Ecosystem service synergies refers to the relationship among multiple ecosystem services whereby services either increase together or decrease together (Bennett et al., 2009). Ecosystem service trade-offs refers to situations whereby one service increases and another decreases. Synergies and trade-offs occur through one of two different mechanisms proposed by Bennett et al. (2009): simultaneous response to the same driver, or interactions among the ecosystem services themselves.

Functional traits are specific characteristics of organisms which have demonstrable links to their role or function in an ecosystem (de Bello et al., 2010). Functional traits may be divided into response traits (the traits that demonstrate how a driver affects an organism) and effect traits (traits which result in an effect on the ecosystem) (Lavorel and Garnier, 2002).

Channelization in this dissertation refers to the process of channel formation in wetlands through erosion (Brown, 1988).

1.5 Scope of Research

When dealing with ecosystem services, I use the Common International Classification of Ecosystem Services (CICES, Haines-Young and Potschin, 2013) rather than the typical Millennium Ecosystem Assessment classification (MEA, 2005). This is because CICES considers only 'final ecosystem services', which makes more sense when dealing with the mutually exclusive concepts of 'ecosystem function' (traditionally classified as 'supporting ecosystem services') and 'ecosystem services'. The CICES system classifies ecosystem services into three major categories: provisioning, regulating and cultural.

I use the concept of functional traits to try to understand ecosystem functioning. This implies that functional traits of all organisms are considered. However for logistical and financial reasons, this research did not consider all trophic levels and trophic interactions. The research focused on the functional traits of plants, given that autotrophs play a key role in ecosystem function. Functional traits of other organisms, especially soil microbes and macrofauna, are acknowledged to play a key role in ecosystem function, and this omission is a limitation of this research.

1.6 Study systems: palmiet wetlands

South African palmiet wetlands get their name from a wetland sedge called 'palmiet', *Prionium serratum.* This is a unique species, one of only four in its family (Thurniaceae) (**Plate 1**). Palmiet is a peat-forming plant, thought to be an ecosystem engineer, with unique properties enabling it to survive the high stress valley-bottom environment (Rebelo, 2012; Sieben, 2012). Palmiet wetlands are dominated by Palmiet and interspersed with fynbos wetland communities. Palmiet wetlands occur throughout the Cape Floristic Region of South Africa, which has a mediterranean-type climate characterised by summer drought and winter rainfall resulting from the passage of cold fronts (Midgley et al., 2003). The soils of the Cape Floristic Region are mainly highly leached dystrophic lithosols (soils without clearly defined layers) associated with the sandstone mountains of the Cape Supergroup (Midgley et al., 2003).

Plate 1. Palmiet, *Prionium serratum*, the species dominating palmiet wetlands. The image on the top right shows the sieve like structures that dead leaves form, and the image on the bottom left shows the peat that forms.

In this dissertation, three palmiet wetlands in three different catchments located throughout the Cape Floristic Region were selected for fieldwork: the Theewaterskloof and Goukou wetlands (Western Cape) and the Kromme wetland (Eastern Cape) (**Plate 2, Fig. 1**). Despite being situated as much as 470 km apart, these wetlands are remarkably similar in vegetation composition. They occur on low gradients below altitudes of 400 m. All three wetlands have accumulated peat layers between 0.5-10 m deep, thought to decrease in thickness in a downstream direction (Job, 2014; Nsor, 2007).

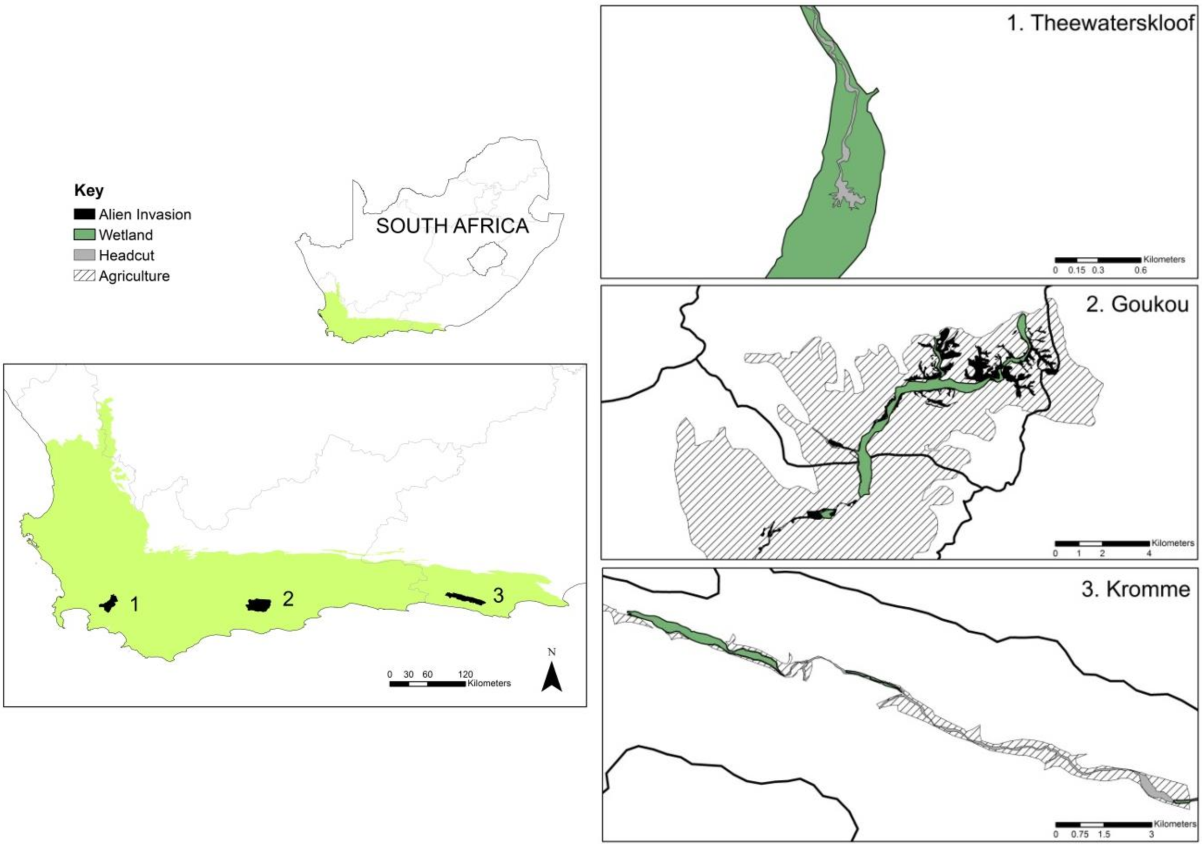

Figure 1. The three study palmiet wetlands in their respective catchments (labelled 1-3) in the Cape Floristic Region of South Africa (light green).

Plate 2. Panoramic photographs of three relatively pristine sections of the study wetlands: (a) Theewaterskloof, (b) Goukou and (c) Kromme showing the valley-bottom nature of these unchannelled palmiet wetlands.

Major Threats to Palmiet wetlands

The value of palmiet wetlands in terms of water purification, amongst other ecosystem services, has been overlooked in favour of their potential for fertile soil for food provision. Therefore, many of these palmiet wetlands have been ploughed up for agriculture, either for orchards or grazing. The remaining wetlands are threatened by a plethora of different problems, including: land-use change (wetlands removed to make place for agriculture), gully/channel erosion, pollution from agricultural runoff (lime, fertilizers), invasion by alien vegetation, increasingly extreme flood events (climate change), and inappropriate fire regimes (Beukes et al., 2012; Job, 2014; Rebelo, 2012; Rebelo et al., 2015) (**Plate 3**).

Arguably one of most pressing threats to palmiet wetlands is gully/channel erosion due to headcuts which undermine existing peatbeds (**Plate 4**). Any disturbance to wetland vegetation, such as vegetation removal for agriculture, a road or railway crossing intersecting the wetland, can cause a knick-point whereupon erosion acts. The high intensity floods that pass through these valley-bottoms create headcuts, resulting in large amounts of sediment washing downstream (Rebelo 2012) (**Plate 3**). These headcuts can be 3-5 m deep and several meters wide in places; this represents a substantial amount of sediment that cannot be replaced. This erosion is destructive for many reasons: it is hard to halt, it decreases water quality, causes sedimentation of dams and may result in a lowering of the water table. The latter ultimately perpetuates the cycle of degradation and can render adjacent agricultural land unusable. This wetland drainage would also result in decomposition and a net export of carbon dioxide into the atmosphere, contributing to global warming (Krüger et al., 2015).

Plate 3. Left: an aerial photograph of erosion damage taken after a flood event in the Kromme catchment (Pierre Joubert). The peatbeds and alluvium (a few meters deep) of this once existing palmiet wetland has been washed downstream after a severe flood event, typical for these valley-bottoms. Right: a satellite image of a section of the remaining Kromme palmiet wetland bordered by irrigated agriculture on both sides (Google Earth). Fringes of *Phragmites australis* (indicated by red arrows) stand testament to the runoff of fertilizers into the wetland. Upstream the wetland is channelized, and downstream a concrete restoration weir can be seen.

Plate 4. Left: Erosion damage to a valley-bottom palmiet wetland (Theewaterskloof). The peat beds are eroding, becoming exposed, drying out and further eroding, thus lowering the water table in the surrounding wetland, leading to wetland drainage. Right: erosion to bedrock (Kromme).

1.7 Significance of Research

This dissertation aims to advance the theoretical understanding of the linkages between biodiversity, ecosystem function and ecosystem services. Furthermore this research aims to extend the work of others on measuring ecosystem services through a replication of existing methodology, and possibly by improving these methods or developing new ones. There are substantial gaps in the literature in both theoretical and practical aspects of ecosystem service science, and this research aims to address these gaps using South African palmiet wetland ecosystems.

This research is important because decision makers need accurate, scientific measurements of ecosystem services as well as good spatial understanding of stocks and flows of ecosystem services, and information on synergies and trade-offs between different ecosystem services. These results could feed into conservation and restoration planning, and possibly policy, with real implications for the protection of ecosystems and biodiversity (Cowling et al., 2008). One successful example of the mainstreaming of the ecosystem services concept is that of the Catskill Catchment in New York (Postel and Thompson, 2005). When faced with watershed restoration or the building of a new water treatments work for the city of New York, decision makers chose for restoration of the Catskill Catchment. As a result, holistic farm planning was developed as an attempt to decrease pollution of the watershed, and farmers were incentivized to pollute less. Through collaboration, cost efficiency was achieved and private as well as social benefits realized. Two of the three palmiet wetlands considered in this research are situated upstream of large municipal reservoirs which provide water for two of South Africa's larger cities: Cape Town and Port Elizabeth. Therefore protecting and conserving these wetlands will have direct, tangible benefits to society.

1.8 Chapter Overviews

The content of this PhD will be focusing from the broad to the fine scale; the first data chapter being at the most coarse scale (global), and the final chapters at the landscape scale (**Fig. 2**).

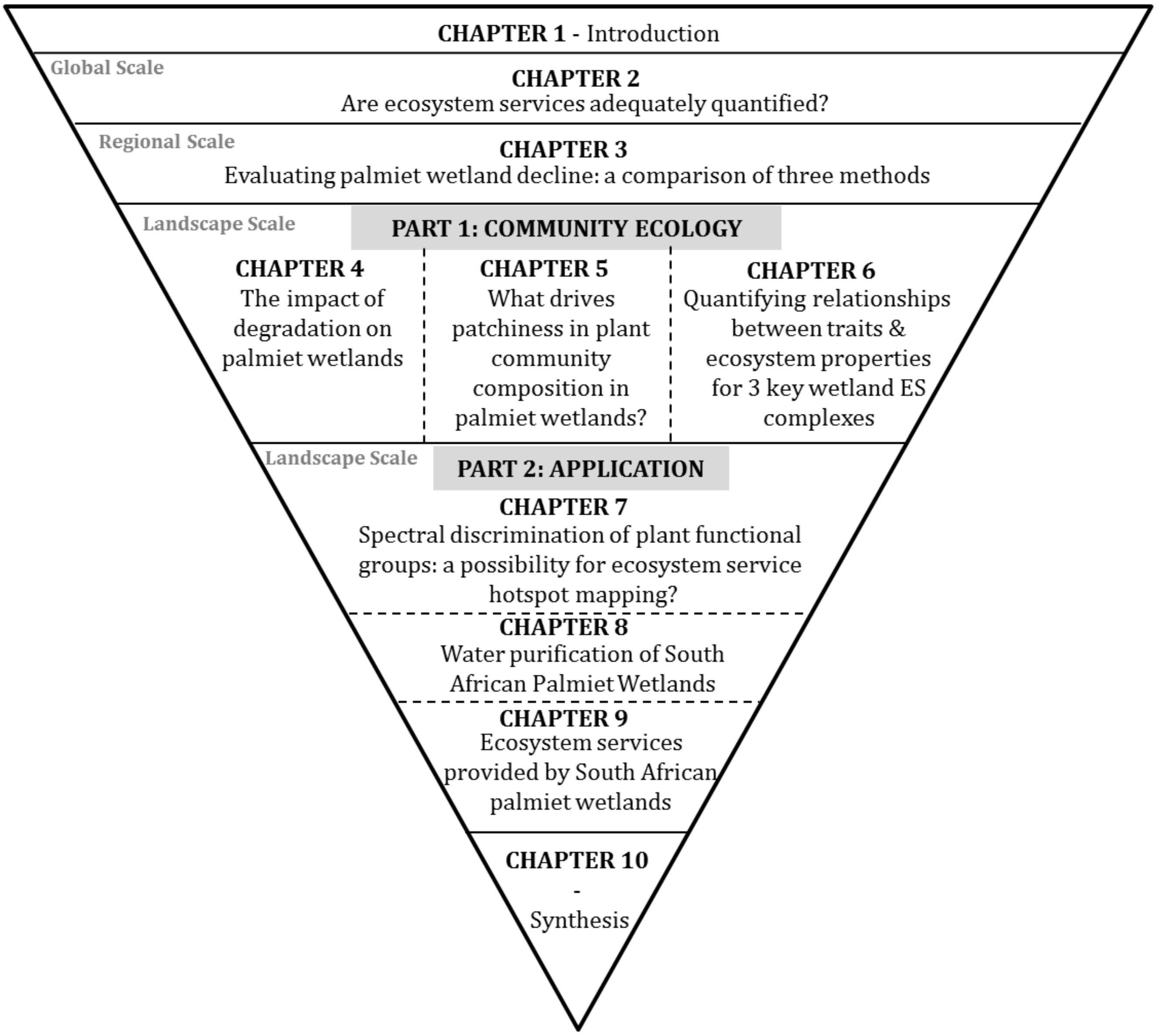

Figure 2. The conceptual framework of this thesis

Chapter 1 – Introduction

Chapter 2 – Are ecosystem services adequately quantified? This chapter forms the literature review for this PhD dissertation. It is presented in the form of a meta-analysis of the field of ecosystem services and includes an in-depth analysis on the robustness of methods used to measure ecosystem services. *Published: Journal of Applied Ecology.*

Chapter 3 – Evaluating palmiet wetland decline: a comparison of three methods. South African palmiet wetlands are highly threatened and many have already been destroyed, however their current and historical extents are not known. This chapter aims to investigate the spatial distribution of palmiet wetlands in South Africa, using a combination of remote-sensing, mapping and modelling techniques. *Published: Remote Sensing Applications: Society and Environment*

Chapter 4 – The impact of degradation on South African palmiet wetlands. The aim of this chapter was to investigate the impact of wetland degradation, primarily channel/gully erosion, on wetland properties and plant communities.

Chapter 5 – What drives patchiness in plant community composition in South African palmiet wetlands? Here I investigated possible abiotic explanations for plant community composition in palmiet wetlands as well as whether any plant functional traits could shed light on the trends observed.

Chapter 6 – Quantifying relationships between traits and ecosystem properties for three key wetland ecosystem service complexes. In this exercise, I aimed to understand key abiotic or biotic properties/processes underpinning the supply of three ecosystem services in palmiet wetlands: water regulation, water purification and carbon sequestration.

Chapter 7 – Spectral discrimination of plant functional groups: a possibility for ecosystem service hotspot mapping? The first aim of this chapter was to relate spectral signatures of dominant wetland species in South African palmiet wetlands to their traits. Secondly, I aimed to see whether functional groups, or species, were spectrally distinct. If this proved possible, it could have implications for ecosystem hotspot mapping in these wetland systems. *Submitted: Remote Sensing of Environment*

Chapter 8 – Water purification of South African Palmiet Wetlands. This short chapter aims to quantify the ecosystem service of water purification provided by South African Palmiet Wetlands in detail. These results feed into **Chapter 9**.

Chapter 9 – Ecosystem services provided by South African palmiet wetlands. This chapter firstly aims to perform a rapid assessment of ecosystem services provided by South African palmiet wetlands. Secondly this chapter aims to compare three of these rapidly measured services to more detailed methods of quantification. The three ecosystem services considered are: water regulation, water purification and carbon sequestration.

Chapter 10 – Synthesis. In closing, this synthesis chapter aims to draw together key findings across all scales, and consider the importance of the findings for restoration activities, conservation, and policy.

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2

Is the biophysical reality of ecosystem services adequately quantified?

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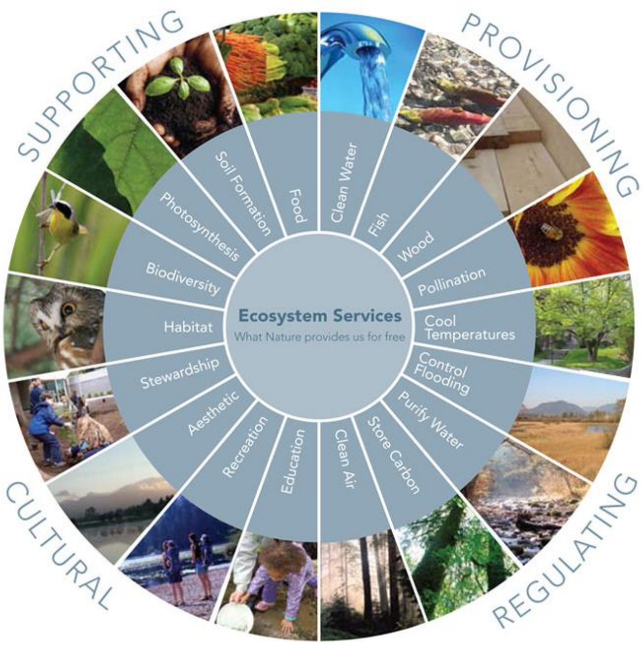


Picture credit: https://freshwaterwatch.thewaterhub.org/content/ecosystem-services:

Abstract

Quantification of ecosystem services is an important step in operationalizing the concept for management and decision making. With the exponential increase in ecosystem service research, ecosystem services have become a "catch-all phrase" which some suggest has led to a poorly defined, impractical and ambiguous concept. An overview of the methods used in ecosystem service quantification is needed to examine their scientific rigor and provide guidelines for selecting appropriate measures. We present a systematic review of 408 peer-reviewed ecosystem service research papers to address the question: is the biophysical reality of ecosystem services adequately quantified? We summarized all the measures used for each ecosystem service and two methods of analysis were used to answer the research question. Firstly we considered whether ecosystem service measures are scientifically robust by looking at four predefined criteria (e.g. uncertainty quantified or validation done). Secondly, using a novel approach, we determined which part of the ecosystem service cascade was measured: the ecosystem property, function, service, benefit or value. Our results showed that each ecosystem service had on average 24 different measures, suggesting a lack of consensus. We found that uncertainty is often not included and validation and stakeholder engagement mostly missing. When analyzing which part(s) of the ecosystem service cascade each measure corresponded to we found that for regulating ecosystem services, ecosystem properties and functions (ecological aspects) are more commonly quantified (67% of measures) compared to benefits and values (socio-economic aspects) for provisioning ecosystem services (68%). Cultural ecosystem services are predominantly quantified using scores (35%). In conclusion the biophysical reality of ecosystem services appears to be poorly quantified in many cases, as often only one side of the cascade is considered (either the ecological or socio-economic side) and oversimplified and variable indicators used. Policy implications: This review provides a detailed overview of ecosystem service quantification (ranging from simple scores to very advanced methods) with the aim to support future ecosystem service quantification and ultimately successful application of the ecosystem service concept.

2.1 Introduction

Ecosystem services are widely defined as "the benefits that humans derive from nature" (MEA, 2005; TEEB, 2010) and are seen as the link between biophysical reality (ecological system) and human wellbeing (socio-economic system) (Haines-Young and Potschin, 2010; TEEB, 2010). The ecosystem service cascade, originally developed by Haines-Young & Potschin (2010), provides a useful conceptual framework for operationalizing this, such that ecosystem properties (biophysical structure or stock), produce ecosystem functions (flows) which provide ecosystem services, that have benefits to mankind, to which a value (economic) can be attributed. This currently accepted ecosystem service cascade with its five parts has been widely adapted by many other researchers in varying degrees of complexity (e.g. Hernández-Morcillo et al., 2013; van Oudenhoven et al., 2012). Saarikoski et al. (2015) offer perhaps the most complicated ecosystem service cascade, dividing it into seven distinct entities by splitting ecosystem services into 'final' and 'intermediate' ecosystem services, and benefits into 'benefits' and 'human well-being'. On the other hand, Luederitz et al. (2015), when operationalizing the ecosystem service cascade, found ecosystem services and benefits to be synonymous. Whichever ecosystem service cascade is used, it is agreed that a full analysis of each ecosystem service requires that the essential parts of the cascade should be considered, as well as the relationships between them (de Groot et al., 2010; Haines-Young and Potschin, 2010).

The broad definition of ecosystem services has resulted in it becoming a "catch-all phrase" which some suggest has resulted in a poorly defined, impractical and ambiguous concept (Nahlik et al., 2012; Seppelt et al., 2011). However some consider that this same ambiguity promotes transdisciplinary research and encourages creativity (Schröter et al., 2014). Various methods are used to measure ecosystem services, ranging from simple scoring systems or rapid assessments to complex field-specific measurements. As ecosystem services are difficult to measure, indicators are often used as a proxy (Kandziora et al., 2013; Layke et al., 2012). The high diversity in measures used for the same ecosystem service, results in a lack of consistency, and many researchers often do not succeed in measuring the ecosystem service itself (Saarikoski et al., 2015). A full quantification of ecosystem services is difficult as multiple aspects of the ecosystem service cascade require inclusion and it is therefore not possible to have a single measure per ecosystem service (Kandziora et al., 2013; Van Oudenhoven et al., 2012). Some studies have addressed this by providing separate indicators for each part of the cascade with the aim to contribute towards a better quantification of ecosystem services (Hernández-Morcillo et al., 2013; Kandziora et al., 2013; Luederitz et al., 2015; Saarikoski et al., 2015; Van Oudenhoven et al., 2012).

There are also concerns about the scientific rigour of ecosystem service research which might be linked to the poor understanding and operationalization of the ecosystem service concept (Nahlik et al., 2012; Seppelt et al., 2011; Van der Biest et al., 2015). Common flaws include the confusion between the quantification of stocks and fluxes, for example measuring carbon stocks instead of carbon sequestration for the ecosystem service Climate Regulation (Boyd and Banzhaf, 2007), or the use of over-simplified proxies (Eigenbrod et al., 2010). Other problems are related to the type of data used in ecosystem service studies, which may not always be appropriate for the specific research question (e.g. data from databases, coarse mapping or data from literature) or scale (Busch et al., 2012; de Groot et al., 2010; Pinto et al., 2010). Additionally many studies do not distinguish between potential and actual supply of ecosystem services by an ecosystem (Van der Biest et al., 2014). In many cases maps, models and remote-sensing analyses are not validated, and in many studies there is no indication of uncertainty (Seppelt et al., 2011). In studies measuring more than one ecosystem service, interactions (trade-offs/synergies) among these ecosystem services are often not considered (Pinto et al., 2010; Seppelt et al., 2011; Smith et al., 2013).

When it comes to implications for policy and real-world application, stakeholder involvement is crucial but often lacking in ecosystem service research (Seppelt et al., 2011). Quality of ecosystem service studies depends to a large extent on constraints such as time, money, and data availability (Busch et al., 2012; de Groot et al., 2012; Layke et al., 2012), and in cases where these are limiting, rapid assessments are often used (de Groot et al., 2010). To help operationalize the concept, there is a need for an overview of the measures and indicators used in the field of ecosystem services. To address this we conduct a systematic review of the ecosystem services literature to examine the measures currently used to quantify each ecosystem service. The central research question of this review is: are current methods adequately quantifying the biophysical reality of ecosystem services? We address this question using two methods (1) we use a number of criteria to assess the scientific robustness of each measure, and (2) we use the five essential elements of the ecosystem service cascade to assess whether the ecosystem service is quantified in its entirety.

2.2 Methods

Based on nineteen key papers, reviews and meta-analyses of ecosystem service measures and indicators we selected 21 ecosystem services from three ecosystem service categories based on the typology from the TEEB (TEEB, 2010) and CICES (Haines-Young and Potschin, 2013) lists. We selected three ecosystem service categories, excluding supporting ecosystem services to avoid double counting and to ensure that only those traditionally considered as final ecosystem services were selected (Haines-Young and Potschin, 2013). Therefore 'nutrient cycling', 'biodiversity' and 'habitat' were not included as ecosystem services. We performed a systematic literature search in Elsevier's Science Direct database using the terms "ecosystem service" and "[the name of the ecosystem service]" e.g. "climate regulation" in abstracts, titles and keywords in April 2014. Where appropriate, key components of each ecosystem service were used in addition, to ensure that all literature on each ecosystem service was found (e.g. "carbon" for Climate Regulation) (**Table 1**). We identified 553 English language peer-reviewed papers which were divided and read. We excluded gray literature and books as this would build in a bias towards reports written in languages mastered by the authors. Any papers not explicitly measuring ecosystem services were excluded, resulting in a final number of 408 papers which were reviewed and captured in a database.

Table 1: List of ecosystem services and additional search terms used in the literature review

		Ecosystem Service	Additional Search Terms
Provisioning	1	Food Production	nutrition; fish
	2	Water Provision	drinking; irrigation
	3	Materials & Fibre	timber; raw material; wood
	4	Energy & Fuel	biomass; fuel
	5	Genetic Resources	
	6	Medicinal Resources	medicin*
	7	Ornamental Resources	
Regulating	8	Water Purification	water waste treatment; water nutrient; water quality
	9	Water Regulation	water flow; water quantity; flood prevention /attenuation; drought mitigation /prevention; storm protection; water retention
	10	Air Quality Regulation	fine dust (capture); air pollutants; dry deposition
	11	Soil Quality Regulation	soil formation; soil fertility; nutrient cycling (soil nutrients); weathering; recycling; microbial processes; decomposition
	12	Soil Retention	erosion; sedimentation (soil conservation)
	13	Climate Regulation	carbon; sequestration; gas
	14	Pollination	
	15	Life Cycle Maintenance	nurser* (nursery, nurseries)
	16	Biological Control	pest
Cultural	17	Recreation & Tourism	entertainment; amenity
	18	Scientific & Educational Services	cognitive development
	19	Heritage, Cultural, Bequest, Inspiration & Art	
	20	Aesthetic Services	well-being
	21	Symbolic, Sacred, Spiritual & Religious Services	

For each paper all studied ecosystem services were identified and key information recorded, including: paper descriptors (e.g. citation, year and journal), the ecosystem, scale and geographical information (location, country, and continent). The state of the ecosystem was noted if it was possible to discern from the paper whether the sites were pristine, degraded, restored or a combination of these. Lastly it was noted whether the paper had performed economic valuation. For each ecosystem service all measures presented in each paper were identified. The name of each measure, the method described and the units were recorded. Many papers considered more than one ecosystem service and many ecosystem services had more than one measure per paper. Therefore we have many more entries than the total number of papers (n= 1637 measures). All measures found per ecosystem service were summarised in a table (**see Supplementary Material**). Additional data included: whether the actual or potential ecosystem service is measured, whether interaction effects between ecosystem services were considered (only if more than one ecosystem service is considered in one paper), and whether scenarios were investigated. We also looked at potential societal impact by checking whether recommendations for policy makers or managers were included and whether stakeholders were involved in the project.

To determine whether the biophysical reality of ecosystem services are adequately quantified we used two key criteria. Firstly we considered whether the measures were scientifically robust by looking at whether uncertainty was calculated, whether validation was done (when relevant e.g. mapping, modelling, and remote-sensing studies) and what type of data were used. We included eight categories of 'data types': four 'active' (actual field measurements, mapping, modelling, and remote sensing), three 'passive' methods (theoretical studies, data from databases or literature) and additionally expert judgement. We also considered whether 'real' data are available (i.e. were data presented in the paper, or was the study theoretical or a simple score used). Secondly we looked at which part of the ecosystem service cascade was measured. We use the ecosystem service cascade structure of Van Oudenhoven et al. (2012) because they separate ecosystem properties from functions and do not confuse 'processes' and 'functions'. We defined the five categories according to strict definitions taken from widely accepted sources. Ecosystem properties, are defined as the biophysical structure of an ecosystem whereas ecosystem functions or processes are 'any change or reaction which occurs in an ecosystem (biophysical, chemical or biological) (TEEB, 2010). 'Ecosystem services' are defined as the "benefits mankind derive from nature" (MEA, 2005), whereas 'benefits' are 'positive changes in wellbeing from the fulfillment of needs and wants' (TEEB, 2010). Lastly 'value' is defined as the 'economic worth of the change in wellbeing'. Measures were assigned to each part of the ecosystem service cascade according to these accepted definitions and the consistency was controlled by an internal cross checking to minimize misclassifications. We included two additional categories, 'score' for all studies using scores either from social surveys, biophysical assessments or expert judgement, and 'other' for measures which did not fit into any of these categories (e.g. disservices). Some researchers considered more than one aspect of the ecosystem service cascade and each of these was recorded and these papers were noted.

2.3 General overview of ecosystem service research

The number of papers published in the field of ecosystem service science has been exponentially increasing since 2005 with about 90% of the research taking place from 2009 onwards (365 out of 408 papers in our review). These 408 papers are from a total of 74 journals, with three journals dominating (27%): Ecological Indicators, Ecological Economics and Agriculture, Ecosystems and Environment respectively. The five most studied ecosystem services are mainly regulating services (48%) and the five least studied ecosystem services are mainly provisioning (26%) and cultural ecosystem services (26%). Most papers studied only one or two ecosystem services (59%), only 25% investigated more than three and only one considered all 21. There appears to be a slight increasing trend in the number of papers studying more than three ecosystem services together since 2007. Ecosystem service studies have been conducted in many countries world-wide (83 countries in total), although a disproportionate number of studies (40%) have been done in only five countries (**Fig. 1**): the USA, China, UK, Australia and Germany. However this appears to be an artefact of population or country size. The majority of studies are carried out at a local or regional scale (81%) and in ecosystems that are the most intensively used by humans such as agriculture, forest, grassland and human settlements (e.g. built-up land, mines) (84%). Nevertheless, very few (20%) studies explicitly consider the state of the site (e.g. degraded, pristine or restored) or make a comparison between different states (13%). All ecosystems appear to be equally well represented in the studies on each continent.

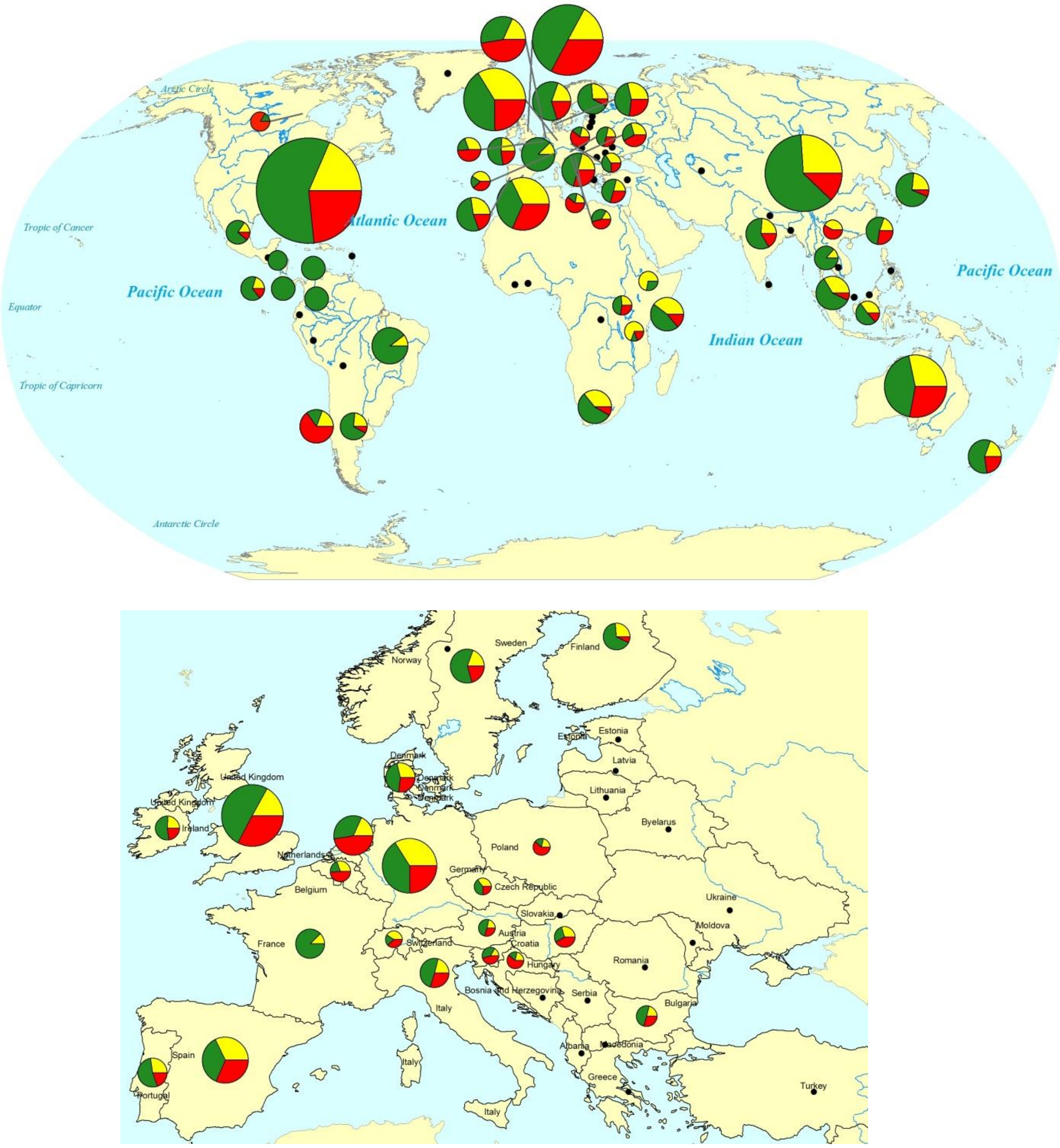


Figure 1: The distribution of ecosystem service studies globally (above) and in Europe (below). All markings represent the 83 countries globally and the 35 countries in Europe respectively in which ecosystem service studies have been conducted. Pie charts show the relative proportion of ■ provisioning ■ regulating and ■ cultural ecosystem services which have been studied, corrected by the number of ecosystem services in each category (seven provisioning, nine regulating and five cultural). Black circles (•) indicate countries where only one study has been done. The size of the pie charts is representative of the number of ecosystem service studies done in each country with for (above) the greatest being 60 in the USA and the smallest two (e.g. Canada) and for (below) the greatest being 27 in the UK and the smallest two (e.g. Switzerland).

2.4 Application of the ecosystem service concept

There are several key issues that all studies should take into consideration to make them applicable for use in practice. Firstly, it is important to distinguish between potential, actual and sustainable supply and demand for ecosystem services and to be consistent and transparent about this. Half of all studies measured potential ecosystem services which can be problematic because this might not always reflect what an ecosystem actually supplies or sustainably could supply, or what is actually or sustainably used by society. Only 3% of studies considered both actual and potential ecosystem services, which could give more clear information about the sustainability of ecosystem service delivery in those cases. Secondly, and similarly to other studies, we found that only 26% of studies considering more than one ecosystem service investigate the relationships between those ecosystem services (Pinto et al., 2010; Seppelt et al., 2011; Smith et al., 2013). Therefore most studies are considering ecosystem services in isolation and neglect underlying complex interaction effects. These might have significant impacts and are especially critical to understand when performing an ecosystem service assessment for decision making purposes. Third, it appears that few studies considered scenarios (24%) and forth, stakeholder involvement (16%), as was also found by Seppelt et al. (2011) (**Table 2**). Lastly we found that 60% of studies gave some recommendations for management or decision-making in varying degrees of detail. There is a slight increase in this over time, however given the application-based nature of the field, this should still be improved (**Table 2**).

2.5 Analysis of ecosystem service measures

A very diverse set of measures was obtained for each of the 21 ecosystem services studied (range: 5-59). For example Climate and Water Regulation both had 59 different measures, whereas Food Production, equally frequently studied, had only 23 (**Table 2; Supplementary Material**). This high diversity of measures may either be an indication of the complexity of an ecosystem service (for example well-studied ecosystem service with many components, such as Climate Regulation) or an indication of a lack of consensus or understanding of how a particular ecosystem service should be measured (for example poorly studied ecosystem services such as Ornamental Resources). This high diversity of measures has consequences for the comparability of studies. To further determine whether the biophysical reality of ecosystem services are adequately quantified we used two key criteria: firstly whether the measures were scientifically robust, and secondly which part of the ecosystem service cascade researchers measured.

Criterion 1: Scientific robustness of ecosystem service measures

We found four major areas of concern in ecosystem service research which call the scientific rigour of the field as a whole into question. The first concern is that very few studies (23%) consider measures of uncertainty for their results and although this is improving slightly with time, the proportion for the most recent years is still very low (**Table 2**). Secondly, there is also a high percentage of studies that do not report any kind of validation for mapping, modelling or remote-sensing exercises (33%). The third concern is that only a fifth of studies used actual field measurements, and only roughly half of all studies use active methods (i.e. generated any new primary data). This is slightly more common for regulating ecosystem services (52%) and studies at a local and regional scale (55%). Studies using data from literature and databases make up about 41% of the total. Lastly, as many as 31% of studies do not report any data (e.g. they display only ranges on a map, or data converted to scores) which is problematic for information transfer and quality control purposes. Overall, to gain more credibility as a field of science in its own right, there is a great need for more critical appraisal of ecosystem services research and greater efforts at quality control.

Table 2: Information about the impact of the research and the scientific robustness of ecosystem service measures, per ecosystem service and the average overall. The percentage of studies and number of measures gives an indication of the diversity of measures for each ecosystem service. The applicability of the research was evaluated using two criteria: whether stakeholders were involved and recommendations made. Scientific robustness is evaluated using several criteria, including: uncertainty quantified, validation done where relevant (mapping, remote-sensing and modelling studies), whether active methods were employed (actual field measurements, mapping, modelling, and remote sensing), and whether real data were used (actual data presented as opposed to a theoretical study). Each of the six criteria is expressed as a percentage of the total number of measures for each ecosystem service.

Ecosystem Service	**Percentage of Studies (%)**	**Diversity (No. of Measures)**	**Stakeholder Involvement (%)**	**Recommendation (%)**	**Uncertainty (%)**	**Validation (%)**	**Active Methods (%)**	**Real Data (%)**
Food Production	10.1	23	15.7	67.4	20.8	33.3	38.1	68.0
Water Provision	5.9	27	20.3	69.6	30.4	13.9	43.1	73.4
Materials & Fibre	5.5	15	25.0	72.4	23.7	38.5	45.6	71.1
Energy & Fuel	2.4	13	8.5	66.0	12.8	33.3	40.2	55.3
Genetic Resources	1.0	8	18.8	56.3	25.0	0.0	40.0	81.3
Medicinal Resources	0.7	5	55.6	55.6	33.3	50.0	46.7	55.6
Ornamental Resources	0.3	5	60.0	40.0	0.0	-	33.3	80.0
Water Purification	8.5	49	11.8	58.8	27.9	43.2	50.0	71.3
Water Regulation	8.7	59	14.3	48.6	20.7	22.2	48.0	62.1
Air Quality Regulation	2.1	11	16.7	70.0	20.0	40.0	44.7	63.3
Soil Quality Regulation	9.0	42	2.6	43.2	22.6	75.0	64.5	79.5
Soil Retention	8.3	38	13.0	52.8	25.9	39.4	54.5	73.1
Climate Regulation	13.6	59	9.2	61.7	27.0	29.0	50.4	78.1
Pollination	3.6	24	8.7	71.7	30.4	28.6	53.2	73.9
Biological Control	2.5	19	15.6	65.6	21.9	25.0	51.3	68.8
Life Cycle Maintenance	0.7	6	12.5	75.0	37.5	100.0	27.3	75.0
Recreation & Tourism	7.9	16	19.0	61.3	13.1	28.2	45.7	61.3
Scientific & Educational Services	1.7	18	20.8	54.2	8.3	0.0	39.0	45.8
Heritage, Cultural, Bequest, Inspiration & Art	2.7	28	33.3	64.3	19.0	25.0	49.3	52.4
Aesthetic Services	3.3	27	25.5	56.9	17.6	30.0	42.0	52.9
Symbolic, Sacred, Spiritual & Religious Services	1.6	15	35.7	57.1	14.3	15.4	63.3	57.1
Average	**4.8**	**24.1**	**15.5**	**59.7**	**22.9**	**32.8**	**48.3**	**69.1**

Criterion 2: Cascade Analysis

Overall, for all 21 ecosystem services, four of the parts of the ecosystem service cascade (properties, functions, benefits and values) are equally well quantified (**Supplementary Material**). Interestingly, no measures have been developed for the 'ecosystem service' part of the cascade, when categorizing measures according to the accepted definitions. For provisioning ecosystem services, benefits and values are more commonly measured (60%) (**Fig. 2**). For regulating ecosystem services, properties and functions are the dominant measures (62%) whereas cultural ecosystem services are mainly quantified using scores (43%). Most measures were based on only one part of the ecosystem service cascade: properties (17.2%), functions (16.7%), benefits (8.6%), and values (16.4%). This differs from the findings of Luederitz et al. (2015) who found that more urban ecosystem service studies considered multiple parts of the ecosystem service cascade, thereby operationalizing the ecosystem service cascade more successfully. We found that the parts of the cascade most commonly studied together were benefits and values (8.4%), followed by functions and values (4.0%), properties and functions (3.5%) and functions and benefits (0.2%). Studying more than two parts of the ecosystem service cascade was very rare (0.7%). The final 20% of measures used scores, or other means to quantify ecosystem services.

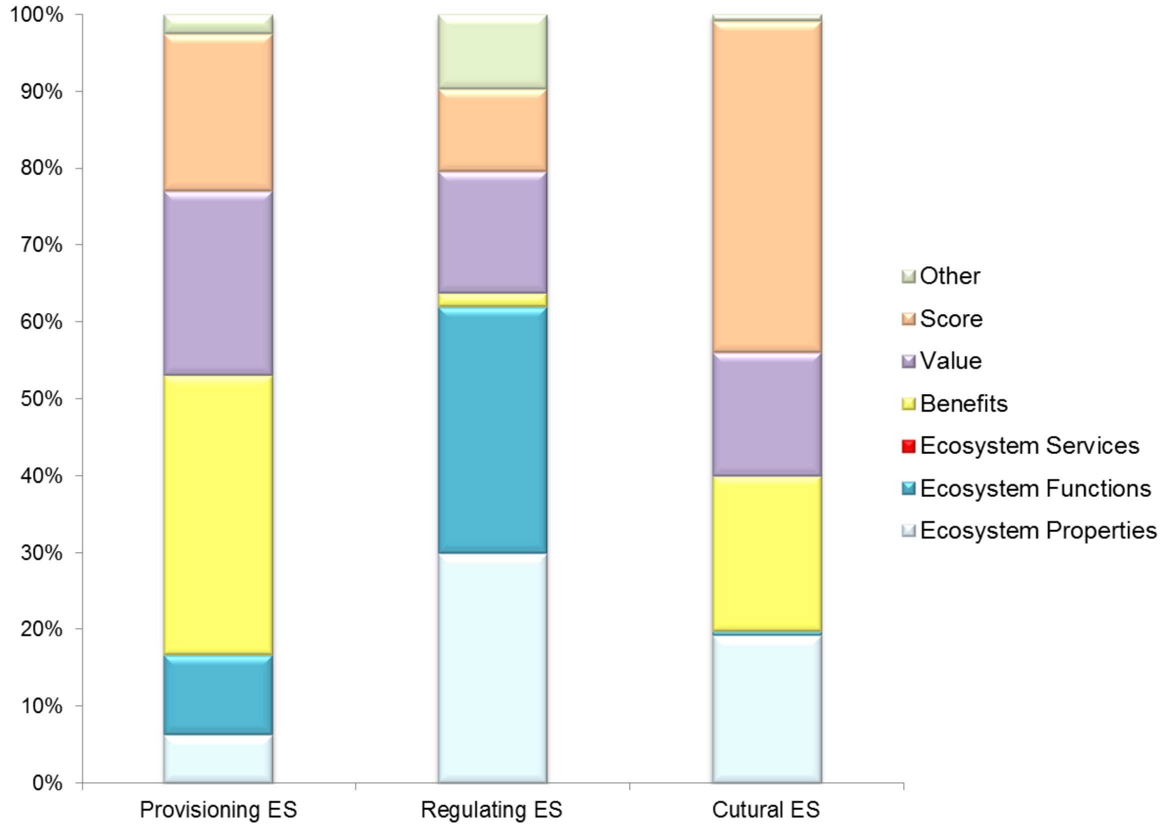
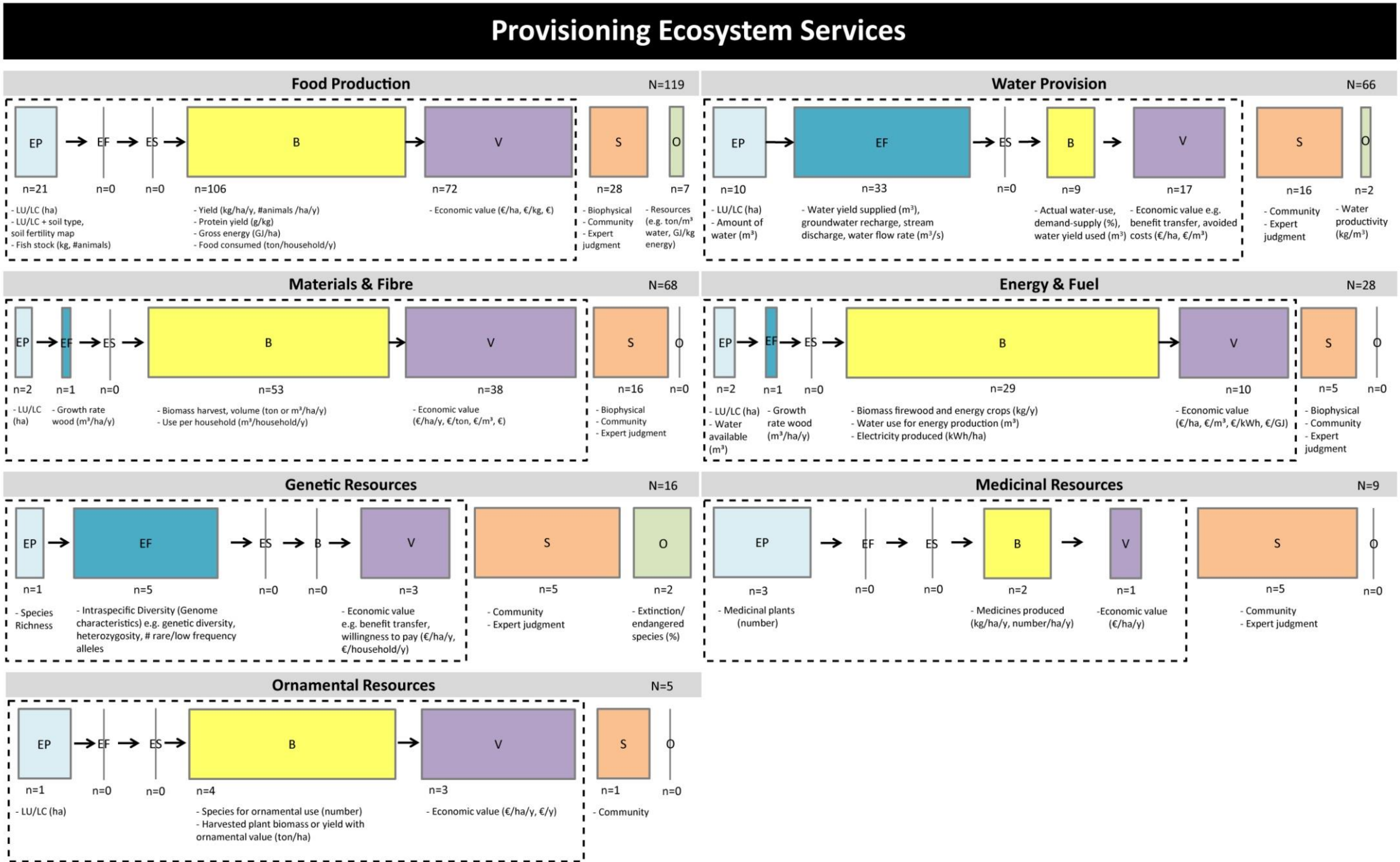
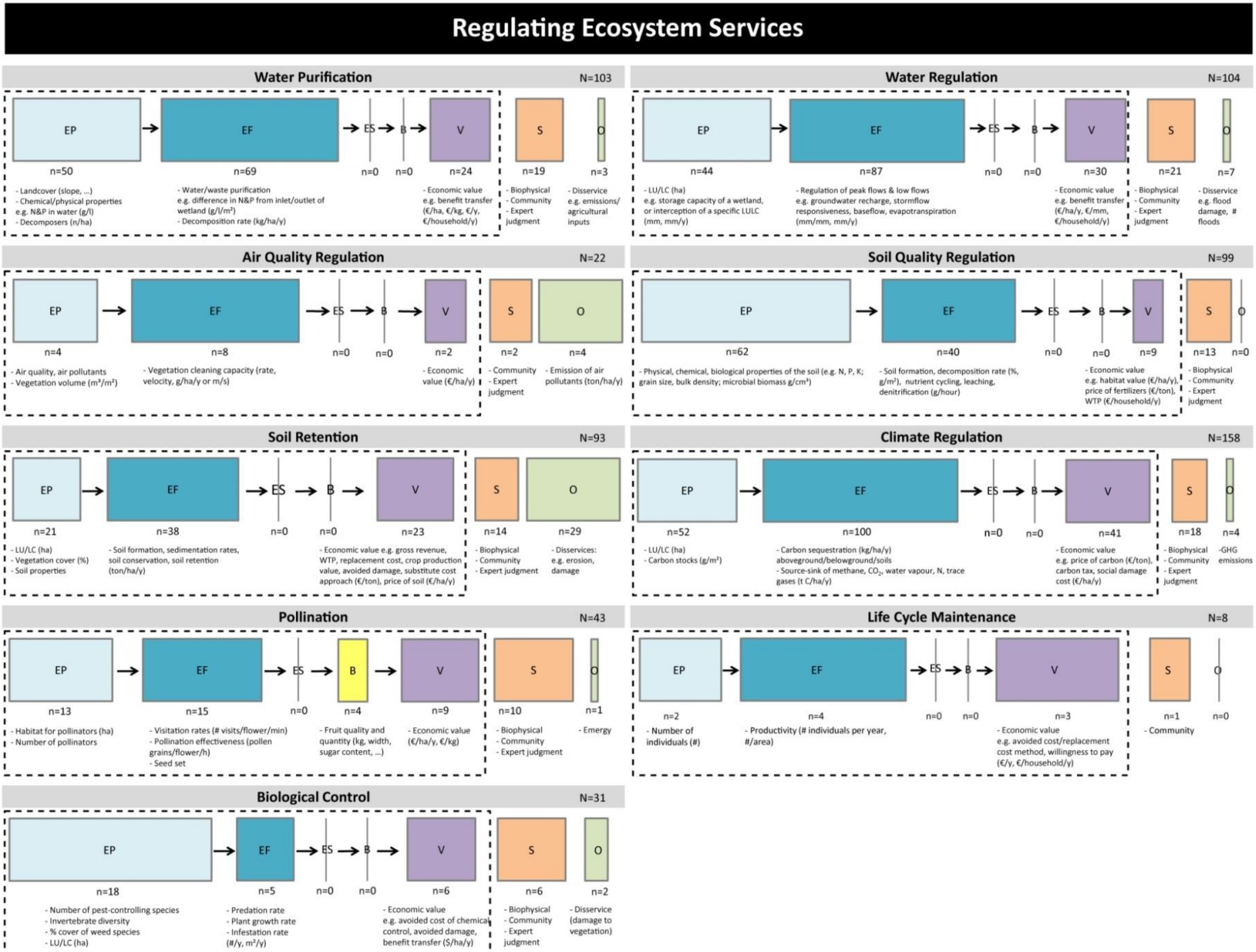


Figure 2: The percentage of measures in each part of the cascade for the three ecosystem service (ES) categories, for all 21 ecosystem services. Where measures are from more than one part of the ecosystem service cascade they are accounted for in each of these parts.

(a)


Provisioning Ecosystem Services
Food Production
N=119
EP
EF
ES
B
V
S
O
n=21
n=0
n=0
n=106
n=72
n=28
n=7
- LU/LC (ha)
- LU/LC + soil type, soil fertility map
- Fish stock (kg, #animals)
- Yield (kg/ha/y, #animals /ha/y)
- Protein yield (g/kg)
- Gross energy (GJ/ha)
- Food consumed (ton/household/y)
- Economic value (€/ha, €/kg, €)
- Biophysical
- Community
- Expert judgment
- Resources (e.g. ton/m³ water, GJ/kg energy)
Water Provision
N=66
EP
EF
ES
B
V
S
O
n=10
n=33
n=0
n=9
n=17
n=16
n=2
- LU/LC (ha)
- Amount of water (m³)
- Water yield supplied (m³), groundwater recharge, stream discharge, water flow rate (m³/s)
- Actual water-use, demand-supply (%), water yield used (m³)
- Economic value e.g. benefit transfer, avoided costs (€/ha, €/m³)
- Community
- Expert judgment
- Water productivity (kg/m³)
Materials & Fibre
N=68
EP
EF
ES
B
V
S
O
n=2
n=1
n=0
n=53
n=38
n=16
n=0
- LU/LC (ha)
- Growth rate wood (m³/ha/y)
- Biomass harvest, volume (ton or m³/ha/y)
- Use per household (m³/household/y)
- Economic value (€/ha/y, €/ton, €/m³, €)
- Biophysical
- Community
- Expert judgment
Energy & Fuel
N=28
EP
EF
ES
B
V
S
O
n=2
n=1
n=0
n=29
n=10
n=5
n=0
- LU/LC (ha)
- Water available (m³)
- Growth rate wood (m³/ha/y)
- Biomass firewood and energy crops (kg/y)
- Water use for energy production (m³)
- Electricity produced (kWh/ha)
- Economic value (€/ha, €/m³, €/kWh, €/GJ)
- Biophysical
- Community
- Expert judgment
Genetic Resources
N=16
EP
EF
ES
B
V
S
O
n=1
n=5
n=0
n=0
n=3
n=5
n=2
- Species Richness
- Intraspecific Diversity (Genome characteristics) e.g. genetic diversity, heterozygosity, # rare/low frequency alleles
- Economic value e.g. benefit transfer, willingness to pay (€/ha/y, €/household/y)
- Community
- Expert judgment
- Extinction/ endangered species (%)
Medicinal Resources
N=9
EP
EF
ES
B
V
S
O
n=3
n=0
n=0
n=2
n=1
n=5
n=0
- Medicinal plants (number)
- Medicines produced (kg/ha/y, number/ha/y)
-Economic value (€/ha/y)
- Community
- Expert judgment
Ornamental Resources
N=5
EP
EF
ES
B
V
S
O
n=1
n=0
n=0
n=4
n=3
n=1
n=0
- LU/LC (ha)
- Species for ornamental use (number)
- Harvested plant biomass or yield with ornamental value (ton/ha)
- Economic value (€/ha/y, €/y)
- Community

(b)


Regulating Ecosystem Services
Water Purification
N=103
EP
EF
ES
B
V
S
O
n=50
n=69
n=0
n=0
n=24
n=19
n=3
- Landcover (slope, ...)
- Chemical/physical properties
e.g. N&P in water (g/l)
- Decomposers (n/ha)
- Water/waste purification
e.g. difference in N&P from inlet/outlet of wetland (g/l/m²)
- Decomposition rate (kg/ha/y)
- Economic value
e.g. benefit transfer (€/ha, €/kg, €/y, €/household/y)
- Biophysical
- Community
- Expert judgment
- Disservice
e.g. emissions/ agricultural inputs
Water Regulation
N=104
EP
EF
ES
B
V
S
O
n=44
n=87
n=0
n=0
n=30
n=21
n=7
- LU/LC (ha)
e.g. storage capacity of a wetland, or interception of a specific LULC (mm, mm/y)
- Regulation of peak flows & low flows
e.g. groundwater recharge, stormflow responsiveness, baseflow, evapotranspiration (mm/mm, mm/y)
- Economic value
e.g. benefit transfer (€/ha/y, €/mm, €/household/y)
- Biophysical
- Community
- Expert judgment
- Disservice
e.g. flood damage, # floods
Air Quality Regulation
N=22
EP
EF
ES
B
V
S
O
n=4
n=8
n=0
n=0
n=2
n=2
n=4
- Air quality, air pollutants
- Vegetation volume (m³/m²)
- Vegetation cleaning capacity (rate, velocity, g/ha/y or m/s)
- Economic value (€/ha/y)
- Community
- Expert judgment
- Emission of air pollutants (ton/ha/y)
Soil Quality Regulation
N=99
EP
EF
ES
B
V
S
O
n=62
n=40
n=0
n=0
n=9
n=13
n=0
- Physical, chemical, biological properties of the soil (e.g. N, P, K; grain size, bulk density; microbial biomass g/cm³)
- Soil formation, decomposition rate (%, g/m²), nutrient cycling, leaching, denitrification (g/hour)
- Economic value
e.g. habitat value (€/ha/y), price of fertilizers (€/ton), WTP (€/household/y)
- Biophysical
- Community
- Expert judgment
Soil Retention
N=93
EP
EF
ES
B
V
S
O
n=21
n=38
n=0
n=0
n=23
n=14
n=29
- LU/LC (ha)
- Vegetation cover (%)
- Soil properties
- Soil formation, sedimentation rates, soil conservation, soil retention (ton/ha/y)
- Economic value e.g. gross revenue, WTP, replacement cost, crop production value, avoided damage, substitute cost approach (€/ton), price of soil (€/ha/y)
- Biophysical
- Community
- Expert judgment
- Disservices:
e.g. erosion, damage
Climate Regulation
N=158
EP
EF
ES
B
V
S
O
n=52
n=100
n=0
n=0
n=41
n=18
n=4
- LU/LC (ha)
- Carbon stocks (g/m²)
- Carbon sequestration (kg/ha/y) aboveground/belowground/soils
- Source-sink of methane, CO₂, water vapour, N, trace gases (t C/ha/y)
- Economic value
e.g. price of carbon (€/ton), carbon tax, social damage cost (€/ha/y)
- Biophysical
- Community
- Expert judgment
-GHG emissions
Pollination
N=43
EP
EF
ES
B
V
S
O
n=13
n=15
n=0
n=4
n=9
n=10
n=1
- Habitat for pollinators (ha)
- Number of pollinators
- Visitation rates (# visits/flower/min)
- Pollination effectiveness (pollen grains/flower/h)
- Seed set
- Fruit quality and quantity (kg, width, sugar content, ...)
- Economic value (€/ha/y, €/kg)
- Biophysical
- Community
- Expert judgment
- Emergy
Life Cycle Maintenance
N=8
EP
EF
ES
B
V
S
O
n=2
n=4
n=0
n=0
n=3
n=1
n=0
- Number of individuals (#)
- Productivity (# individuals per year, #/area)
- Economic value
e.g. avoided cost/replacement cost method, willingness to pay (€/y, €/household/y)
- Community
Biological Control
N=31
EP
EF
ES
B
V
S
O
n=18
n=5
n=0
n=0
n=6
n=6
n=2
- Number of pest-controlling species
- Invertebrate diversity
- % cover of weed species
- LU/LC (ha)
- Predation rate
- Plant growth rate
- Infestation rate (#/y, m²/y)
- Economic value
e.g. avoided cost of chemical control, avoided damage, benefit transfer ($/ha/y)
- Biophysical
- Community
- Expert judgment
- Disservice (damage to vegetation)

(c)

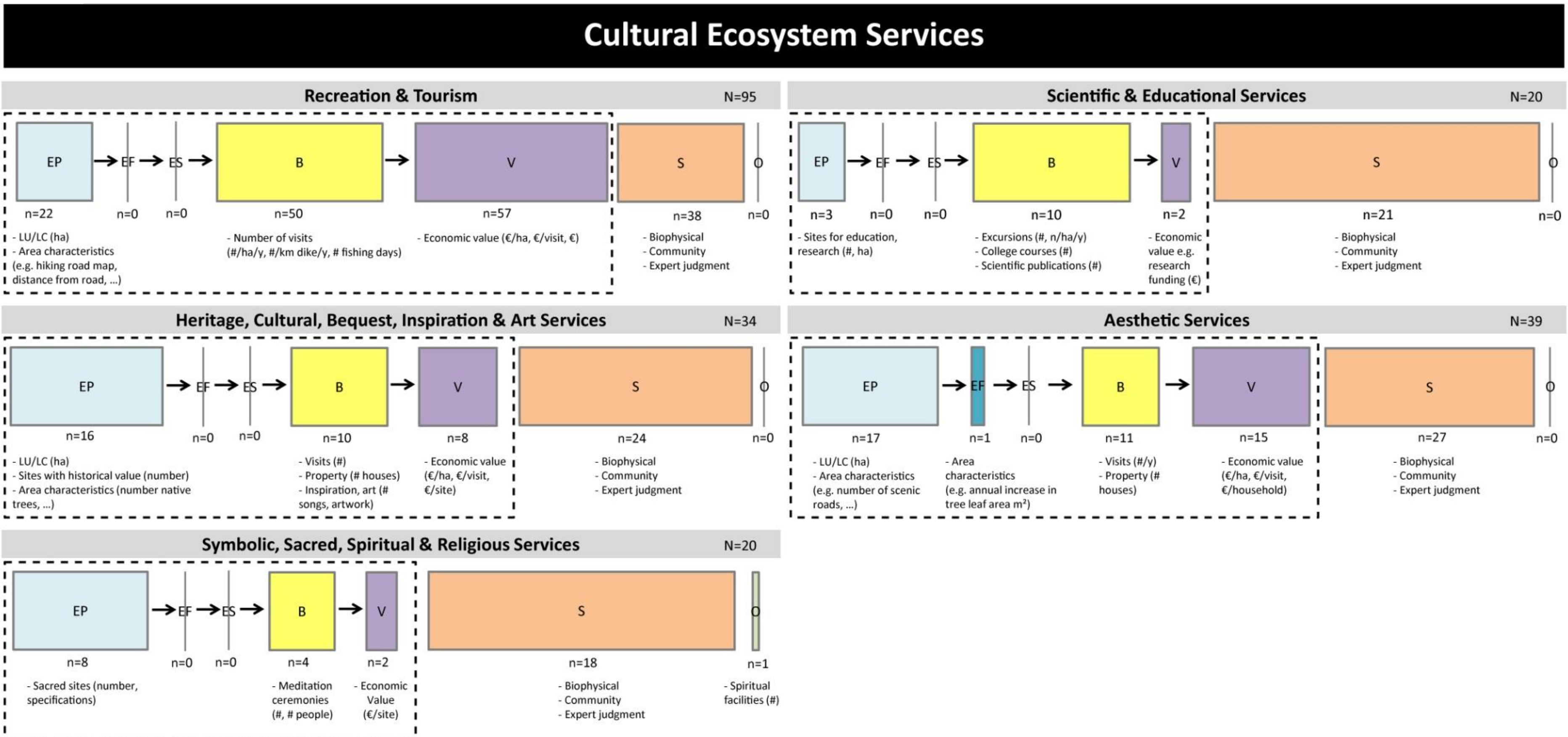


Figure 3: The cascade analysis for (a) provisioning, (b) regulating, and (c) cultural ecosystem services. The bar graph in each diagram indicates which parts of the cascade are most commonly measured and the text beneath gives examples of the main types of measures used. The stippled line indicates the extent of the traditional cascade. EP: ecosystem properties, EF: ecosystem functions, ES: ecosystem services, B: benefits, V: value, S: score, O: other. 'N' refers to the number of papers, and 'n' refers to the number of measures.

PROPERTIES

The properties of an ecosystem are not directly related to the supply of an ecosystem service to society as this is determined by many other factors, such as environmental parameters (both biotic and abiotic), infrastructure, sustainable yield and demand. The most frequently used measures for ecosystem properties are land-use/land-cover or habitat (%/ha) which is sometimes combined with additional information such as soil type, vegetation biomass/volume (**Fig. 3; Supplementary Material**). However even adding these abiotic parameters to land-use/land-cover maps has been shown to yield little improvement in ecosystem service estimation (Van der Biest et al., 2015). Another common measure is the stock of various ecosystem properties, which is inappropriate as ecosystems are constantly changing. The most common example is that of using standing biomass as a measure of carbon sequestration for the ecosystem service Climate Regulation. For Water Purification, ecosystem properties such as total N, total P or turbidity are frequently measured instead of the contribution of the system to regulate water quality (i.e. what part of the change is a result of the ecosystem filtration mechanism). For all ecosystem services that depend on biodiversity, such as Genetic Resources, Biological Control, Pollination and Life Cycle Maintenance, simple measures or indicators of biodiversity and population size are often used. For example, Genetic Resources are estimated using species richness (Ford et al., 2012), however the two are not necessarily directly related. Overall the relationship between biodiversity and ecosystem services is poorly understood, and more research on this is needed so that indicators for these, often less understood, ecosystem services can be developed (Schröter et al. 2014, although see Gascon et al. 2015).

FUNCTIONS

Where measuring ecosystem properties alone is weak, measures of ecosystem functions are stronger as they give a better idea of ecosystem service supply and how this fluctuates spatiotemporally. The processes and functions underpinning each ecosystem service are diverse and comprise many different aspects (components) (Smith et al., 2013). The discussion on measures for ecosystem functions is grouped into six categories. First, for water-related ecosystem services, measures for Water Provision include: water yield, groundwater recharge, and water flow rate (for details see **Fig. 3** and **Supplementary Material**). Measures for Water Regulation are similar, but also include the regulation of these fluxes such as: regulation of peak flows and low flows, and stormflow responsiveness. Water Purification is measured by changes in nutrients spatially (e.g. differences between inlet/outlet), or decomposition rates. Second, for soil-related ecosystem services, measures include soil formation, conservation and erosion regulation (Soil Retention) and decomposition rate, biological respiration, soil formation and nutrient cycling (Soil Quality Regulation). Third, there are three main types of measures for Climate Regulation, and these relate to carbon sequestration (above or below ground), greenhouse gas sequestration/emission, and net primary productivity. Fourth, Air Quality Regulation is usually quantified by estimating vegetation cleaning capacity either by dry deposition rate/velocity, or pollution removal rate by plants. Fifth, for ecosystem services related to biodiversity, measures include intraspecific diversity (Genetic Resources), pollination effectiveness and visitation rates (Pollination) and predation rate, plant growth rate and infestation rates (Biological Control). Lastly, only one measure relating to ecosystem functions was found for cultural ecosystem services, specifically the annual increase in tree leaf area (Aesthetic Services). Overall, there are some isolated cases of misrepresentation, where incorrect methods are used (e.g. measuring carbon stocks for carbon sequestration).

ECOSYSTEM SERVICES

No measures were found for the ecosystem service part of the cascade.

BENEFITS

Benefits are most commonly measured for provisioning ecosystem services because they are tangible, and often have well-developed markets, both of which make them easier to quantify (Layke et al., 2012; Luederitz et al., 2015). Measures for benefits can be divided into two main groups: those related to societal demand (e.g. harvest of food or number of species available for ornamental or medicinal use) and those linked to actual use, expressed, for example, per household (e.g. food consumed, actual water use or number of visits). Some other measures for benefits include outputs, such as the number of publications, or the number of paintings/songs inspired by an ecosystem. For regulating ecosystem services, only one example was found (quality and quantity of fruit supplied as benefit of Pollination). By definition, benefits also have many components, e.g. food provision, nutrition, health, and the appreciation of food for the ecosystem service Food Production. Some would argue that ecosystem services are separate from benefits, and instead they generate many different benefits (e.g. nutrition, enjoyment of food *etc.* as benefits) while the ecosystem service would then be ‘amount of food’. However the very definition for ecosystem services contradicts this: ‘the benefits mankind derives from nature’ (MEA 2005). Furthermore, having this extra step in the ecosystem service cascade seems redundant (for example the nutritional value of food ($g.kg^{-1}$ or $Joules.m^{-2}$) is simply multiplying the weight of the food by a calorific value).

VALUE

Only one fifth of ecosystem service studies performed a monetary valuation, which seems surprisingly low. For all ecosystem services some form of monetary value is studied, but it is most frequently done for provisioning ecosystem services and Recreation & Tourism. Measures for value of ecosystem services are confined to economic valuation methods of which four main types appear. Firstly, the most simple and rapid measure is the ‘unit value per habitat type’ which is often based on benefit transfer (€.$ha^{-1}.y^{-1}$). Furthermore many of these studies use the global values from Costanza et al. (1997) which are rough guidelines. For this approach it is essential that the case study, from which values are taken, is comparable to the study in question. Second, many studies use the market price method, but to determine the ‘added value’ of an ecosystem service, the net value is more appropriate and this is the market price corrected for the production costs (€.ton^{-1}, €.m^{-3}). In some other cases the total value of a sector (e.g. fish sector, agricultural sector) for a specified area (€.ha^{-1}) or the research funds or budget (Scientific & Educational Service) are used. Third, avoided cost or replacement cost are commonly used, such as: avoiding flood damage (avoided cost), or avoiding the cost of a water treatment plant (replacement cost). Lastly, the 'willingness-to-pay' method (a stated preference method) is used (€.household^{-1}, €.person^{-1}, €.visit^{-1}). Overall, but particularly for regulating ecosystem services, we occasionally found that the supply of ecosystem services is valued but the benefit to society (demand) is not considered. This is problematic as it may give an overestimation of the economic value of an ecosystem service.

SCORES

Using simple indicators like scores can be an effective way to incorporate information from stakeholders into an ecosystem service assessment and can also be a valuable method to compare different ecosystem services and include ecosystem services for which no good measures exist. Scores often take the form of the "perceived" importance of an ecosystem service ('non-economic valuation') and are derived from interviews with community members and local people or experts (scientists or practitioners from government or industry), or biophysical assessments. Biophysical scoring systems can either be simple, rapid assessments (qualitative categories, indicators) or more complex models (e.g. INVEST). There are some limitations to using scores, such as their subjectivity, vagueness, over-simplification and sometimes lack of transparency. Depending on the purpose of the assessment, where more objectivity is needed, proper ecosystem service quantification may be more appropriate. There are some ecosystem services for which few measures exist besides scores, such as Scientific & Educational Services and Symbolic, Sacred, Spiritual & Religious Services (**Supplementary Material**). This suggests that these ecosystem services are poorly understood and that adequate measures are difficult to derive. In some cases there is a need for more research to understand what exactly these ecosystem services are, and whether they are important; if not, a rethinking of the list of ecosystem services may be required.

OTHER

There are a number of measures which do not fit into the five parts of the ecosystem service cascade, nor are they scores. This information is useful as extra information, but it is inappropriate when used as quantification of the ecosystem service. The most common measures of this type relate to ecosystem disservices, such as: emissions/pollution from an ecosystem, number of fires or floods, number of endangered species and extinction. Disservices are not related to the ecosystem service, however they might in some cases shed light on the demand for the ecosystem service. Another abstract measure is one where the resources used to obtain the benefit are measured and expressed as productivity (e.g. the volume of water or energy needed to produce a kg of crops). In the case of cultural ecosystem services, measures can, for example, be based on manmade facilities needed for recreation, symbolic or spiritual activities. Another example of an abstract measure is using net migration of people to desirable areas as a measure for Aesthetic Services.

2.6 Rethinking the ecosystem service cascade

As the number of papers dealing with ecosystem services is booming, so too is the confusion and lack of consensus about how to measure and quantify ecosystem services. We argue that this is due to overlap and lack of clarity on definitions of parts of the ecosystem service cascade. When following the accepted definitions, no measures emerged specifically quantifying the ecosystem service part of the cascade. Rather measures are linked to quantification of the functioning of the ecosystem (ecological side of the cascade), or to the quantification of the benefits (socio-economic side). A typical regulating ecosystem service example is carbon sequestration ($kg.y^{-1}$ or $kg.m^{-2}.y^{-1}$) which gives an indication of the functioning of the ecosystem in relation to the ecosystem service Climate Regulation. This is a commonly accepted measure for the ecosystem service, but it is purely indicative of the capacity of the ecosystem to supply the ecosystem service without considering the benefits to society (socio-economic side of the cascade, e.g. health improvements, or safety from extreme events linked to climate change). A typical example of the provisioning ecosystem service Food Production is fish landings (kg, or number of fish) which give an indication of the total amount used by society, but not of the sustainable capacity of the ecosystem to deliver the ecosystem service (ecological side of the cascade). This demonstrates that the link between ecosystems and human well-being is currently not well made.

We present a revised ecosystem service cascade which emphasizes the point that one measure for an ecosystem service is insufficient - at least two measures are needed, one for the ecosystem function (supply of ecosystem services) and another for the benefit to mankind (demand of ecosystem services) (**Fig. 4**). These two measures for the ecosystem service are connected by a transfer function, which cannot be quantified. This is why we present the cascade without a fifth block in the center called "ecosystem services", but rather encompassed by a dotted line which represents both the supply and demand of the ecosystem service as a whole. A similar conclusion was reached by Mononen et al. (2016) where they assigned indicators to four parts of the ecosystem service cascade, and they considered the ecosystem service to be the summation of these four parts. The aim of this cascade is to provide clarity on which aspects are important for sustainable ecosystem service delivery and hence what can and should be measured for each ecosystem service. We believe that the solution to the confusion is not to produce more detailed and complex cascades, but to keep it simple and the definitions clearly defined.

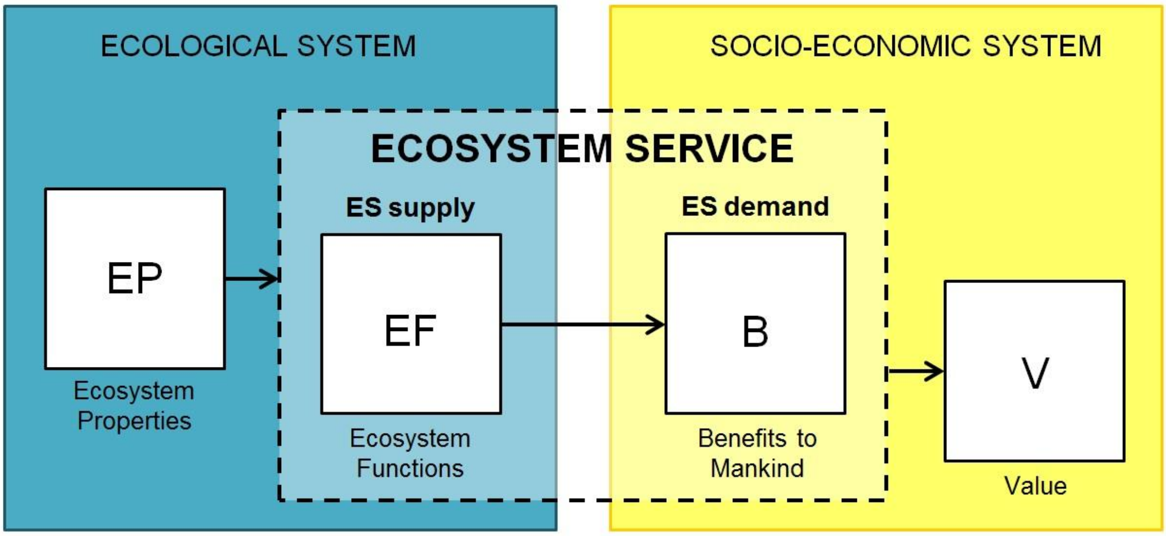


Figure 4. New proposed conceptual framework for ecosystem services based on the ecosystem service cascade from Haines-Young & Potschin (2010)

2.7 Recommendations

1. Bridging the gap between ecological and socio-economic aspects

To quantify the sustainable supply of an ecosystem service it is necessary to quantify the properties and functions of an ecosystem (ecological side of the cascade), whereas to quantify the importance to society it is necessary to understand and quantify the benefit to society (socio-economic side). Many researchers are only considering one side of this cascade and therefore are not succeeding in understanding the whole picture. Do all future studies need to quantify each side of the ecosystem service cascade? This will largely depend on the aim of each individual study (Martinez-Harms et al., 2015), however we argue that researchers should be aware of and be explicit about which aspect of the cascade they are considering and recognize the limitations of quantifying only one side of the ecosystem service cascade.

2. Relationships between ecosystem services

The fact that all 21 ecosystem services very clearly clustered either to the ecological or socio-economic side of the cascade would suggest that the functioning of some ecosystem services underpins the delivery of other ecosystem services. Our analysis shows which ecosystem services are limited to measures of function and for these, benefits are mostly not considered. On the other hand measures for other ecosystem services are limited to benefits and functions are not measured. One example is that the ecosystem service Soil Quality Regulation and Soil Retention underpin the delivery of *inter alia* Food Production, which is the tangible benefit to society. For a detailed account of this, Dominati et al. (2014) study the role of soil in ES delivery for agro-ecosystems. We expect that there is a large amount of specialized research on ecosystem functions underpinning ecosystem services for which measures of function are scarce, but this is not taking place within the field of ecosystem services. Therefore there is a need for more integration between the field of ecosystem services and more specialized fields. If it is not possible to find measures of both function and benefit for an ecosystem service, then it is possible that it is not a true ecosystem service. We recommend more discussion on the relationships between ecosystem services to elucidate which ecosystem services are true ecosystem services and are essential to consider in ecosystem service assessments.

3. *Tighter definitions for ecosystem services*

It is argued that the vagueness and imprecision in the definitions of ecosystem services and the ecosystem service concept as a whole encourages creativity and transdisciplinary collaboration (Schröter et al. 2014). While this is possible, there are many studies where this has led to confusion about what constitutes an ecosystem service, lack of transparency and inappropriate methods of quantification. For example, some studies split ecosystem services into sub-services and report these as multiple ecosystem services (e.g. Food Production split into eight different ecosystem services based on different fish species, Kozak et al., 2015). Some studies are not explicit about what constitutes an ecosystem service nor how they measure them (Niu et al., 2012) and there are also examples of parameters being included as ecosystem services which are clearly not ecosystem services, for example 'productivity' (Dobbs et al., 2014). Another example is that many researchers are using the exact same measure for all cultural ecosystem services, demonstrating that the differences between the cultural ecosystem services are not clear. On the other hand, different researchers use different measures for each cultural ecosystem service and this wide diversity indicates a lack of consensus on what the ecosystem service actually is (similar to findings of Luederitz et al. 2015). This definition confusion may lead to an over-estimation of ecosystem service delivery, and ultimately double-counting as well as problems with comparability. In spite of the argument that a final classification is perhaps neither possible nor necessary (Fisher et al., 2009), given the multiple examples of confusion resulting from loose definitions, we call for some naming conventions, for example corporately accepting one of the ecosystem service classifications (e.g. TEEB or CICES). While creativity is to be encouraged, transparency is essential. We recommend that ecosystem service papers should have a clear section in their methods stating exactly *which* ecosystem services they measured, and *how* they did this (for an example see table 5 in Perring et al. 2012).

4. *Components of ecosystem services*

All of the ecosystem services reviewed in our study are complex concepts made up of many different components although in many studies only one component is measured. The classic example is that of Climate Regulation, where carbon sequestration is often the only component measured although there are other essential components including climate moderation, and sequestration of methane and NO_2. Our results show a high diversity of measures for many ecosystem services (especially regulating ecosystem services), which could in part be explained by researchers variously measuring the many different components making up each ecosystem service. It is wrong to select just one of these components without evidence that this component is representative of the ecosystem service as a whole. Depending on the aim and scope of the study, there may be some cases where considering all components may not be relevant (e.g. a terrestrial study would not need to quantify fish landings for Food Production). The fundamental question here is: what is necessary for an ecosystem service to be considered quantified? Should all components be measured? Either way, researchers should be clear about exactly which components are measured, and what is missing. We recommend further discussion on this topic and that some field-wide standards are chosen.

5. *Selecting good quality ecosystem service measures and indicators*

Given that ecosystem services are so complex, having four different measureable parts from the cascade, each of which have different components which are difficult to measure, it would be impractical and probably impossible for every study to fully quantify each ecosystem service. Similar challenges of complexity in the field of ecology have resulted in the development of 'indicators' (Müller and Burkhard, 2012). Indicators are not arbitrarily chosen proxies, but are carefully selected and tested to ensure that they adequately reflect the reality of the measure they are approximating, that they are scientifically robust and practically applicable (Kandziora et al., 2013, after Müller and Burkhard, 2012). Indicators have been proposed for ecosystem services and indeed even for each part of the ecosystem service cascade and different components within this (Kandziora et al., 2013; Layke et al., 2012). However the rigor of these indicators should be adequately assessed as some indicators are very weak. For example, from our analysis it is clear that measures or indicators for ecosystem functions and benefits should be rates (with units $g.ha^{-1}.y^{-1}$ or $m.s^{-1}$) and not stocks (g or ha or $g.ha^{-1}$) (**Supplementary Material**). We call for indicators to be developed and tested for each part of the ecosystem service cascade either for each component, or an indicator which is demonstrated to be representative of all components within the ecosystem service (based on relationships). One suggestion would be that researchers use indicators that have been developed in specialized fields within each ecosystem service, for example the field of hydrology for measures relating to Water Regulation.

6. *Scientific rigour in ecosystem service science*

Finally there is a need to improve the scientific rigour of ecosystem service studies. More effort needs to be made by journals and reviewers to perform quality control: to ensure that methods are reported transparently (de Groot et al., 2012), that validation is done where appropriate, and that some effort is made to estimate uncertainty. In general there appears to be a large need for field validation of studies. In addition, when economic valuation is done, it is advisable that several methods are used to give a range of results, where the most conservative estimate should be chosen.

2.8 Conclusion

It is likely that researchers will never succeed in perfectly measuring the biophysical reality of all ecosystem services and hence will forever rely on some kind of indicator. Ecosystem service research is looking for simple tools to translate ecological studies to something useful for policy, and our review provides an overview of current gaps and six recommendations of how to improve the current measures to achieve a more realistic quantification of the reality.

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3

Evaluating palmiet wetland decline: a comparison of three methods

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Channel/gulley erosion in the Kromme River. The floodwaters have eroded the valley-bottom down to the bedrock which is visible on the floor of the valley. The knick-point for erosion is located to the left (not pictured). Once this erosion begins, active rehabilitation is necessary for the system to recover.

Abstract

Small valley-bottom wetlands (<5 km^2) are often overlooked in conservation and restoration efforts due to the difficulty to discriminate them in large regions. However due to their position in the landscape they are both critical for ecosystem service provision as well as highly threatened. Therefore there is a need to detect and map the extent of small valley-bottom wetlands to aid conservation and restoration efforts. We investigated five research questions concerning small, valley-bottom palmiet wetlands in the Cape Floristic Region, South Africa: (1) What is the best technique to detect palmiet wetlands?, (2) what is the best approach to map their extent?, (3) how best to analyse their potential extent and historical changes?, (4) what is their current extent and distribution and how has this changed historically?, and (5) what are the main drivers of this change? We used three different approaches to answer the various questions: multispectral imagery (the Landsat series) combined with Support Vector Machine classification, aerial photograph analysis with photographs from three time-steps and predictive modelling of wetland habitat suitability (using the MaxEnt model). Our main findings suggest that (1) multispectral classification using Landsat8 was best for palmiet wetland detection (76% accuracy), whereas (2) aerial photographs were the most useful in mapping extent. (3) Analysing changes in extent over time was best achieved using aerial photography, due to their high resolution and long historical record in South Africa (1940 compared to 1970 in the Landsat series). (4) South African palmiet wetlands are in decline, having decreased by on average 31% in area since the 1940/50s (overall loss of 6.36 km^2). Palmiet wetlands have also become increasingly fragmented, with weighted wetland perimeter increasing by 29% over the same period. (5) The major driver of this appears to be gully erosion triggered by land-use change. The wider implication of these findings is that it is possible to detect small wetlands using freely available Landsat8 data which could be useful to support local or regional conservation and restoration initiatives.

3.1 Introduction

Globally, wetlands are acknowledged to be valuable ecological infrastructure as they provide many essential ecosystem services to humans (Mitsch and Gossilink, 2000; Russi et al., 2013; Simonit and Perrings, 2011). Due to this value, many wetlands have been exploited or unsustainably used, resulting in estimated declines in global wetland extent of between 64 – 71% in the 20th century alone (Gardner et al., 2015). Countries that have ratified the Ramsar Convention (Ramsar, 1971) are obliged to implement planning to promote the wise use of wetlands and to develop policies for management and conservation (Gardner et al., 2015). Despite 169 countries signing this agreement, there are still negative trends; wetlands are continuing to be lost or degraded, and populations of wetland species are declining (Gardner et al., 2015). Additionally, the Convention on Biological Diversity (CBD, 1992) obliges contracting parties to rehabilitate and restore degraded ecosystems and manage biological resources which are important for the conservation of biological diversity (Glowka et al., 1994). To effectively manage and conserve wetlands, nations require up-to-date, accurate inventories of wetland occurrence and distribution and means of monitoring this (Li and Chen, 2005; Rebelo et al., 2009).

Satellite remote sensing is a useful tool for wetland detection, both in terms of distribution and extent. Certain wetland types (open inundated areas, bogs or fens) are frequently mapped using areas of inundation, focussing on the near infra-red part of the spectrum (Gala and Melesse, 2012; Knight et al., 2009), or a combination of this and chlorophyll indices, such as the normalised difference vegetation index (NDVI) (Landmann et al., 2010). Other types of wetlands (permanent wetlands, marshes, swamps), where soil inundation is obscured by dense wetland vegetation, are mapped using vegetation spectral signatures (Kameyama et al., 2001; Thomas et al., 2015). No single sensor is ideal, and there are always trade-offs to consider (temporal frequency, spectral resolution, spatial resolution, cost). Digitization of aerial photography is perhaps the most accurate method of mapping wetland extent for small wetlands (Harvey and Hill, 2001); however the trade-off is that this needs to be a targeted approach, targeting a specific wetland once it has been located, and therefore is not a useful technique for wetland detection. In addition to using imagery, predictive models and Bayesian Networks have also been successful in mapping and detecting wetlands at local to regional scales. The MaxEnt species distribution model, based on the principal of maximum entropy, has been used to predict the occurrence of wetland communities with reasonable success (Hunter et al., 2012). Wetland occurrence is determined by complex interactions between geographic variables, such as altitude, gradient, and geology which influence groundwater, soils and climatic variables.

South Africa has ratified the Ramsar and Biological Diversity conventions, however wetlands continue to be degraded with over 65% threatened and half estimated to be destroyed (Nel and Driver, 2012). One of the nation's greatest challenges in wetland conservation is the lack of a comprehensive overview of the extent, diversity, distribution, status and relative importance of its wetlands (Rountree et al., 2009). The

South African National Wetland Inventory, a national wetland classification system has been developed at a national scale and contains a set of 791 wetland ecosystem types (Driver et al., 2012). More recently, the National Freshwater Ecosystem Priority Areas (NFEPA) project was developed using GIS applications (Nel et al., 2011). However due to the large size of South Africa, 1.2 million km^2, both of these national-scale inventories are coarse, and result in many important and threatened wetland systems being overlooked (van Deventer et al., 2016). If restoration strategies in South Africa, such as the current 'Working for Wetlands programme" (van Wilgen et al., 2012), are to succeed in prioritizing wetlands for restoration and conservation, it is essential to have a finer scale inventory of wetlands. Wetland occurrence in South Africa has been determined at finer scales, both for certain provinces (using modelling techniques such as Bayesian belief networks (Hiestermann and Rivers-Moore, 2015)) and for individual cities (e.g. City of Cape Town; Holmes & Pugnalin (2016)), but there are still important gaps.

We used three techniques to investigate the following five research questions concerning South African palmiet wetlands: (1) What is the best technique to detect palmiet wetlands?, (2) what is the best approach to map their extent?, (3) how best to analyse their potential extent and historical changes?, (4) what is their current extent and distribution and how has this changed historically?, and (5) what are the main drivers of this change? Palmiet wetlands are a unique, typically small ($<5\ km^2$) unchannelled valley-bottom wetland system occurring throughout the Cape Floristic Region of South Africa. They get their name from the endemic wetland plant and ecosystem engineer: palmiet (*Prionium serratum*). Palmiet wetlands are thought to provide multiple ecosystem services to society, including flood attenuation (Rebelo et al., 2015), water purification and carbon sequestration (Rebelo, 2017). They are typically underlain by peatbeds between 0.5-10 m deep (Job, 2014; Nsor, 2007), and this is the ecological infrastructure that stores carbon, provides habitat for microbes which are thought to play a role in purifying water, and in combination with palmiet vegetation, dissipates the force of floodwaters (Rebelo, 2017). Despite the inherent value of these wetlands and their threatened status, there is no comprehensive understanding of where they remain, where they have been destroyed and what the main drivers of change are. The results of the comparison of techniques may be useful for other research at local or regional scales. The findings specific to palmiet wetlands would support the setting of restoration and conservation priorities within the Cape Floristic biodiversity hotspot.

3.2 Methods

Study region & wetlands

The Cape Floristic Region of South Africa is one of 35 global biodiversity hotspots (Mittermeier et al., 2011; Myers et al., 2000) and covers 87,892 km^2 at the south-western tip of southern Africa (Cowling and Heijnis, 2001) (**Fig. 1**). It is characterized by exceptionally high botanical diversity and endemism which is under threat (Myers et al., 2000; van Wyk and Smith, 2001). The Cape Floristic Region has a mediterranean-type climate in the west with varying degrees of summer drought and winter rainfall resulting from the passage of cold fronts (Midgley et al., 2003). Further towards the east there is more of a bimodal rainfall pattern. One of the greatest threats to the biodiversity of the Cape Floristic Region is the rapid expansion of towns and cities as well as the accompanying habitat transformation associated with agriculture, plantations and alien plant invasions (Cowling et al., 2003; Rebelo et al., 2011; Rebelo and Siegfried, 1992).

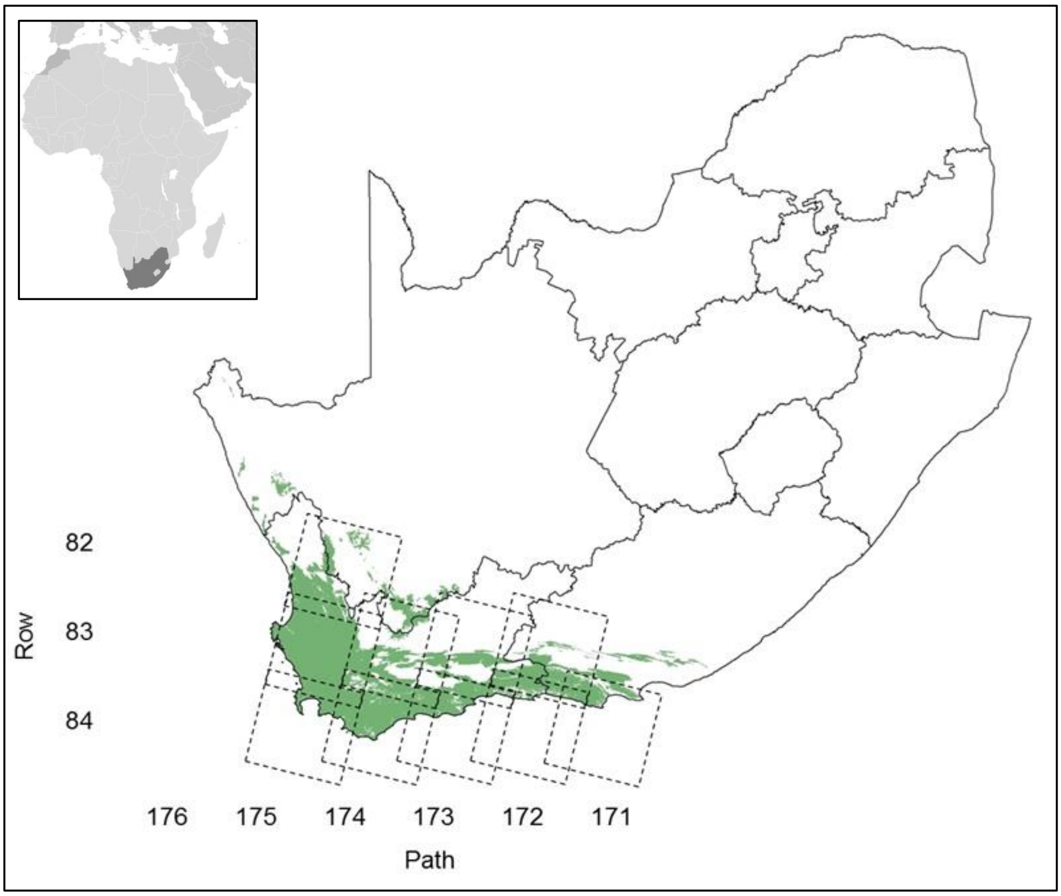


Figure 1. The location of the Cape Floristic Region (green) within South Africa (inset) and the coverage of the 10 Landsat8 scenes selected for this study.

We used three techniques: (i) multispectral remote sensing techniques, (ii) maximum entropy distribution modelling and (iii) aerial photograph analysis to answer the five research questions. We first used Landsat imagery to determine whether multispectral remote-sensing was a suitable technique to map small wetlands (both in terms of detection, and accurately mapping extent) (research question 1&2) currently (Landsat8) and historically (Landsat1-3, 5). We used the output from the Landsat8 classification to select palmiet wetland fragments to use in aerial photograph analysis to compare the accuracy and effectiveness of this technique to the Landsat time-series analysis (research question 3). It was apparent from the earliest aerial photographs that some of the degradation had taken place prior to the first available imagery. Therefore to understand what the original extent of palmiet wetlands might have looked like, we attempted to model ‘potential habitat distribution’ using MaxEnt species distribution modelling.

(i) Technique 1: Multispectral remote sensing

(a) Image acquisition and classification

Palmiet wetlands are sparsely distributed over the Cape Floristic Region, often forming long narrow bands in the bottom of valleys, varying from 30 - 550 m in width, and typically from a few hundred to a thousand metres in length. Therefore we selected the Landsat series due to their large swath width and historical archives. Ten Landsat8 images (level 1T terrain corrected) covering the study area were downloaded from the Earth Explorer website from 2014 (**Fig. 1**). We tried to select images from spring to early summer (August-December 2014), as after the rainy winter season, the wetlands would be at their highest water levels and be easier to detect in the landscape (Ozesmi and Bauer, 2002). However in some cases this was not possible, due to extensive cloud cover. Therefore the scenes ranged in date from February to October. Images were converted from digital numbers to reflectance (except for the thermal bands which are preserved as temperature) in Grass7 using the i.toar-routine, and the Fmasks procedure was applied separately for cloud detection.

Regions of interest were collected from each of these ten scenes to represent the main land-use/land-cover classes throughout the images and, most importantly, for pure pixels containing palmiet wetlands. Regions of interest were selected visually using the regions of interest tool in ENVI, either in true colour mode (bands 2, 3, 4: blue, green, red), or false colour (bands 4, 6, 7: red, SWIR1, SWIR2), or both. Land-use/land-cover classes included agriculture (irrigated and dryland), towns/cities, sand, rock, water, cloud, mountain fynbos vegetation, karoo vegetation, plantations, riparian alien tree invasions, and native forest. All non-palmiet regions of interest were grouped together prior to classification. The classification was performed by the Support Vector Machine algorithm, which has demonstrated its use in the analysis of remotely sensed images (Asadzadeh and de Souza Filho, 2016). However, as the palmiet wetland class is very small, a presence-only variant was selected to identify its occurrence. More specifically, the one-class extension by Schölkopf et al. (2000) was used in the implementation of LibSVM (Chang and Lin, 2011). We used the same techniques to map the recent historical palmiet wetland occurrence at two points in time: 1970s and 1980s using Landsat1-3 and Landsat5 respectively (**Table 1**). We transferred regions of interest from the 2014 scenes onto those from the 1970s and 1980s and edited these to tailor them to the land-use/land-cover of the time, using the satellite images as a reference.

Table 1. Specifications of the products used in this study for various time steps

Product	Decade	Number of bands	Resolution	Swath Width/Area	Scale
Landsat8	2010	11	30x30 m	185 km	-
Landsat5	1980	4	60x60 m	185 km	-
Landsat1-3	1970	4	60x60 m	185 km	-
Aerial photographs	2010	-	0.5 m	6x5 km	-
	1980	-	2.6-4.7 m (mean 3.6 m)	7.5x7.5 km or 12.5x12.5 km	1:30 000 – 1:50 000
	1940/50	-	1.9-2.9 m (mean 2.5 m)	5x5 km or 7x7 km	1:18 000 – 1:30 000

(b) Classification validation and ground-truthing

For each classification, 80% of the ground reference points (pixels of the regions of interest for palmiet wetlands) were set aside for training data. Of this 80%, 50% were used for training and 50% for validation. In the validation step, the available non-palmiet regions of interest were included for parameter estimation, in order to reduce over-classification. The remaining independent 20% were used to test the accuracy of the classifications. F1-scores were calculated from the test set and are given as a score from 0-1 depending on the accuracy of the classification (% true positives). An additional accuracy score (%) was calculated for non-palmiet classification (% true negatives). The final result of the Landsat8 classifications was also ground-truthed using two independent techniques. The first was using visual analysis through Google Earth Pro, which had a high enough resolution to allow the assessment of the wetland classification results. Random GPS coordinates were generated (321 in total) and each point on the classification was compared to Google Earth imagery. The second method used independent data on palmiet presence collected through the citizen science platform: iSPOT (https://www.ispotnature.org/communities/southern-africa). In total palmiet vegetation was recorded 55 times throughout the study region by citizen scientists. These 55 locations were checked on the imagery to determine whether the classifications had correctly classified palmiet, and an accuracy score (%) was calculated. The classifications from the 1980s and 1970s were not possible to ground-truth, given that no data on wetland occurrence were found for these time periods.

(ii) Technique 2: Habitat suitability modelling

The purpose of using habitat suitability modelling was to construct a probability map of the possible original occurrence and extent of palmiet wetlands within the Cape Floristic Region, before colonialists arrived in South Africa in the 17th century, dramatically changing land-use/land-cover in South Africa (e.g. see Skead (2009)). We did this by only including input relating to its natural distribution (e.g. geology, soil, climate) and excluding input that would explain its decline (e.g. land-use/land-cover, pollution). Modelling a wetland community, rather than species, using MaxEnt, has been shown to be possible (Hunter et al., 2012). Therefore we used the MaxEnt species distribution model, which is based on the ecological niche concept (Phillips et al., 2006). MaxEnt is a general-purpose machine learning method based on the principal of maximum entropy (Phillips et al., 2006). MaxEnt produces a results map showing the probability of species occurrence, ranging from 0-1.

(a) Input data and settings

Relevant model input variables were selected and data obtained from various organizations such as national government and research institutions (**Table A1**). The output of the most recent (2010) aerial photograph analysis (raster file; technique 3) was converted to points (shapefile) in ArcMap and used as the input for wetland presence in the MaxEnt model. Sampling bias was controlled by inputting information on survey effort across the study region into the model (Merow et al., 2013). Since no palmiet wetland absence data exist, we used the non-palmiet regions of interest input from the multispectral remote sensing analysis. We used random seeding and set the number of replicates, from which the results could be averaged, to 15. In addition we chose to withhold 25% of the data for testing the performance of the model, using a sub-sampling approach. We set the number of iterations to 5000, allowing the model enough time to converge. All other MaxEnt settings were left at their default values. The spatial resolution of the analysis is determined by that of the coarsest data set (1.6x1.6 km), although all rasters were resampled to 46x46 m.

(b) Model validation and assessment

MaxEnt has a number of inbuilt cross-validation options where the presence locations are divided into training and validation datasets (used for K-fold cross validation). Goodness-of-fit statistics, or area under the receiver-operating characteristic curve (AUC), is the most popular model evaluation for MaxEnt (Merow et al., 2013). Alternatively, binary presence-absence predications can be generated from the model output using thresholds and this can be ground-truthed using independent data sets. We used AUC and the 10th percentile training presence logistic threshold to define the minimum probability of suitable habitat. Since no data exist on the historical extent of palmiet wetlands, the distribution cannot be ground-truthed. However the output was visually compared with current wetland extent to assess whether the modelled results are feasible.

(iii) Technique 3: Aerial photograph analysis

(a) Image acquisition and digitization

Palmiet wetland fragments were identified for further analysis using the results of the Landsat8 classification combined with expert knowledge. True palmiet wetlands were identifiable as relatively larger areas of dense pixels, whereas palmiet wetlands falsely identified by the algorithm tended to be made up of single pixels, sparsely spread. Eight wetland fragments were selected for further analysis. Aerial photographs from three time slices: 1940/50s, 1980s and 2010s were acquired from the Chief Directorate of National Geo-spatial Information (Cape Town, South Africa) for these eight sites. Wetland fragments range from about 2.75-13 km in size (wetland length). Aerial photographs were selected from three time steps (**Table 1**). The aerial photographs from 2010 were already rectified and georeferenced. These photographs were used to rectify and georeference the historical photographs in ArcMap. Wetland vegetation in each of the aerial photographs was digitized, making effort to consider the same wetland fragment in all three time slices for each site. Alien trees, erosion and agriculture in the valley-bottoms were excluded, but besides this no effort was made to distinguish healthy (pristine) wetland vegetation from degraded vegetation, nor to distinguish wetland vegetation types; as this would not have been possible to discriminate in the historical imagery. Wetland area and perimeter were calculated in ArcMap using the 'calculate geometry' tool, and the relative perimeter was calculated (perimeter/area).

Analysis & statistics

All resulting maps of historical and current palmiet wetland occurrence were collated in ArcMap and screened for reliability and accuracy. We chose the most reliable of the three approaches to analyse changes in wetland area and distribution over time. The statistical difference in change of wetland area and perimeter was tested using linear mixed models in R and an F-test with Kenward-Roger correction, after testing for normality. To establish which years differed from each other, a Tukey post hoc test was used. Where wetlands were predicted to be present historically, but are no longer present, the land-use/land-cover replacing them were obtained from Google Earth Pro and recorded. These findings were analyzed to determine the main drivers of palmiet wetland decline within the Cape Floristic Region. The frequency with which these drivers affected each wetland was recorded, and from this a percentage was calculated to indicate the relative importance of each driver.

3.3 Results

Technique 1: Landsat classification results

Landsat8 classification produced reasonable results for the current occurrence of palmiet wetlands within the Cape Floristic Region of South Africa (**Fig. 2, Table 2**). There was some slight over-classification, especially at higher altitudes, where there are no palmiet wetlands present (**Fig. 2**). There was also some over-classification within wetlands themselves as the algorithm sometimes struggled to discriminate between palmiet wetland vegetation, and other wetland vegetation types/alien vegetation. From the ground-truthed results using iSPOT records, a score of 63% for true positives was obtained, whereas from the 321 randomly generated points checked in Google Earth, the accuracy score was 100% for true negatives. Using Landsat8 imagery to detect and map small wetland fragments seems to be a feasible technique.

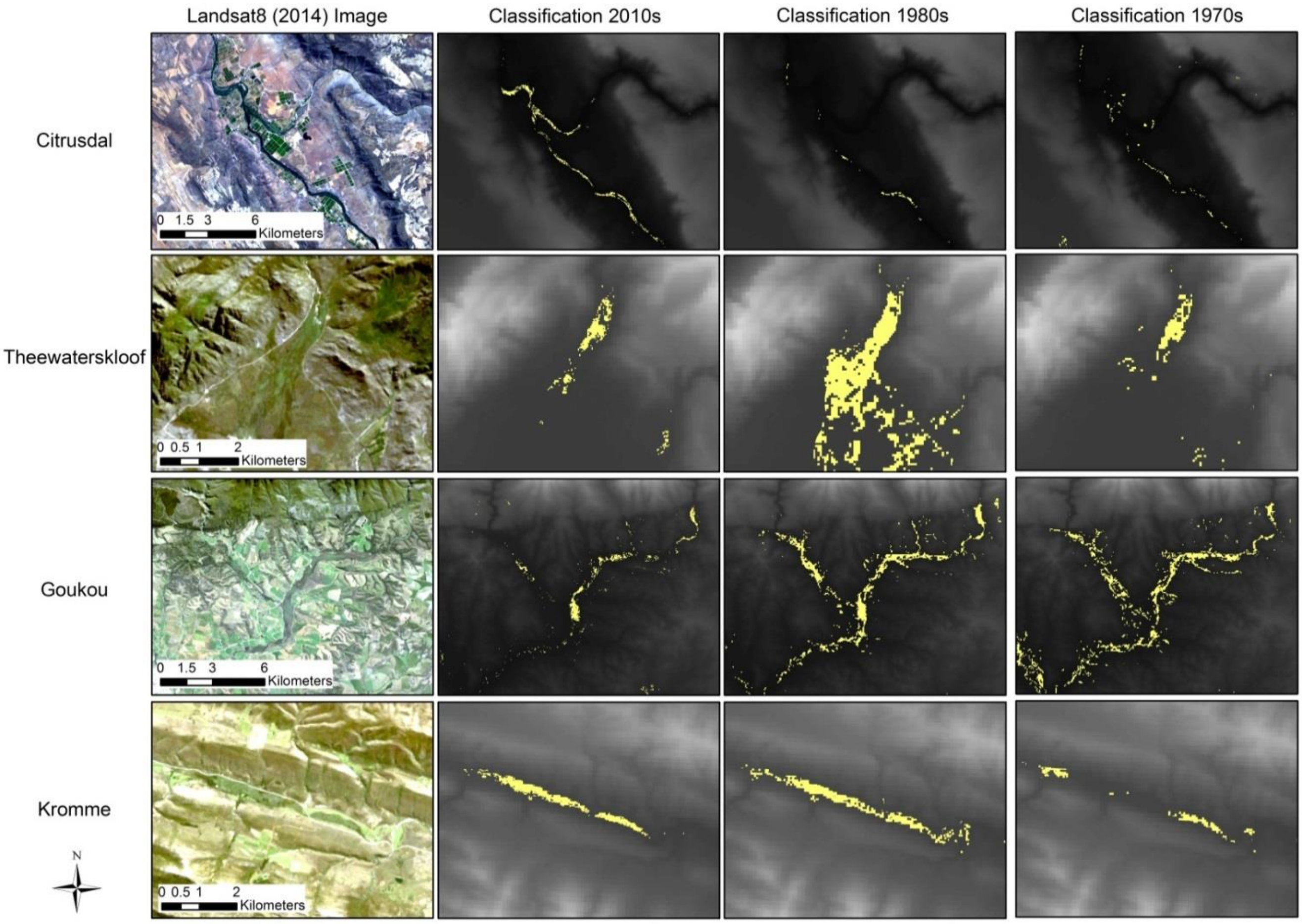


Figure 2. Results of the Landsat classifications for the 1970s, 1980s and 2010s from Landsat1-3, Landsat5 and Landsat8 respectively for four palmiet wetland sites in the Cape Floristic Region of South Africa. For the location of these sites within the Cape Floristic Region, see **Fig. 5.**

Overall for the historical imagery, Landsat5 and Landsat1-3 classification results were not as promising (**Table 2, Fig. 2**). The coarser spatial (60x60 m) and spectral (4 bands) resolutions made the classification of small wetland fragments challenging. Palmiet wetlands were still detectable; however there was significant over-classification, especially for Landsat5 imagery (**Fig. 2**). Therefore the results of classifications from the 1980s and 1970s were not used in further analyses to detect change in wetland extent over time. Landsat historical imagery appears to have limitations for accurately mapping the extent of small wetland fragments.

Table 2. Accuracy of classifications: F1-scores refer to the accuracy in terms of true positives (palmiet correctly classified) whereas % accuracy refers to the accuracy in terms of true negatives (non-palmiet correctly classified). The numbers in bold are the names of the images.

			Landsat8 2014			**Landsat5 1983-1987**			**Landsat1-3 1972-1978**		
#	**Path**	**Row**		**F1-Score**	**Accuracy (%)**		**F1-Score**	**Accuracy (%)**		**F1-Score**	**Accuracy (%)**
1	175	84	**115**	0.60	53.00	**131**	0.42	77.02	**335**	0.57	46.38
2	175	83	**291**	0.82	75.32	**131**	0.64	58.82	**313**	0.67	64.71
3	175	82	**291**	0.83	60.38	**289**	0.60	50.00	**260**	0.32	50.00
4	174	84	**236**	0.71	63.24	**218**	0.40	68.75	**298**	0.40	43.90
5	174	83	**268**	0.54	52.00	**330**	0.64	54.55	**312**	0.73	66.67
6	173	84	**245**	0.74	73.23	**115**	0.85	79.57	**347**	0.64	54.05
7	173	83	**277**	0.75	42.31	**115**	0.30	69.56	**347**	0.73	65.22
8	172	84	**174**	0.86	75.00	**204**	0.31	61.76	**070**	0.53	63.33
9	172	83	**174**	0.88	76.67	**321**	0.66	55.26	**274**	0.71	58.97
10	171	84	**279**	0.84	76.19	**314**	0.73	58.70	**15**	0.33	65.00
			mean	0.76	64.73		0.56	63.40		0.56	57.82

Spectral signatures

Spectral signatures can be useful in untangling the causes of over-classification of satellite remote sensing imagery. In the case of Landsat8 imagery, certain classes were more difficult to discriminate than others (i.e. had similar spectral signatures). Spectral signatures for palmiet were most similar to irrigated agriculture, plantations/alien invasion, Afromontane Forest, Albany Thicket and some Fynbos types (**Fig. 3, Fig. 4**). From the average spectra collected and displayed in **Fig. 4**, it seems that the spectral signature for palmiet wetlands is most similar to stands of dense trees, either alien (plantations/invasions) or indigenous (Afromontane Forest, Albany Thicket) or irrigated agriculture. This may be due to the high vegetation biomass or high water-use of these land-use/land-cover types, or a combination of both, rendering them similar to palmiet wetland spectra.

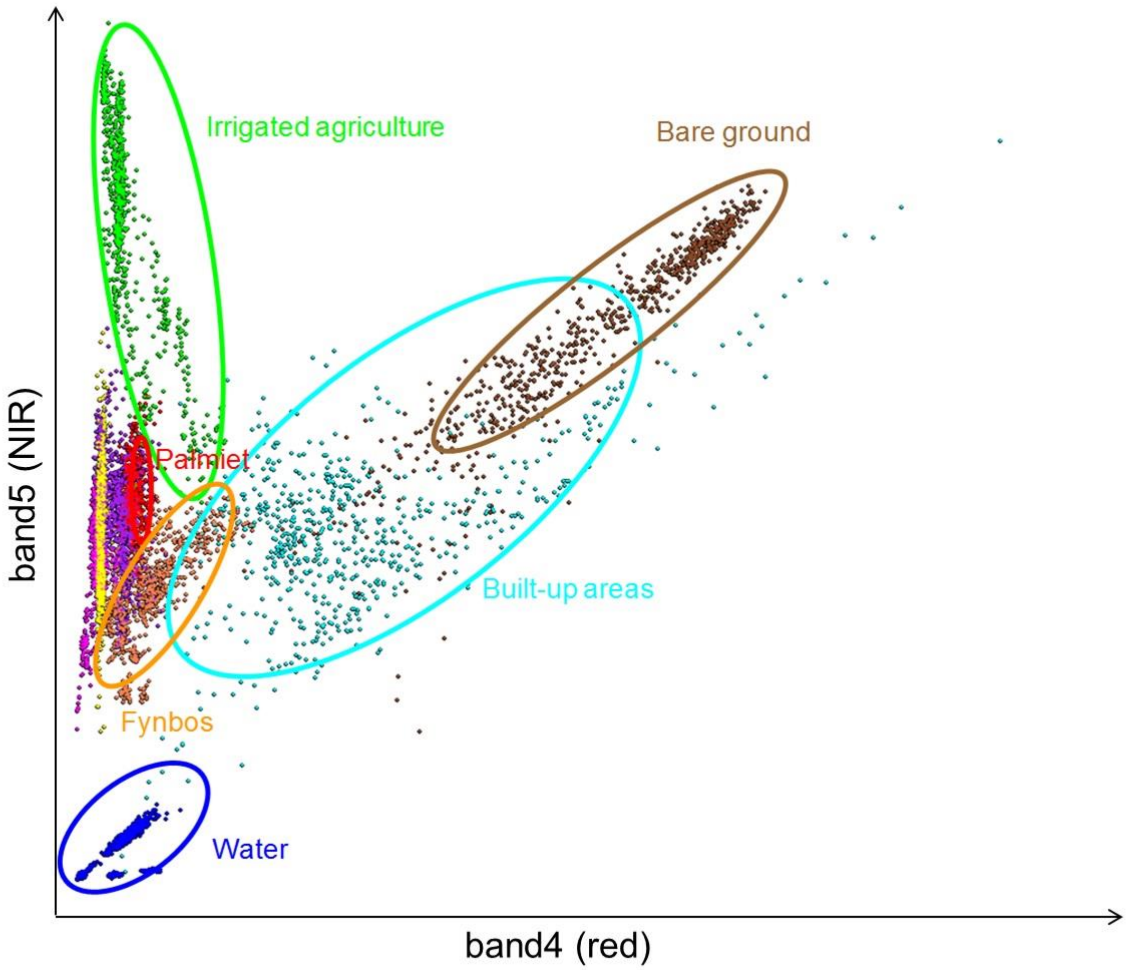
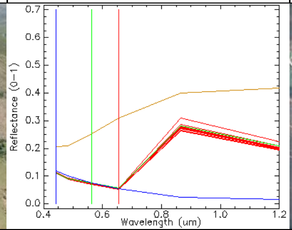
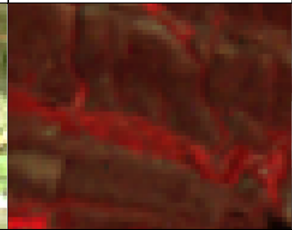
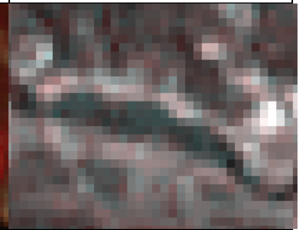
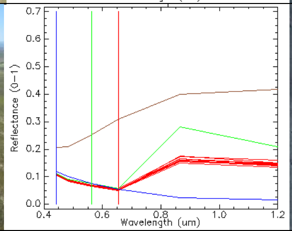
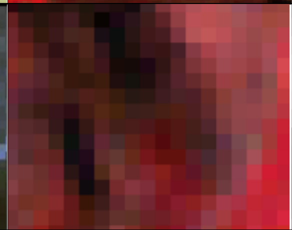
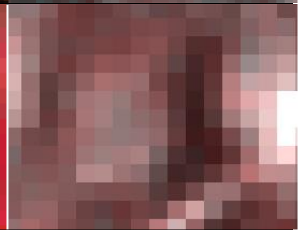
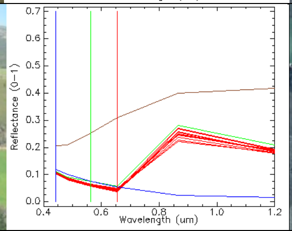
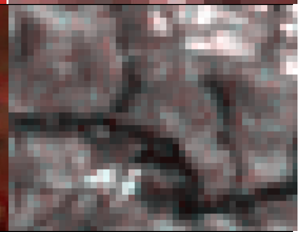
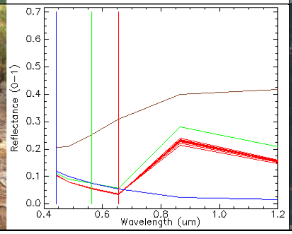
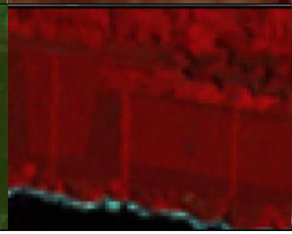


Figure 3. Spectral signatures of the major land-use/land-cover classes within the Cape Floristic Region, South Africa extracted from regions of interest taken from 2014 Landsat8 imagery. Two bands are plotted against each other: band4 (red) and band5 (near infra-red). The easily distinguishable classes are indicated on the figure, but all classes are listed here: ■ palmiet wetlands, ■ irrigated agriculture, ■ plantations/alien invasion, ■ Afromontane Forest, ■ bare ground, ■ water, ■ built up areas, ■ Fynbos, ■ Albany Thicket.

Land-use/Land-cover Class	Photo	Spectral Signature	Google Earth (2012-2016)	Landsat8 (2014)	Landsat5* (1984-1986)	Landsat1-3* (1972-1978)
Palmiet valley-bottom wetland (Kromme Wetland)						
Mountain seep wetland (Langkloof, Eastern Cape)						
Alien invasion (e.g. Black Wattle: *Acacia mearnsii*)						
Plantation (e.g. *Pinus* sp.), Tsitsikamma, Western Cape						

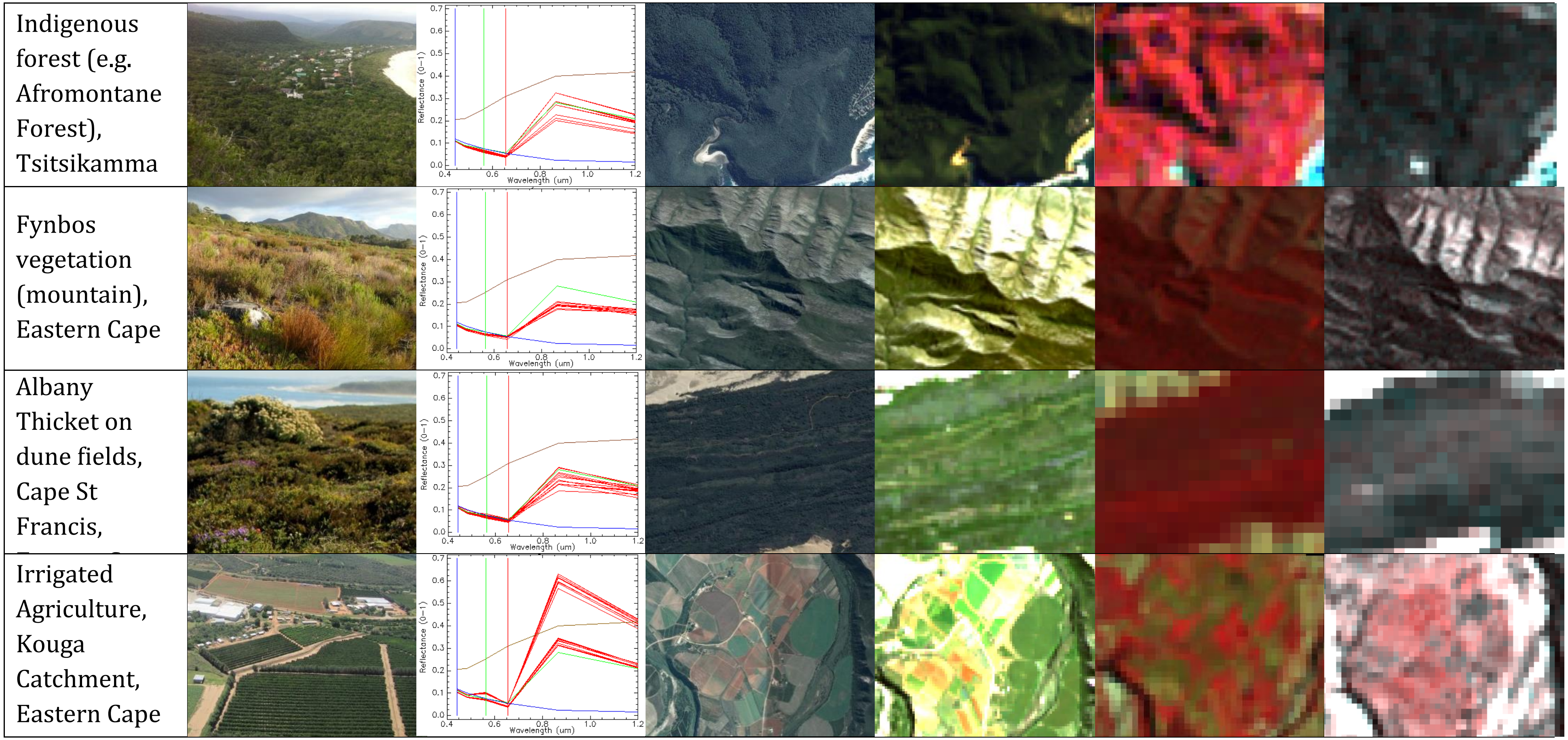


Figure 4. Discriminating between major land-use/land-cover classes in palmiet wetland classifications from the Cape Floristic Region, South Africa. All satellite imagery are displayed as true colour unless the land-use/land-cover is too difficult to discriminate; in which case it is displayed as false colour (*), where red is indicative of high vegetation biomass. Ten spectral signatures are collected from one image (**Fig. 1**, path 171, row 84) and are given in red, contrasted with 3 reference spectra (averaged from hundreds of spectra): ■ water, ■ bare ground and ■ palmiet. Two sets of spectra are given for agriculture: representing two main different types (orchards and fodder crops).

Technique 2: Habitat suitability modelling

Overall the MaxEnt model successfully identified some fragments of existing palmiet wetland patches as 'suitable' habitat (**Fig. 5**). It had an area under the receiver-operating characteristic curve of 0.81 (0.5 is considered no better than random, 1 is considered good model performance). However it was not able to extrapolate this information to where these wetlands may once have occurred (e.g. where they are known to have been replaced by an impoundment or agriculture). Overall this model –with the currently available spatial layers (input data) - does not successfully predict the historical extent of small valley-bottom wetland patches.

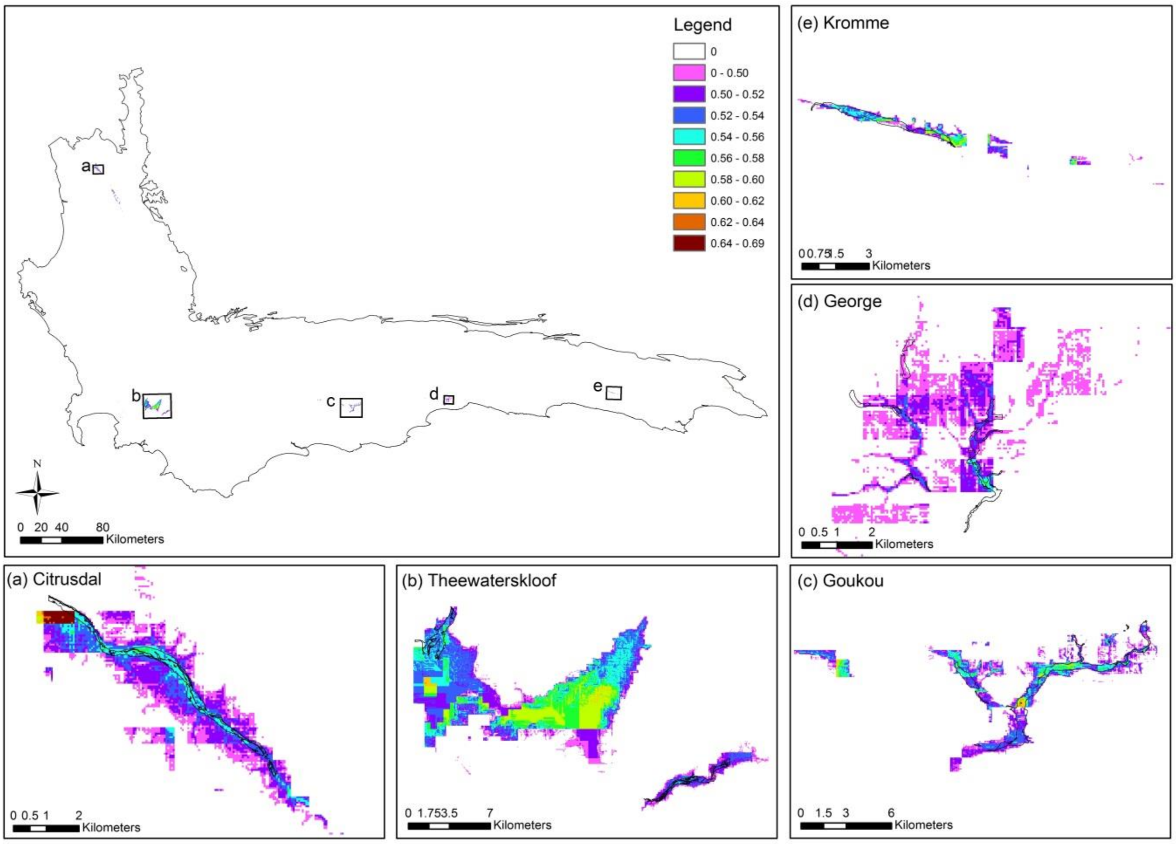


Figure 5. Predicted probability of palmiet wetland occurrence within the Cape Floristic Region, South Africa (scale: 0-1). This figure shows close-ups of five wetland fragments; the black lines indicate the current extent of these wetlands. The colour scale shows probability of wetland occurrence, cut off at 0.48, the 10th percentile training presence logistic threshold.

Ten variables were the most important in predicting palmiet wetland habitat suitability, accounting for 90% of the predictive contribution (**Table 3**). However not all of these variables and thresholds are the most sensible. For example, the threshold that the model set for slopes that are suitable for palmiet wetlands was too high. The model set the threshold at between 5-18° where we have found palmiet wetlands not to occur above slopes of about 5°. This accounts for some of the over-classification observed in **Fig. 5**. Secondly, one of the important variables is found to be 'precipitation of the driest quarter', which clearly separates the western and eastern parts of the Cape Floristic Region, being low in the west (9-80 mm) and high in the east (80-241 mm), resulting in a spatial bias due to the two different climatic regions. However palmiet wetlands occur in both regions, and therefore it is strange that this was selected by the model to be important in predicting palmiet wetland occurrence.

Table 3. Cumulative percentage contribution of environmental variables to the prediction of palmiet wetland occurrence in the Cape Floristic Region, South Africa. Thresholds are based on cumulative response curves.

Environmental variable	Contribution (%)	Thresholds
Groundwater depth (mamsl)	22.1	>300mamsl (35%)
Altitude (DEM)	43.4	<400m (100%); <100 (50%)
Mean diurnal temperature range (mean of monthly)	60.4	>11.5°C (35%)
Groundwater recharge (mm/a)	68.4	50-150mm (26-36%)
Precipitation of driest quarter (mm)	75.9	<80mm (56%)
Slope (degrees)	80.3	-5-18° (18-36%)
Mean annual runoff (mm)	83.4	>100mm (36%)
Borehole yield (l/s)	86.2	>8 l/s (36%)
Max temperature of warmest month (°C)	88.7	24-36°C (35%)
Min temperature of coldest month (°C)	90.2	4-7°C (20-45%)

Technique 3: Aerial photograph analysis

Eight remaining palmiet wetland fragments were identified in the Cape Floristic Region from the Landsat8 classification results, and these were used in aerial photograph analysis. This technique was found to be the most accurate in examining historical changes in wetlands, yielding results which were comparable from one time period to the next, unlike the historical Landsat analysis. Wetland change is shown visually for four wetland fragments in **Fig. 6** (details in **Table 4**). In contrast the MaxEnt modelling output is shown, giving an impression of the coarseness of the results. Also shown is the classification of these wetland fragments according to the South African National Freshwater Ecosystem Priority Areas (NFEPA) project (Nel et al., 2011). In each case these wetlands are miss-classified in NFEPA, either as ‘channelled’ valley-bottom wetlands, or as floodplain wetlands. These wetlands are all unchannelled valley-bottom wetlands, with the exception of the Citrusdal wetland. This Citrusdal wetland has likely artificially been channelized before the 1940s when extensive systems of canals were dug parallel to the wetland system, and a municipal dam was built. The NFEPA classifications also do not recognise wetland degradation, or where the wetland no longer exists due to agriculture (**Fig. 6**).

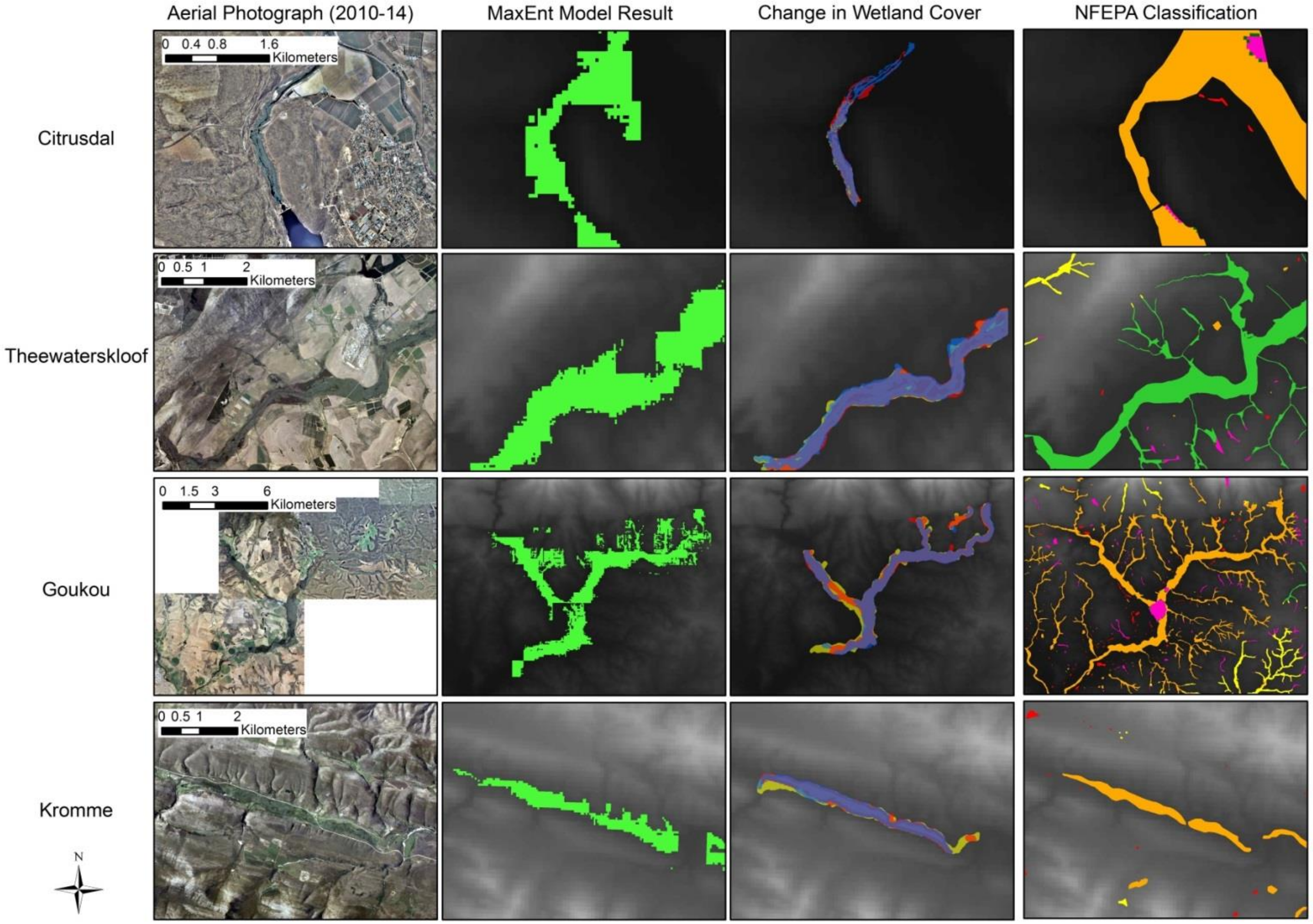


Figure 6. Comparison of aerial photograph and MaxEnt model output to an existing South African wetland product used for management and conservation (NFEPA) for four palmiet wetland sites in the Cape Floristic Region of South Africa. Change in wetland cover is shown by displaying the aerial photograph analysis results for: ■ 1940/50s, ■ 1980s and ■ 2010s. The NFEPA Classification has five different categories shown here: ■ channelled valley-bottom wetland, ■ flat, ■ floodplain wetland, ■ seep, and ■ unchannelled valley-bottom wetland.

Wetland change analysis

Palmiet wetland extent within the Cape Floristic Region has significantly declined over the past 60-70 years ($F = 5.21$, $df = 14$, $p < 0.05$). Overall decline in area is 31%; at some sites wetland area does not change at all and in other sites it declines by over half over the last 60-70 years (55%) (**Table 4**). Most of these significant changes took place between the 1940/50s and the 1980s ($t = 2.4$, $df = 7$, $p < 0.05$), though it is clear from the earliest photographs that major changes to these systems had already been made before the first aerial photographs were available (1940s). Wetland weighted perimeter (relative to the area of the wetland) increased significantly by 29% over the last 60-70 years ($F = 5.20$, $df = 14$, $p < 0.05$), indicating that remaining palmiet wetlands are becoming increasingly fragmented (**Table A2**). Every palmiet wetland experienced increased fragmentation, ranging from 5-39%.

Table 4. The change in palmiet wetland extent over three time-steps for eight palmiet wetland fragments within the Cape Floristic Region, South Africa. The primary catchment and drainage region (in brackets) are given. A negative change indicates an increase in area and positive a decrease. Letters in the bottom row denote significance of differences for the total change.

		Palmiet wetland extent (km^2)			
Location	**Catchment**	**1940/50s**	**1980s**	**2010s**	**Change (%)**
Citrusdal	Berg Catchment (G)	0.18	0.26	0.27	-0.09 (51%)
		1.26	1.23	1.26	0.00 (0.2%)
Theewaterskloof	Breede Catchment (H)	4.24	3.64	2.43	1.81 (43%)
		2.21	2.14	2.00	0.21 (9%)
Duivenhoks		1.16	0.68	0.52	0.64 (55%)
Goukou		8.44	6.67	5.80	2.64 (31%)
George	Tsitsikamma Catchment (K)	1.56	0.84	0.73	0.83 (53%)
Kromme		1.52	1.13	1.19	0.33 (22%)
Total		20.57 ^{a}	16.58 ^{ab}	14.21 ^{b}	6.36 (31%)

The major drivers of wetland change in South Africa can be divided into two categories: those indirectly affecting wetland extent by altering hydraulics and those directly affecting wetland extent by replacing wetland surface area (Rebelo et al., 2015). Bisecting roads are one of the most common drivers negatively impacting palmiet wetlands, affecting each of the eight wetland fragments investigated (**Table 5**). Roads cause knick-points in these wetland systems, often resulting in erosion, which eventually drains the wetland (Job, 2014). Once this erosion begins, it is impossible for the system to recover without active rehabilitation, which is costly. This wetland drainage results in a shift in vegetation communities, often encouraging the recruitment of alien vegetation. Other drivers impacting wetland hydraulics include water canals which drain palmiet wetlands, and dams: either small farm dams, or large municipal ones. Examples of the second type of driver include irrigated agriculture and alien plant invasion. Sections of palmiet wetlands have been replaced by agriculture, and others have become invaded by non-native plants, either trees (e.g. *Acacia mearnsii*, *Eucalypt* sp., *Pinus* sp. or *Quercus* sp.), or weedy plants such as *Rubus* sp.

Table 5. Main drivers of palmiet wetland change within the Cape Floristic Region, South Africa. The percentages indicate the relative importance of each driver in terms of the frequency with which it is recorded in the study wetlands.

Drivers	Contribution (%)
Roads bisecting wetland	28.6
Irrigated agriculture	25.0
Alien plant invasion	21.4
Dams	14.3
Water canals	10.7

3.4 Discussion

Comparison of techniques to map small wetlands

We found Landsat8 imagery combined with Support Vector Machine classification to be highly effective at detecting palmiet wetlands in a large region. This result was refined using aerial photograph analysis, by selecting eight of the largest remaining palmiet wetland fragments, and performing digitization at high resolution to accurately map current wetland extent. Historical wetland mapping using multispectral remote sensing was more challenging. The results from the Support Vector Machine classification of historical Landsat imagery were unreliable, a result of differing rates of over-classification per image and per time-step which rendered the outputs incomparable over time. Therefore using the Landsat series to examine change of small wetlands over time was unsuccessful in this study. Other studies have also found aerial photographs to deliver a superior product relative to multispectral imagery (Harvey and Hill, 2001). This is in contrast to studies using the Landsat series to classify larger wetland areas, which are often more successful (Han et al., 2015; MacAlister and Mahaxay, 2009).

We therefore used historical aerial photograph digitization for the eight palmiet wetland fragments to accurately examine change in wetland extent over time –since the 1940s. However we realised that some of the damage to these wetlands had been done before the first aerial photographs had been taken (pre-1940s). To understand wetland dynamics and to form restoration targets, it is essential to understand original wetland extent, and their original hydrological classification: whether these wetlands were originally channelled or unchannelled valley-bottom wetlands (although see argument of Grenfell et al. 2009). Therefore it was essential to have some information on where these wetlands may once have occurred, and to have an idea of their original extent. To that end we performed predictive modelling (MaxEnt) using the input data from the aerial photograph analysis. We found that this modelling technique was not optimal for mapping historical extent of palmiet wetlands, probably due to the low resolution of some of the predictors available. Overall, the best technique for small wetland detection, extent mapping and analysing temporal changes proved to be a combination of multispectral remote-sensing and aerial photograph analysis.

Implications for management, rehabilitation and conservation

The outlook for palmiet wetlands in the Cape Floristic Region is not positive. Existing wetlands have declined by on average 31% since the 1940's, although we have little information on the original extent of these wetlands. Nel and Driver (2012) estimate that over 50% of South African wetlands have been lost. This is slightly lower than the global average of 64-71% (Gardner et al., 2015). It is also important to note that the quality of these valley-bottom palmiet wetlands has declined over the past 60-70 years, becoming increasingly fragmented and channelized. According to the analysis of major drivers, this is largely due to roads bisecting and destabilizing the alluvium of the wetlands, causing headcut erosion and eventually channelization of these typically unchannelled systems. Similar causes of wetland degradation, wagon tracks and roads, in the Karoo have been deduced (Boardman, 2014). Hydraulic changes to these wetland systems by erosion are by far the most severe type of degradation and are difficult and expensive to rehabilitate (Grenfell et al., 2009). By draining the wetlands, these hydraulic changes also facilitate the invasion by alien species, often trees, which further perpetuates the cycle of degradation. Agriculture either alongside the wetland, or on the alluvium itself, poses another great threat to wetland integrity.

In terms of implications for management, degradation caused by roads or other infrastructure bisecting palmiet wetlands mostly took place before the 1980s. In the South African case, it is unlikely that more roads will be constructed through or over these wetlands. However for other valley-bottom wetlands globally, it is recommended that disturbance of the wetland should be avoided at all costs, and where possible bridges should be constructed, with high clearance and no culverts or obstructions beneath. Provision is made for protection of wetlands in the case of road construction in South Africa in two main ways: through compliance with section 24(7) of the National Environmental Management Act 107 of 1998 (environmental impact assessment required) and through the National Water Act 36 of 1998 which requires a water-use licence if the flow of water is diverted. Perhaps of greater concern currently, is the management of agriculture encroaching on or into palmiet wetlands, or of drainage canals being dug for agriculture. These practises are still continuing at present, and should be monitored and prevented, in accordance with the National Environmental Management, the National Water Act and the Conservation of Agricultural Resources Act.

One important observation that was made during the historical mapping is that palmiet wetlands seem to be remarkably stable over periods of up to 70 years, unless the alluvium is destabilized, in which case headcut erosion takes place rapidly. In case 1 (**Fig. 7**), a road bisecting the top end of the palmiet wetland, the point at which a steep mountain stream becomes unconfined and enters a broader valley bottom, caused a knick-point, resulting in channel erosion. This channel is on average 10 m wide and 3-4 m deep. Between 2004 and 2014 the channel had lengthened by 446.24 m, an average of 45 m per year. According to historical imagery available on Google Earth Pro, the change is not gradual, year-by-year, but rather as the result of extreme flood events, which happen on average once a decade. In case 2, the stability of palmiet wetland systems is demonstrated. This channel, whether natural or man-made, has remained open in this palmiet wetland for the past 60 years, demonstrating that once these systems reach an equilibrium, they are highly stable over time. Similar observations were made in a geomorphological study of the Goukou palmiet wetland system, where sections of the wetland were found to be remarkably stable between 1941 and 1991 (Job, 2014). This has important management and rehabilitation implications, as it means that once damage has occurred, causing a knick-point, it should be rehabilitated before the next large 10-year floods occur, otherwise substantial wetland loss is risked. Therefore timing is critical in these rehabilitation projects. Ultimately as these wetlands become channelized and the alluvium and peat is washed away, valuable ecosystem services are lost (Rebelo et al., 2015).

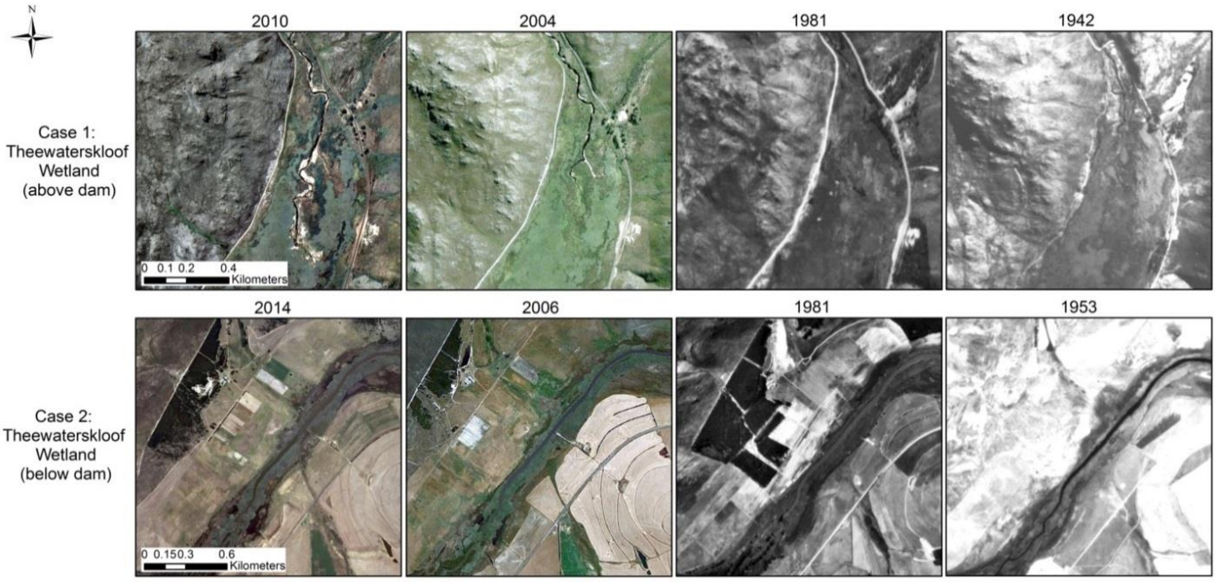


Figure 7. Wetland change over time: two interesting cases in point, illustrated over four time-steps for the last 61-68 years. The first wetland is the upper Theewaterskloof wetland, and the second is the lower Theewaterskloof wetland, above and below the municipal dam respectively, in the Cape Floristic Region, South Africa. The first case shows the progression of a head-cut through the wetland, and the second shows the persistence of a channel. It is unknown whether this is man-made or natural.

Lastly, it is apparent that palmiet wetlands are not adequately represented in the South African National Freshwater Ecosystem Priority Areas (NFEPA) Atlas. Many of these palmiet wetlands are misclassified, and there is no information available on the condition of these wetlands. Many are degraded or no longer exist, and yet are indicated as wetlands in the atlas. Similar results were found in a congruency assessment between the South African National Wetland Map and two sites which had wetlands mapped on 1:10 000 aerial photographs: the Overberg Municipal District and the City of Cape Town Metro (van Deventer et al., 2016).The data from small scale studies such as this one, can be used to supplement coarser national-scale wetland inventories, improving the knowledge of wetland distribution, type and condition. This is essential for prioritizing wetland rehabilitation and conservation. At least half of the eight wetlands which were chosen for wetland change analysis are in a critical condition, threatened by headcut erosion. If steps are not taken immediately to stop this erosion, it is likely that these wetlands will be drained or lost in the next 50 years. Most of these palmiet wetlands are underlain by peatbeds, known to have important water purification abilities (**Chapter 10**). Additionally many of these wetlands are located above dams, providing municipal water to millions of South Africans. If these wetlands are lost or become degraded, there is likely to be an impact on the water quality of these important regional water resources.

3.5 Conclusion

Historical aerial photograph analysis showed that South African palmiet wetlands are in decline, and due to drivers such as erosion, agriculture and alien plant invasion, are becoming increasingly degraded and fragmented. Structural wetland rehabilitation to stop the progression of gully erosion is recommended prior to the next large respective local flood events, to prevent substantial loss and high rehabilitation costs. The comparison of three techniques to detect and map extent of small wetlands demonstrated that a combination of techniques yields the best results. We found classification of Landsat8 imagery to be the most successful technique for initial wetland detection, which can be refined using aerial photographs where greater accuracy is needed. This addresses a major challenge in mapping small wetlands at a landscape level.

3.6 Acknowledgements

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3.8 Appendix

Table A1. Original MaxEnt model input variables for consideration, their labels, units, data type, cell size, file type and source. CFR: Cape Floristic Region.

Variable type	Variable	Label	Units	Data Type	Cell size	Extent	File	Source
Climate	Annual Mean Temperature	bio1	°C*10	Continuous	0.8km	Global	raster	WorldClim[1]
	Mean Diurnal Range (Mean of monthly (max temp - min temp))	bio2	°C*10	Continuous	0.8km	Global	raster	WorldClim[1]
	Isothermality (*100)	bio3	°C*10	Continuous	0.8km	Global	raster	WorldClim[1]
	Temperature Seasonality (stdev*100)	bio4	°C*10	Continuous	0.8km	Global	raster	WorldClim[1]
	Max Temp. of Warmest Month	bio5	°C*10	Continuous	0.8km	Global	raster	WorldClim[1]
	Min Temp. of Coldest Month	bio6	°C*10	Continuous	0.8km	Global	raster	WorldClim[1]
	Temperature Annual Range	bio7	°C*10	Continuous	0.8km	Global	raster	WorldClim[1]
	Mean Temp of Wettest Quarter	bio8	°C*10	Continuous	0.8km	Global	raster	WorldClim[1]
	Mean Temp of Driest Quarter	bio9	°C*10	Continuous	0.8km	Global	raster	WorldClim[1]
	Mean Temp of Warmest Quarter	bio10	°C*10	Continuous	0.8km	Global	raster	WorldClim[1]
	Mean Temp of Coldest Quarter	bio11	°C*10	Continuous	0.8km	Global	raster	WorldClim[1]
Hydrology	Annual Precipitation	bio12	mm	Continuous	0.8km	Global	raster	WorldClim[1]
	Precipitation of Wettest Month	bio13	mm	Continuous	0.8km	Global	raster	WorldClim[1]
	Precipitation of Driest Month	bio14	mm	Continuous	0.8km	Global	raster	WorldClim[1]
	Precipitation Seasonality (Coefficient of Variation)	bio15	mm	Continuous	0.8km	Global	raster	WorldClim[1]
	Precipitation of Wettest Quarter	bio16	mm	Continuous	0.8km	Global	raster	WorldClim[1]
	Precipitation of Driest Quarter	bio17	mm	Continuous	0.8km	Global	raster	WorldClim[1]
	Precipitation of Warmest Quarter	bio18	mm	Continuous	0.8km	Global	raster	WorldClim[1]
	Precipitation of Coldest Quarter	bio19	mm	Continuous	0.8km	Global	raster	WorldClim[1]
	Mean annual runoff	bio20	mm	Continuous	1.6km	RSA	raster	SWSA
Groundwater	Groundwater recharge	bio21	mm/a	Continuous	0.8km	RSA	raster	GR2, GEOSS, SARVA
	Groundwater electrical conductivity	bio22	mS/m	Continuous	46m	RSA	raster	GR2, GEOSS, SARVA
	Borehole yield	bio23	l/s	Continuous	46m	RSA	raster	GR2, GEOSS, SARVA

	Depth to groundwater	bio24	(mamsl)	Continuous	0.8km	RSA	raster	GR2, GEOSS, SARVA
Geology & Soils	Geology	bio25	-	Categorical	0.5km	RSA	raster	WR90
	Soils	bio26	-	Categorical	0.5km	RSA	raster	WR90
Digital elevation model derived	Altitude (dem)	bio29	m amsl	Continuous	46m	CFR	raster	90 m SRTM DEM
	Slope	bio30	Degrees	Continuous	46m	CFR	raster	90 m SRTM DEM
	Aspect	bio31	Degrees	Continuous	46m	CFR	raster	90 m SRTM DEM
	Flow accumulation	bio32	-	Continuous	46m	CFR	raster	90 m SRTM DEM
	Flow direction	bio33	Degrees	Categorical	46m	CFR	raster	90 m SRTM DEM
Biotic	Palmiet wetland occurrence data		Presence				point	
	Background File		Presence & Absence				point	

[1] Hijmans, R.J., S.E. Cameron, J.L. Parra, P.G. Jones and A. Jarvis, 2005. Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25: 1965-1978.

Table A2. The change in palmiet wetland weighted perimeter (km) over three time-steps for eight palmiet wetland fragments within the Cape Floristic Region, South Africa. The primary catchment and drainage region (in brackets) are given. All wetlands show an increase in weighted perimeter (negative change). Letters denote significance of differences of the totals.

Wetland Location	Catchment	1940/50's	1980's	2010's	Change (%)
Citrusdal	Berg Catchment (G)	48.51	46.27	78.78	-30.27 (38%)
		33.58	39.26	37.98	-4.40 (11%)
Theewaterskloof	Breede Catchment (H)	9.81	11.73	14.86	-5.05 (34%)
		17.45	16.07	28.73	-11.28 (39%)
Duivenhoks		45.33	44.19	68.21	-22.87 (34%)
Goukou		7.54	9.74	9.88	-2.35 (24%)
George	Tsitsikamma Catchment (K)	27.59	32.79	34.72	-7.13 (21%)
Kromme		11.41	14.92	12.10	-0.70 (5%)
Total		201.22 [a]	214.96 [a]	285.26 [b]	-84.04(29%)

4

The impact of degradation on South African palmiet wetlands

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Submitted

Channel erosion in the Theewaterskloof wetland. Dense wetland vegetation once covered layers of peat and soil where this channel is today. The channel is lengthening at a rate of 45 m per year on average and is roughly 10 m wide and about 3-4 m deep. Alien trees invade along the channels borders.

Abstract

Wetlands provide a disproportionate amount of ecosystem services to society relative to their size, and yet these ecosystems are amongst the most threatened globally. There are many different types of wetland degradation, such as that which affects the physical structure of wetlands, pollution, land-cover change, disturbances and climate change, which have various impacts, depending on the type of wetland, soils, internal biochemistry amongst other factors. We researched a unique, poorly-studied South African valley-bottom peatland that is dominated by the ecosystem engineer palmiet: *Prionium serratum*. We ask the question: what is the impact of degradation on biochemistry and plant community composition of palmiet wetlands? Types of degradation faced by palmiet wetlands include land-cover change, gully/channel erosion, invasion by alien plants and pollution by agricultural runoff. In 39 plots from three palmiet wetlands situated approximately 200 km apart we measured key soil, groundwater and vegetation parameters, as well as vegetation community composition. Overall we found that channel erosion, through a loss of alluvium, seems to have resulted in highly leached soils with lower soil organic matter and water content, unable to retain nutrients and cations. This has probably resulted in groundwater with higher electrical conductivity and pH than pristine wetlands and a decrease in soil cation exchange capacity (±20.6 to ±7.7 meq/100g). The loss of alluvium typically resulted in a completely new plant community, composed mostly of pioneer species and several alien species. An increase in base saturation (±17.6 to ±30.2%) and soil pH (±4.9 to ±5.1) was thought to be the result of liming practices. Wetland degradation will have a bearing on ecosystem service provision, including: reduction of carbon sequestration, decrease in flood attenuation, and reduction in the water purification capacity of palmiet wetlands. To preserve ecosystem service provision of remaining pristine fragments of this unique South African valley-bottom wetland system, protection and conservation is recommended.

4.1 Introduction

Wetlands make up less than 3% of the area of the globe, and less than 8.6% of land, and yet half of the worlds wetlands have been estimated to have been lost and many more have been degraded (Ferreira and Lacerda, 2016; Meli et al., 2014; Meng et al., 2017; Nel et al., 2007; Rebelo et al., 2015; Zedler and Kercher, 2005). There are many different types of wetland degradation, and some types of degradation trigger further impacts. Wetland degradation can be grouped into five loose categories: degradation that affects wetland physical structure, pollution, land-cover changes, disturbances (e.g. fire - Zedler and Kercher (2004)), and climate change (Meng et al., 2017; Zedler and Kercher, 2005). Degradation affecting physical structure of wetlands may include drainage; either by humans or as a result of other damage (Krüger et al., 2015; Watters and Stanley, 2007; Zedler and Kercher, 2005), peat excavation (Cabezas et al., 2014; Nsor, 2007; Winde, 2011), and erosion (e.g. channel or gully erosion) (Boardman, 2014; de Haan, 2016; Rebelo et al., 2015). Wetland pollution may be in the form of agricultural runoff, wetland fertilization, or point source pollution (Carpenter and Bennett, 2011; Jordan et al., 2003; Winde, 2011; Zedler and Kercher, 2005). Types of land-cover changes include vegetation changes (Brooks et al., 2003), alien invasion (Zedler and Kercher, 2005, 2004) or land conversion, for example to agriculture (de Haan, 2016; Rebelo et al., 2015). Ultimately the degradation of wetlands results in a loss of biodiversity and ecosystem services (Meli et al., 2014; Zedler and Kercher, 2005) which may have economic consequences for local communities (Schuyt, 2005).

Different types of wetland degradation affect wetland biochemistry, community composition and ecosystem functioning differently, however commonalities exist. Wetland degradation generally increases soil bulk density and causes a decline in organic matter/carbon content (Huo et al., 2013; Krüger et al., 2015; Salimin et al., 2010; Sankura et al., 2014). In contrast, impact on soil pH depends on the system and type of degradation, in some cases decreasing (Sankura et al., 2014) and in others increasing with degradation (Aggenbach et al., 2013; Emsens et al., 2015; Salimin et al., 2010). Wetland drainage of Northern Hemisphere ecosystems has been cited to cause a chain reaction of impacts, such as the loss of biodiversity, peat decomposition leading to the leaching of nutrients into rivers, as well as dust storms (Krüger et al., 2015; Zedler and Kercher, 2005). Wetland drainage may also cause erosion, dramatically altering wetland form, eventually leading to channel formation (Watters and Stanley, 2007). In South Africa, channel erosion has been postulated to be the result of damage caused by roads bisecting wetlands or the landscape in general, however the processes behind this degradation are poorly understood (Boardman, 2014; de Haan, 2016; **Chapter 3**). Overall wetland degradation has significant consequences for ecosystem service provision; loss of soil organic matter or carbon results in a release of carbon into the atmosphere (Krüger et al., 2015). Gully erosion, on the other hand, increases siltation of dams and increases flood risk to downstream landowners (Job, 2014; Rebelo et al., 2015).

South African wetlands and associated river systems are in a critical state, with over 65% estimated to be damaged, and over half destroyed (Nel et al., 2007). One such threatened wetland, a unique valley-bottom peatland, occurs within the Cape Floristic Region of South Africa. These peatlands are dominated by a wetland species endemic to southern Africa and listed as declining on the red list of South African plants: palmiet (*Prionium serratum*). Palmiet is thought to be an ecosystem engineer (Sieben, 2012). Due to its deep, extensive rooting structure and clonal nature, it is hypothesized to have stabilized river valleys within the Cape Floristic Region, creating a local base level and water ponding, forming unchannelled valley-bottom wetlands and allowing the accumulation of peat beds (Job, 2014). Palmiet wetlands are highly threatened with degradation, having declined by almost 31% since the 1940's (**Chapter 3**). The main threats faced by these wetlands are channel erosion, land-cover change (wetlands to agriculture), pollution from agricultural runoff (potentially both fertilizers and effluent from liming) and invasion by alien vegetation. These threats are often operating together and as a result it is very difficult to select sites which exclusively face only certain types of degradation and it is equally difficult to disentangle their effects.

Removal of wetland vegetation for agriculture is perhaps one of the more extreme changes to palmiet wetlands and since wetland vegetation is completely removed and sites are heavily manipulated with fertilizers, liming and irrigation, these impacts were not investigated in this study and these sites were avoided. The second most dramatic impact to these wetlands is channel erosion, which might be expected to draw down the water table in adjacent wetland habitat, resulting in an increase in soil bulk density and a decline in organic matter/carbon content (Huo et al., 2013; Krüger et al., 2015; Salimin et al., 2010; Sankura et al., 2014). This would increase soil oxygen in the root zone making soil nutrients available, which, combined with lower organic matter may result in the release of these nutrients into the groundwater (Krüger et al., 2015; Zedler and Kercher, 2005). The impacts of alien plant and tree invasion on palmiet wetlands is difficult to study since in many places alien vegetation has been removed by restoration programmes such as Working for Water. Therefore we did not explicitly consider these effects in this study. There has been research on the impacts of invasion by alien Acacias on riparian systems, which has shown an increase in nitrogen availability in the soil as well as enhanced phosphorus mineralization rates (Naudé, 2012). Impacts from agricultural runoff may include an increase in bioavailable nutrients from fertilizers as well as an increase in pH due to liming practises common in agriculture in the Cape Floristic Region (Beukes et al., 2012). In this study, we ask the question: what is the cumulative impact of this complex, multifaceted wetland degradation on biochemistry and vegetation community composition of palmiet wetlands?

4.2 Methods

Study region & wetlands

The Cape Floristic Region has a predominantly mediterranean-type climate characterised by summer drought and winter rainfall resulting from the passage of cold fronts (Midgley et al., 2003). The soils of the Cape Floristic Region are mainly highly leached dystrophic lithosols associated with the sandstone mountains of the Cape Supergroup (Midgley et al., 2003). Three palmiet wetlands were selected as study sites within the Cape Floristic Region: the Theewaterskloof and Goukou wetlands (Western Cape) and the Kromme wetland (Eastern Cape) (**Table 1**). Despite being situated as much as 470 km apart, these wetlands are remarkably similar in vegetation composition. They occur on low gradients below elevations of 400 m. Mean annual precipitation is highly variable, highest in the Theewaterskloof catchment and lowest in the Goukou catchment. Mean annual runoff is also highest in the Theewaterskloof catchment but lowest in the Kromme catchment. In the case of the Kromme and Goukou, most of this runoff occurs over a short period of time, during flood events (Job, 2014; Rebelo et al., 2015). All three wetlands have accumulated peat layers between 0.5 to 10 m deep (**Table 1**). In some ways, these systems are similar to European bogs, in that they are highly oligotrophic and have a low pH (Wheeler and Proctor, 2000). On the other hand they are also similar to fens in terms of vegetation composition and hydrology. These wetlands are described as being internally dynamic, but overall relatively stable ecosystems (Job, 2014).

Table 1. Site information for the three study wetlands. MAP: mean annual precipitation, MAR: mean annual runoff (Job, 2014; Kotze, 2015; Middleton and Bailey, 2008; Nsor, 2007; Sieben, 2012).

Catchment	Theewaterskloof	Goukou	Kromme
Co-ordinates	33°57'40.32"S, 19°10'10.00"E	34° 0'30.46"S, 21°24'59.97"E	33°52'24.69"S, 24° 2'24.13"E
Elevation (m)	362.4	180.7	353.6
MAP (mm)	1241	645	745
Rainfall 6 months before September 2014 (mm)	644	316	197
Rainfall 6 months before March 2015 (mm)	107	351	148
MAR (mcm)	149.8	52.3	25.4
Rainfall Region/Pattern	winter	winter/coastal zone	bimodal
Peat Depth (m)	0.5-2	3-10	0.5-2.8

Study design

To capture seasonal variation in wetland properties and processes, each wetland was sampled twice: once in September 2014, which was just after winter, and once in March/April 2015, which was just after the summer. Rainfall for the six months preceding the first fieldtrip (winter) was average-to-low for all sites (approximating 50% of the MAP for the Theewaterskloof and Goukou), as a result of a drought. Rainfall for the six months preceding the second fieldtrip (summer) was far lower for Theewaterskloof (**Table 1**). For Theewaterskloof and the Kromme, the second campaign represents a drier season, whereas there is no such difference for the Goukou wetland as the rainfall regime is influenced by its proximity to the coast. At each wetland, both a degraded and an undisturbed (pristine) stretch was sampled, yielding a total of six sites. Degraded stretches were characterized by channelization or erosion with subsequent drainage, which was typically accompanied by alien tree or weed invasion (**Table 2, Fig. 1**). Additionally degraded sites were often situated in an agricultural context, receiving polluted runoff from adjacent fields. Pristine stretches were selected such that there was no channelization or alien vegetation in the immediate vicinity (at least 300 m-1 km away), though it should be noted that all wetlands are transformed to some degree, with channelization occurring upstream or downstream of pristine fragments.

Table 2. Types of degradation at each of the three degraded palmiet wetland fragments.

Wetland	Channel erosion	Agricultural runoff	Alien plant invasion
Theewaterskloof	Channel through the middle of the wetland fragment	None	*Acacia mearnsii* (tree), *Rubus fructicosus* (weed)
Goukou	Channel along the side of the wetland fragment	Yes (irrigated agriculture adjacent to fragment)	*Acacia mearnsii* (tree), *Briza minor, Conyza bonariensis, Hypochaeris radicata, Paspalum dilatatum* (weeds)
Kromme	The entire alluvium of the fragment has been eroded	Yes (irrigated agriculture adjacent to fragment)	*Acacia mearnsii, Acacia saligna* (trees), *Conyza bonariensis, Hypochaeris radicata, Rubus fruticosus* (weeds)

At each site, cross-sectional transects (100-200 m) were made across the wetland, with six plots (3x3 m) placed between 20-50 m apart, yielding a total of 36 plots across the six sites (**Fig. 1**). Transects and plots were chosen in the field to ensure adequate representation of the main vegetation communities. To this end we included one extra pristine site in the Goukou wetland, with only three plots, yielding a final sum of 39 plots. Piezometers (3 m, PVC) were placed adjacent to every second plot, yielding a total of 21 piezometers (**Fig. 1**).

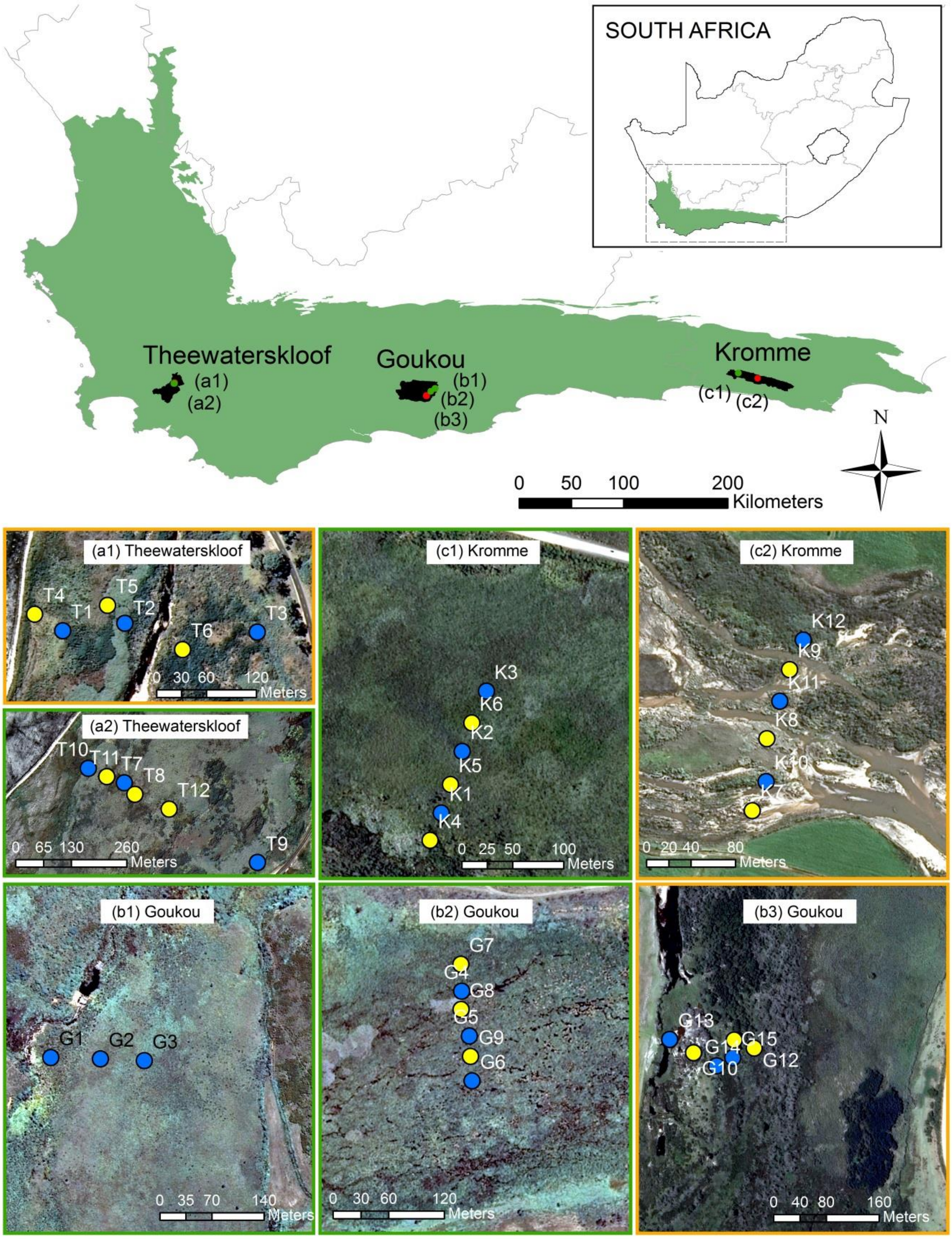

Figure 1. The location of the 39 study sites (circles) and three study wetlands within the Cape Floristic Region (green) of South Africa. Orange borders show wetland fragments that are degraded (often channelized), whereas green borders indicate relatively undisturbed fragments. Blue-filled circles indicate the location of piezometers within the wetlands.

Sampling

a) Plant community composition and vegetation analysis

In each plot, all plants were identified to species level where possible and percentage cover was estimated for each species using the Braun-Blanquet Scale (Mueller-Dombois and Ellenberg, 1974). Vegetation was sampled from three small, randomly selected subplots of 0.28x0.28 m within each plot. Vegetation was weighed after oven drying for 48 hours at 70°C and then ground and homogenised using a mill until it could pass through a 0.5 mm mesh sieve. Plant total carbon and total nitrogen contents were determined by total combustion of 5 mg of each sample on a Flash 2000 CN-analyzer (Thermo Fisher Scientific). Plant total nitrogen and total phosphorus were determined using acid digestion and were measured with a continuous -flow analyzer (CFA) (SKALAR: SAN++) (Walinga et al., 1989). Plant total K, Ca and Mg were analyzed by Inductively Coupled Plasma-emission spectrometry (ICP-OES) (Walinga et al., 1989) after acid digestion of ±0.3 g of dried and finely ground vegetation with H_2SO_4–Se-salicylic acid.

b) Soil sampling and chemical analyses

In each plot, one composite soil sample was taken from 10 points throughout the plot at a depth of 1-10 cm using a hand held auger of 1 cm in diameter. Soil pH-H_2O was measured after adding distilled water to a 10 g soil sample and shaking it for an hour. Additionally in each plot one bulk density sample was taken of the topsoil using a 100 cm^3 metal Kopecky ring. Samples were weighed after oven drying for 48 hours at 70°C and values are expressed as g/cm^3. Soil moisture was calculated gravimetrically by weighing ±20 g of fresh soil before and after drying for 24 hours at 105°C. Soil organic matter content was determined by loss on ignition (4h at 550°C). Total phosphorus and nitrogen were analyzed on a CFA. Soft extractions were done on fresh soil to determine NO_3^--N, NH_4^+-N and PO_4^{3-}-N; samples were extracted and preserved for later analysis on a CFA using AA-EDTA (ammonium acetate – ethylenediaminetetraacetic acid) for PO_4^{3-}-P and AA-KCl (ammonium acetate - potassium chloride) for NO_3^--N and NH_4^+-N respectively (Houba et al., 1989). Nutrient pools were calculated by multiplying nutrient concentrations by bulk density measurements. Total soil K, Ca and Mg were analyzed on the ICP-OES after acid digestion of ±0.3 g of dried and finely ground soil with H_2SO_4–Se-salicylic acid (Walinga et al., 1989).

Cation exchange capacity was determined using the method of Brown (1943) by weighing ±8 g of soil before and after air drying in an incubator at 40°C for 48 hours. Samples were then sieved through a 2 mm sieve, 25 ml ammonium acetate solution (1M) was added to 2.5 g of soil and samples were shaken for one hour. Soil pH was measured and samples were filtered through a 0.45 µm filter before being analyzed for H, Ca, K, Mg, Na, Al, Fe, Mn ions on an ICP-OES. CEC is calculated as the sum of all the ions, and base saturation is calculated as the percentage of base cations (Ca, K, Mg, Na) per CEC. Soil microbial biomass carbon was measured as a proxy for microbial activity in the soil at each site. We used the chloroform fumigation direct extraction protocol for microbial biomass carbon (Beck et al., 1997; Martens, 1995).

c) Groundwater sampling and chemical analyses

Depth to the water table was measured in each piezometer using a sounding device, and the standing water was emptied using a bailer. Once fresh water had refilled the piezometer, a sample was taken for a pH and conductivity reading. Six water samples were taken and filtered (0.45 µm) to test for water quality parameters. The concentration of phosphate (PO_4^{3-}-P), ammonium (NH_4^+-N), total phosphorus (P-tot), and total Kjeldahl nitrogen (Kj-N) were measured on a CFA. Concentrations of sodium, magnesium and calcium were measured on the ICP-OES.

Data analysis

We performed an ANOSIM and SIMPER analysis in R, using the 'Vegan' package for community ecology (Warton et al., 2012). We used analysis of similarity (ANOSIM) to determine whether vegetation communities from degraded and pristine wetland fragments were separable or not, using the Bray–Curtis dissimilarity index. Next we performed a similarity percentage analysis (SIMPER) to determine which species characterised degraded and pristine fragments, as well as different wetlands.

To test the effect of degradation and wetland (Theewaterskloof, Goukou, Kromme) on soil, groundwater and vegetation parameters, we fitted linear mixed models taking season into account (2014, 2015). Plots were entered as a random effect to account for the dependence between observations from within the same plot. Wetland, degradation, season and the interaction between wetland and degradation were entered as fixed effects. First, the significance of the interaction was tested by comparing the fit of this model to a reduced model with only the three main effects. Where the interaction term was significant, we split the dataset by wetland and tested for the effect of degradation in all three wetlands separately. Where the interaction term was not significant, we excluded it from the model and tested the significance of the main effect: degradation. Significance was tested using an F-test with Kenward-Roger correction for degrees of freedom, as implemented in the "pbKRtest" package of R. All variables, except pH and ratios, were log(x+1) transformed to fulfill assumptions of normality and homoscedasticity of linear mixed models.

Lastly a Detrended Correspondence Analysis (DCA) was performed on species abundance data, using the "vegan" package in R. Each season was analyzed separately (2014, 2015). Soil and vegetation parameters that differed significantly between degraded and pristine wetland fragments were correlated to the first and second axes, and overlain on the plot.

4.3 Results

The effect of degradation on abiotic parameters

Degraded wetland fragments had a significantly higher soil pH and significantly lower soil water content than their pristine counterparts (**Table 3**). Degraded wetland fragments also tended to have higher bulk densities and lower soil organic matter contents, though these differences were not significant for the Theewaterskloof wetland. In terms of nutrients, pristine wetland soils had higher nutrient (phosphorus and nitrogen) concentrations overall, as well as available nutrients (PO_4-P, NH_4-N) relative to degraded wetland soils. However pools of total and available nutrients varied inconsistently among sites and among wetlands with the exception of the NO_3-N pool, being significantly higher on degraded wetland fragments. Potassium concentration was significantly higher in pristine wetland soils. Cation exchange capacity was higher, and the base saturation lower in pristine wetland soils, though not significantly so for the Theewaterskloof wetland. Base cations, total soil Ca^{2+} and Mg^{2+} concentrations, therefore follow the same trend as cation exchange capacity, as do cations in general, having higher concentrations in pristine relative to degraded soils.

Table 3. The difference in soil parameters between degraded (n=18) and pristine (n=21) wetland fragments of three South African palmiet wetlands. The significance of the difference between degraded and pristine wetland fragments within each wetland is displayed: * p<0.05, ** p<0.01, *** p<0.001; F and p values are given in **Table A1**. CEC stands for cation exchange capacity. Parameters in bold are those where the effect was the same regardless of location (wetland effect not significant). Values given are mean ± standard deviation.

		Theewaterskloof			Goukou			Kromme		
		Pristine	Degraded		Pristine	Degraded		Pristine	Degraded	
Physical properties	**pH**	**4.5±0.35**	**4.5±0.31**	*	**4.7±0.47**	**5.2±0.2**	*	**5.4±0.18**	**5.6±0.22**	*
	Bulk Density (g/cm3)	0.3±0.12	0.5±0.27		0.3±0.09	1.1±0.24	***	0.4±0.24	1.2±0.16	***
	Soil Water Content (%)	**46.5±20.00**	**23.8±17.07**	***	**61.3±5.07**	**19.5±8.58**	***	**66.3±11.55**	**19.8±4.10**	***
	Soil Organic Matter (%)	23.5±12.53	15.2±10.88		31.1±6.27	3.5±1.19	***	16.4±5.39	2.0±1.51	***
Nutrient concentrations	**N/P Ratio**	**14.4±4.66**	**11.3±4.36**	***	**16.2±1.51**	**8.3±1.86**	***	**12.1±2.16**	**6.4±2.81**	***
	P_{tot} (mg/kg)	338.3±165.69	371.4±229.61		464.3±113.49	103.7±47.91	***	222.5±72.02	56.1±31.10	**
	PO_4-P (mg/kg)	5.0±2.98	7.6±6.01		4.7±2.60	1.6±0.73	**	2.4±1.15	0.8±0.80	**
	N_{tot} (mg/kg)	4848.8±2659.44	3885.9±2650.22		7512.2±1850.63	896.8±571.91	***	2759.7±1040.73	418.1±349.18	**
	NH4-N (mg/kg)	4.0±4.43	4.5±2.22		6.0±2.69	1.9±1.47	***	13.1±21.21	1.5±1.32	**
	NO_3-N (mg/kg)	0.6±0.54	6.8±8.77	*	0.8±0.76	1.6±1.76		0.5±0.61	0.2±0.35	
Nutrient pools	**P pool (mg/L)**	**100.3±46.52**	**160.4±112.55**		**132.9±52.88**	**108.3±44.05**		**70.1±25.64**	**62.4±29.52**	
	PO4-P Pool (mg/L)	**1.6±1.19**	**3.7±3.57**		**1.4±1.11**	**1.6±0.6**		**1±0.99**	**0.9±0.71**	
	N pool (mg/L)	1376.1±641.29	1578.8±711.62		2134.6±771.58	946.7±588.90	***	842.0±311.01	454.1±355.75	
	NH4-N Pool (mg/L)	**1.3±1.56**	**2±1.23**		**1.7±0.72**	**2.1±1.84**		**5.1±8.91**	**1.7±1.44**	
	NO3-N Pool (mg/L)	0.2±0.17	3.4±4.94	**	0.2±0.23	1.8±2.21	*	0.2±0.18	0.3±0.46	
Buffering capacity	CEC (meq/100g)	16.1±6.89	12.5±4.93		25.0±2.37	6.3±2.07	***	20.8±4.11	4.2±2.74	***
	Base Saturation (%)	**9.7±3.79**	**12.3±9.45**	**	**15.0±3.82**	**30.5±5.16**	**	**28.9±3.40**	**47.9±14.38**	**
	Na (mg/kg)	**50.4±28.32**	**22.0±14.25**	***	**124.4±33.09**	**42.1±15.32**	***	**169.0±37.83**	**110.5±129.94**	***
	Ca (mg/kg)	371.6±342.65	350.1±167.55		440.5±115.81	212.9±159.78	**	686.3±257.82	203.6±147.34	**
	Mg (mg/kg)	539.6±293.31	470.9±224.92		1656.1±656.04	852.1±232.56	*	1113.5±286.14	289.9±175.61	**
	K (mg/kg)	4232±2492.94	3881.6±1778.4		5195.3±1503.14	2616.4±610.9	**	2983.6±679.73	822.9±372.85	***

For all groundwater parameters, the interaction effects between the three wetlands were not significant; therefore only results for pristine and degraded wetlands are shown (**Table 4**). Relative groundwater depth fluctuated substantially between sampling sessions in pristine wetland fragments (average fluctuations of 0.85-2.08 m), and to a lesser degree in degraded fragments (0.33-0.96 m). However there was no detectable difference in relative groundwater depth between degraded and pristine sites (**Table 4**). The groundwater of degraded wetland fragments had a significantly higher pH and conductivity than pristine wetland fragments. There were no significant differences in nutrient levels (total or available) in the groundwater of degraded and pristine wetland fragments, except for biologically available nitrogen (NH_4-N) which was significantly higher at degraded sites. Cations (Na^+, Ca^{2+} and Mg^{2+}) were significantly higher in the groundwater of degraded wetland fragments relative to pristine ones.

Table 4. The difference in groundwater parameters between degraded and pristine wetland fragments of South African palmiet wetlands. Significance is displayed: * p<0.05, ** p<0.01, *** p<0.001, NS: not significant. Values given are mean ± standard deviation.

		Pristine	Degraded	Statistics
Physical	pH	5.7±0.39	6.1±0.37	F=7.30, ddf=1, ndf=16, p=0.016*
	Conductivity (uS/cm)	119.4±45.57	377.5±352.96	F=39.93, ddf=1, ndf=16, p=0.000***
	Rel. Groundwater Depth (m)	0.8±0.95	1.1±0.63	NS
Nutrients	Kjeldahl Nitrogen (mg/l)	2.7±3.07	4.2±4.58	NS
	NH_4-N (mg/l)	0.1±0.17	2.6±4.13	F=13.12, ddf=1, ndf=16, p=0.002**
	P_{tot} (mg/l)	0.2±0.23	0.1±0.09	NS
	PO_4-P (mg/l)	0.0±0.04	0.1±0.03	NS
Ions	Na (mg/l)	12.3±5.81	45.7±37.02	F=34.03, ddf=1, ndf=16, p=0.000***
	Ca (mg/l)	3.9±2.71	12.4±16.58	F=8.05, ddf=1, ndf=16, p=0.012*
	Mg (mg/l)	1.6±0.92	12.5±19.03	F=20.66, ddf=1, ndf=16, p=0.000***
	K (mg/l)	4.7±4.14	3.7±3.60	NS

Vegetation on degraded wetland fragments had a significantly higher phosphorus concentration and a lower N/P ratio in their tissues relative to vegetation on pristine fragments (**Table 5**). For the Theewaterskloof and Goukou wetlands, total nitrogen followed the same trend; however there was no difference for the Kromme (**Table 5**). The relative increase in total nitrogen and phosphorus was greatest in Theewaterskloof. Results of potassium concentrations in plant tissues were conflicting, in some cases higher for degraded wetland fragments (Goukou), in other cases higher for pristine (Kromme). Vegetation on degraded wetland fragments had a higher concentration of base cations (higher Mg^{2+}, significantly higher Ca^{2+}) in their tissues relative to pristine fragments.

Table 5. The difference in vegetation parameters between degraded and pristine wetland fragments of three South African palmiet wetlands. The significance of the difference between degraded and pristine wetland fragments is displayed: * p<0.05, ** p<0.01, *** p<0.001; F and p values are given in **Table A2**. Parameters in bold are those where the effect was the same regardless of location (wetland effect not significant). Values given are mean ± standard deviation.

	Theewaterskloof			Goukou			Kromme		
	Pristine	Degraded		Pristine	Degraded		Pristine	Degraded	
N/P ratio	**21.5±7.66**	**20.6±5.61**	**	**27.8±10.86**	**18.5±7.7**	**	**23.6±5.92**	**14.4±3.58**	**
Ptot (mg/kg)	**363.1±200.68**	**625.7±292.01**	***	**259.9±126.07**	**617.1±290.15**	**	**374.7±233.72**	**635.6±238.68**	**
Ntot (mg/kg)	**6789.3±2100.2**	**12186.9±5783.2**	***	**6250.0±1413.5**	**10217.0±2891.6**	**	**8025.4±4319.3**	**8498.7±2181.0**	**
K (mg/kg)	4211.3±2521.04	3094.6±2039.40		4106.8±2436.37	7063.2±3681.11	*	9022.4±4997.93	4844.1±1836.87	
Ca (mg/kg)	**2196.2±1486.6**	**4346.2±1963.3**	***	**2100.3±1099.0**	**4887.4±3063.35**	**	**2878.5±1246.9**	**3176.8±1808.8**	**
Mg (mg/kg)	1355.9±492.18	1797.8±708.87		1111.1±390.60	2324.4±825.81	***	1557.6±392.43	1960.5±500.03	

The effect of degradation on wetland community composition

Degradation results in a change in vegetation communities in South African palmiet wetlands; results of the SIMPER analysis revealed 82% dissimilarity between degraded and pristine fragments. Pristine palmiet wetland fragments were characterized by patches of two main shrub-dominated vegetation communities: *Prionium serratum* communities (mean: 81-86 % cover) and those dominated by a mix of other fynbos wetland species. Several species were able to co-exist with *P. serratum,* albeit at a lower density, and these differentially characterized pristine palmiet wetland patches at each of the three study wetlands. Key species were: *Psoralea aphylla*, *Restio paniculatus*, *Wachendorfia thyrsiflora* (Theewaterskloof), *R. paniculatus*, *Todea barbara* (Goukou) and *Cliffortia odorata* and *Helichrysum odoratissimum* (Kromme). Fynbos patches in pristine wetland fragments were typically more diverse and species more evenly distributed. Some key species characterizing these patches were: *Pteridium aquilinum* and *Isolepis prolifera* (Theewaterskloof), and *P. aquilinum*, *R. paniculatus, C. strobilifera*, and *Epischoenus gracilis* (Goukou).

Degraded palmiet wetland fragments on the other hand were highly dissimilar among the three study wetlands, and were typically characterized by pioneer and alien vegetation (lower percentage cover of shrubs, increased trees and grasses), except where small patches of *P. serratum* communities persisted (**Table 6**). Therefore degraded wetland fragments tended to be more species-rich than pristine fragments. In each of the three wetlands, the key species characterizing degraded fragments were: *P. aquilinum*, *I. prolifera*, *R. fruticosus*, *C. strobilifera*, *Carpha glomerata*, *Psoralea pinnata*, and *Laurembergia repens* (Theewaterskloof), *C. strobilifera*, *A. mearnsii* and *W. thyrsiflora* (Goukou), and *Pennisetum macrourum*, *C. strobilifera*, *H. odoratissimum*, *R. fruticosus*, *J. lomatophyllus*, and *I. prolifera* (Kromme). Microbial biomass was significantly higher in the pristine wetland soils of the Goukou and Kromme relative to degraded soils, though not significantly so for Theewaterskloof wetland.

Table 6. Community composition for degraded and pristine wetland fragments from three South African palmiet wetlands. Totals are given in brackets for: number of species and number of alien species. Microbial biomass carbon is an index for microbial abundance. The significance of the difference between degraded and pristine wetlands is displayed: * $p<0.05$, ** $p<0.01$, *** $p<0.001$; F and p values are given in **Table A3.** Parameters in bold are those where the effect was the same regardless of location (wetland effect not significant). Values given are mean ± standard deviation.

	Theewaterskloof			Goukou			Kromme		
	Pristine	Degraded		Pristine	Degraded		Pristine	Degraded	
# species recorded	**6.8±1.75 (23)**	**6.3±2.18 (20)**		**7.2±3.06 (26)**	**7.7±4.19 (28)**		**6.1±4.29 (23)**	**12.3±5.37 (42)**	
# alien species	**0**	**0.4±0.67 (2)**	**	**0**	**0.9±1.51 (4)**	**	**0.2±0.39 (1)**	**1.3±1.15 (5)**	**
% cover by dominant	72.1±21.05	56.7±18.26		68.1±19.34	75.0±17.19		87.9±23.01	45.8±28.53	*
Microbial carbon	0.4±0.27	0.2±0.16		1.0±0.45	0.1±0.03	***	0.4±0.29	0.0±0.03	**

Relationship between vegetation composition and abiotic parameters

The results of the DCA, based on vegetation community structure from September 2014, show some degree of separation between degraded and pristine wetland sites and to some extent a grouping of sites from the same wetlands (**Fig. 2**). The results from 2015 showed similar trends and are displayed in **Fig. A1**. Degraded wetland sites tend to occupy the upper right quadrant, and pristine sites the lower left quadrant. However three of the degraded Goukou wetland plots were more similar in community structure to pristine wetlands (plots were sampled in surviving patches of *P. serratum*), though their soil and groundwater characteristics were closer to those of degraded plots. In general, the first axis may represent a gradient from annuals (graminoids) and small herbaceous plants (*P. decipens*, *L. repens* etc) on the right to longer-lived, woody perennials on the left (*T. barbara*, *P. serratum* etc). This axis seems to be explained (though not significantly) by soil pH, calcium and NH_4-N. The second axis seems to capture some element of alien/weedy plant invasion, with weedy species (*T. capensis, R. fructicosus*) and alien trees (*A. mearnsii*) at the top of the plot, corresponding with degraded plots. Soil magnesium concentration ($r^2 = 0.4535$, $p = 0.001$), water content ($r^2 = 0.3426$, $p = 0.001$), and total vegetation phosphorus ($r^2 = 0.4660$, $p = 0.001$) correlated weakly with the second axis. Vegetation N/P ratio was strongly positively correlated with many soil parameters: soil water content, potassium, magnesium, calcium and sodium concentration, cation exchange capacity, and soil organic matter. Vegetation tissue calcium and total phosphorus concentrations were positively correlated with soil bulk density, base saturation and nitrate pool.

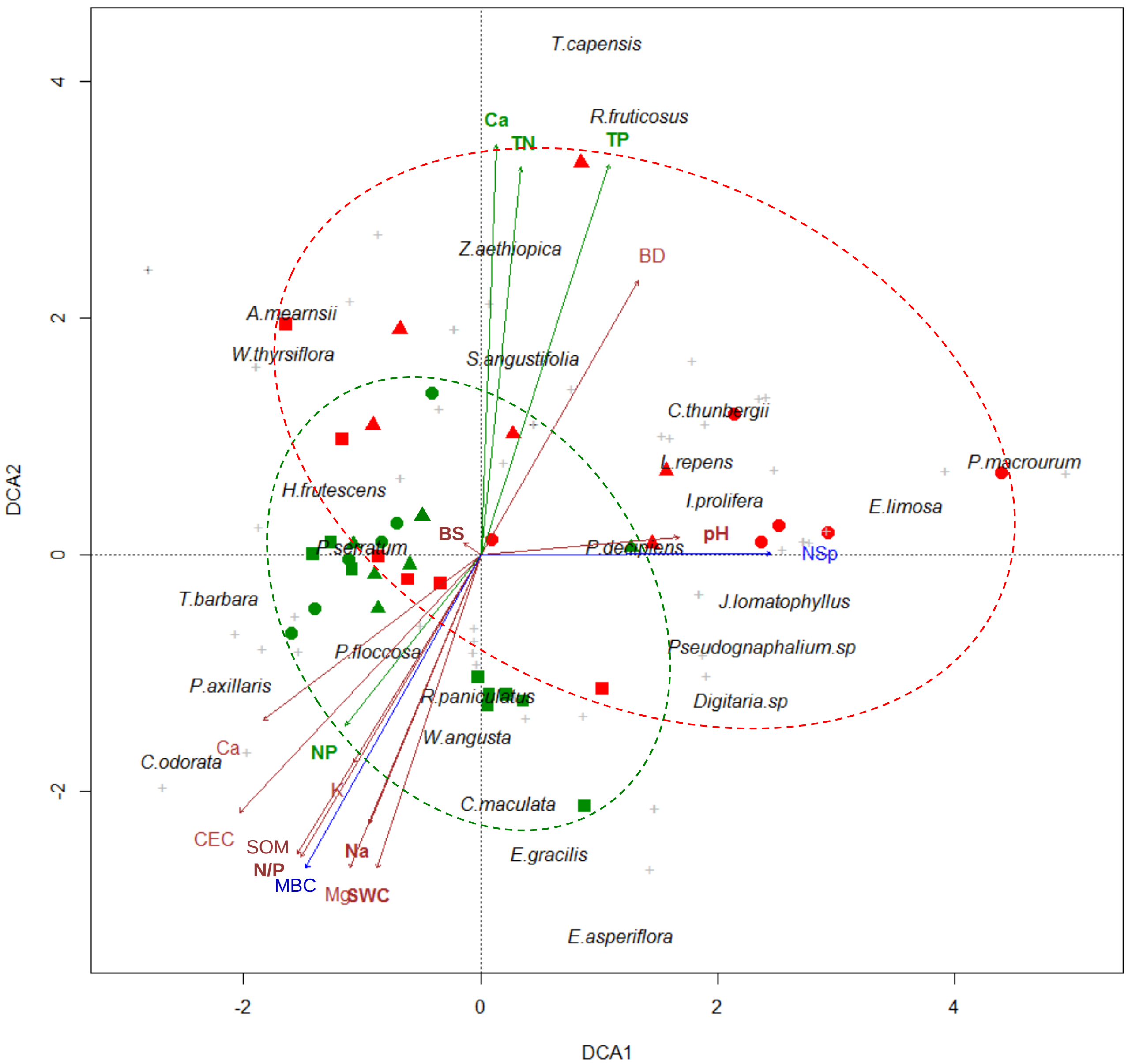

Figure 2. Detrended Correspondence Analysis (DCA) of the vegetation communities on pristine and degraded wetland fragments of three South African palmiet wetlands sampled in September 2014. Degraded sites are in red, pristine in green. Symbols: ▲ Theewaterskloof, ■ Goukou, ● Kromme. Species names are given in black, and + indicates species with a lower abundance that would have masked by other labels. Abiotic parameters that were interesting or significantly different (bold) between pristine and degraded wetland fragments were overlain and are indicated by the arrows. Soil parameters are in brown, vegetation chemical composition in green. Abbreviations: NSp: number of species, MBC: microbial biomass carbon, BS: base saturation, BD: bulk density. Stippled circles encompass sites from pristine and degraded wetland fragments. For full species names see supplementary material.

4.4 Discussion

All three selected fragments of degraded palmiet wetlands were degraded by some degree of channel erosion, and all had some level of invasion of alien plants and trees.

However only the Goukou and Kromme wetlands were situated in an agricultural context, and therefore were potentially impacted by agricultural effluent. These differences are important to consider, given that results are suggestive that these different types of degradation have had differing impacts on wetland biochemistry.

Possible influence of channel erosion on wetland biochemistry and community composition

Some key soil, groundwater and vegetation parameters differed between degraded and pristine palmiet wetland fragments, regardless of the specific wetland. Therefore the site (wetland) effect was not significant, despite these wetlands being located far from each other (as much as 470 km apart). Since the main type of degradation that these three wetlands had in common was channel erosion, with concomitant or resultant invasion by alien vegetation; it can be inferred that these universal differences between degraded and pristine wetland patches are mainly attributable to channel erosion. Channel erosion impacts palmiet wetlands through the physical loss of soil, or alluvium during high flow/flood events (de Haan, 2016; Rebelo et al., 2015, **Chapter 3**). Under extreme channel erosion, the entire valley floor is removed, leaving only coarse sand behind (e.g. sections of the Kromme wetland) (**Chapter 3**). In earlier stages of degradation by channel erosion, either patches of palmiet wetland vegetation may persist within the degraded fragment, retaining the alluvium within that patch (e.g. the degraded Goukou wetland), or the channel has only cut down through the alluvium in one area, leaving the wetland vegetation in the majority of the wetland fragment more-or-less intact (e.g. the degraded Theewaterskloof wetland). However despite this gradient in degradation, degradation resulting from channel erosion had some clear impacts on palmiet wetland biochemistry.

Firstly, channel erosion appears to have caused a decrease in soil water content, which may be a result of loss of soil organic matter (soil water content and organic matter are well correlated; **Table A4**) and/or wetland drainage. However water table draw-down was not found to be significant in this study due to considerable seasonal fluctuations. The bulk density of the soil also increased and soil organic matter decreased with degradation, though not significantly for the Theewaterskloof wetland, which is likely due to the earlier stage of degradation relative to the other two wetlands. For example, plots furthest from the channel in the degraded fragment of the Theewaterskloof wetland are impacted by lower soil water content, but the alluvium is not yet lost over the entire valley floor and therefore bulk density and organic matter content has not yet significantly changed. A decline in soil organic matter or carbon with degradation has been found in many wetland studies (Huo et al., 2013; Salimin et al., 2010). Cation exchange capacity and total soil nitrogen (concentration and pools) may also have decreased as a result of the loss of soil organic matter (**Table A4**). Overall degradation increased soil pH, though, again, these differences in the Theewaterskloof wetland were slight. Conversely, in studies of other wetland systems: restoration was found to increase soil pH of northern temperate fens (Aggenbach et al., 2013; Emsens et al.,

2015) and wetland conversion to cropland or plantations in Ethiopia decreased soil pH (Sankura et al., 2014).

Probably as a result of the increased leaching of the topsoil, the groundwater of degraded wetlands had more base cations (Ca^{2+}, Mg^{2+}, Na^{+}), higher ammonium, higher electrical conductivity and also a higher pH. However the same trend is not seen for potassium, possibly because it is limiting. The legacy effects of this degradation can also be seen in the vegetation community, with vegetation on degraded fragments having almost double the total phosphorus and total nitrogen than that of pristine fragments as well as a lower N/P ratio. The reason that this may be most pronounced at the Goukou and especially the Theewaterskloof wetland may be a result of the early stage of channel erosion compared to the Kromme wetland where the alluvium has already been washed away at the degraded site. It is possible that in this earlier stage of wetland erosion, decomposition makes nutrients, especially nitrates, available for plant uptake before they are leached into the groundwater or washed away.

Higher soil pH has been shown to result in an increase of phosphorus uptake in vegetation in acid soils (Beukes et al., 2012), in this case driving a vegetation community that is less phosphorus limited. This is evidenced by decreasing vegetation N/P ratio and visibly by the higher incidence of alien weeds and competitive tree species such as *Acacia mearnsii* and *Acacia saligna* on degraded fragments (Zedler and Kercher, 2004). Alien species exploiting an increase in nutrient availability have been observed in other aquatic ecosystems (Li et al., 2011; Siemann and Rogers, 2007). It is probable that productivity (though not standing biomass) is higher on degraded sites due to the higher incidence of annuals, though we did not measure this. The results of the DCA are conflicting: the fact that no variable significantly correlated with the first axis suggests that either the main driver of vegetation community structure is not measured, or that the story is too complex to be untangled by correspondence analysis. One reason for this is that vegetation communities and wetland biochemistry may be out of sync, such that vegetation structure may in some cases still reflect more ‘pristine’ conditions, whereas the soil and groundwater reflects its degraded state.

Possible influence of agricultural effluent on wetland biochemistry and community composition

Although the impacts of degradation by channel erosion on palmiet wetland soil, groundwater and vegetation seem clear, some factors differed between wetlands, suggesting other explanations account for the patterns emerging. Several soil parameters differed significantly between degraded and pristine wetland fragments, but only for the Goukou and Kromme wetlands, and not for the Theewaterskloof wetland. We hypothesize that these differences are linked to the impacts of agricultural runoff. We did not measure this, however it is known that fertilizers and lime (usually dolomitic lime) are commonly applied to agricultural fields in the Cape Floristic Region of South Africa, particularly irrigated fields, to increase the pH and nutrient availability of extremely acidic and oligotrophic soils (Beukes et al., 2012). Both the Goukou and

Kromme catchments have intensive irrigated agriculture adjacent to degraded palmiet wetlands.

Degradation as a result of pollution by agricultural runoff is one plausible explanation for the increased pH on degraded fragments of the Goukou and Kromme wetlands, as increased pH cannot be explained by the mechanisms around channel erosion alone. A characteristic of degradation by pollution of agricultural effluent may be the observed increased base saturation. We hypothesize that this is a result of base cations and hydrogen carbonates from the dolomitic lime leaching into the wetland soils from adjacent irrigated fields, resulting in the increase of base cations (Ca^{2+}, Mg^{2+}, Na^{+}) that are evident in degraded palmiet wetland topsoils. We did not measure soils deeper than 10 cm and therefore it is possible that nutrient availability may differ in deeper soil layers. Although carbonates were not measured, we hypothesize that the carbonates from the dolomitic lime applied to agricultural fields also entered the wetland soils, possibly being the mechanism behind the observed increase in pH. It should be noted that these shifts in vegetation communities are less dramatic than those that occur with the loss of the entire alluvium as a result of channel erosion. It is unclear from this study what impact agricultural practices adjacent to palmiet wetlands are having on wetland biochemistry, and this should be investigated further.

4.5 Conclusion

There appear to be two major, compound types of degradation in palmiet wetlands. Channel erosion, often accompanied by invasion of alien species, causes a loss of alluvium and in extreme cases, vegetation and alluvium are washed away. Remaining soil has higher rates of decomposition, which results in lower organic matter. A reduction in organic matter causes a decrease in soil water content and cation exchange capacity, resulting in soil which is highly leached and unable to retain nutrients and cations. As a result, groundwater had higher conductivity and pH. These biochemical changes drive a completely new plant community, composed mostly of pioneer species, with patches of the original *Prionium serratum* wetland vegetation persisting – depending on the severity of degradation. The second type of degradation discussed here, pollution by agricultural effluent, may increase base saturation, possibly as a result of liming practices in agriculture. Loss of soil organic matter implies a release of CO_2 into the atmosphere, loss of alluvium a decrease in flood attenuation and a reduction in cation exchange capacity and bulk density a reduction in the water purification capacity of palmiet wetlands. This implies a marked reduction in ecosystem service provision with palmiet wetland degradation. Once the pristine wetland soils and vegetation communities are lost, it would take tremendous effort and long timescales to restore these palmiet wetlands. This makes a case for the protection and conservation of remaining pristine patches of this unique South African valley-bottom wetland system.

4.6 Acknowledgements

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4.8 Appendix

Table A1: Statistical results of the linear mixed models for soil parameters.

		Theewaterskloof	Goukou	Kromme
Physical properties	**pH**		**F=6.36, ndf=1, ddf=35, p=0.016**	
	Bulk Density (g/cm3)	NS	F=122.48, ndf=1, ddf=13, p=0.000	F=40.57, ndf=1, ddf=10, p=0.000
	Soil Water Content (%)		**F=75.45, ndf=1, ddf=35, p=0.000**	
	Soil Organic Matter (%)	NS	F=224.52, ndf=1, ddf=13, p=0.000	F=46.09, ndf=1, ddf=10, p=0.000
Nutrients	**N/P Ratio**		**F=43.63, ndf=1, ddf=35, p=0.000**	
	P_{tot} (mg/kg)	NS	F=72.14, ndf=1, ddf=13, p=0.000	F=23.09, ndf=1, ddf=10, p=0.001
	PO_4-P (mg/kg)	NS	F=16.75, ndf=1, ddf=13, p=0.001	F=17.22, ndf=1, ddf=10, p=0.002
	N_{tot} (mg/kg)	NS	F=114.58, ndf=1, ddf=13, p=0.000	F=20.08, ndf=1, ddf=10, p=0.001
	NH4-N (mg/kg)	NS	F=49.63, ndf=1, ddf=13, p=0.000	F=13.4, ndf=1, ddf=10, p=0.004
	NO_3-N (mg/kg)	F=9.71, ndf=1, ddf=10, p=0.011	NS	NS
Nutrient pools	**P pool (mg/L)**		**NS**	
	PO4 Pool (mg/L)		**NS**	
	N pool (mg/L)	NS	F=25.88, ndf=1, ddf=13, p=0.000	NS
	NH4 Pool (mg/L)		**NS**	
	NO3 Pool (mg/L)	F=11.02, ndf=1, ddf=10, p=0.008	F=8.43, ndf=1, ddf=13, p=0.012	NS
Buffering capacity	CEC (meq/100g)	NS	F=151.15, ndf=1, ddf=13, p=0.000	F=41.46, ndf=1, ddf=10, p=0.000
	Base Saturation (%)		**F=11.74, ndf=1, ddf=35, p=0.002**	
	Na (mg/kg)		**F=24.61, ndf=1, ddf=35, p=0.000**	
	Ca (mg/kg)	NS	F=17.06, ndf=1, ddf=13, p=0.001	F=11.57, ndf=1, ddf=10, p=0.007
	Mg (mg/kg)	NS	F=6.52, ndf=1, ddf=13, p=0.024	F=21.32, ndf=1, ddf=10, p=0.001
	K (mg/kg)	NS	F=18.13, ndf=1, ddf=13, p=0.001	F=35.35, ndf=1, ddf=10, p=0.000

Table A2: Statistical results of the linear mixed models for vegetation parameters.

	Theewaterskloof	Goukou	Kromme
N/P ratio		**F=8.92, ndf=1, ddf=35, p=0.005**	
Ptot (mg/kg)		**F=38.80, ndf=1, ddf=35, p=0.000**	
Ntot (mg/kg)		**F=24.44, ndf=1, ddf=35, p=0.000**	
K (mg/kg)	NS	F=7.80, ndf=1, ddf=13, p=0.015	NS
Ca (mg/kg)		**F=17.62, ndf=1, ddf=35, p=0.000**	
Mg (mg/kg)	NS	F=26.01, ndf=1, ddf=13,	NS

Table A3: Statistical results of the linear mixed models for community composition parameters.

	Theewaterskloof	Goukou	Kromme
# species recorded		NS	
# alien species		**F=14.50, ndf=1, ddf=35, p=0.001**	
% cover by	NS	NS	F=8.31, ndf=1, ddf=10, p=0.016
Microbial carbon	NS	F=51.32, ndf=1, ddf=13, p=0.000	F=10.49, ndf=1, ddf=10, p=0.009

Table A4: Spearman correlations used to explain trends found in results

Parameter 1	Parameter 2	Spearman's Rho	Significance
Soil organic matter	Soil water content	0.66	p<0.001
Soil organic matter	Cation exchange capacity	0.84	p<0.001
Soil organic matter	Total N pools	0.97	p<0.001
Soil organic matter	Total N concentration	0.75	p<0.001

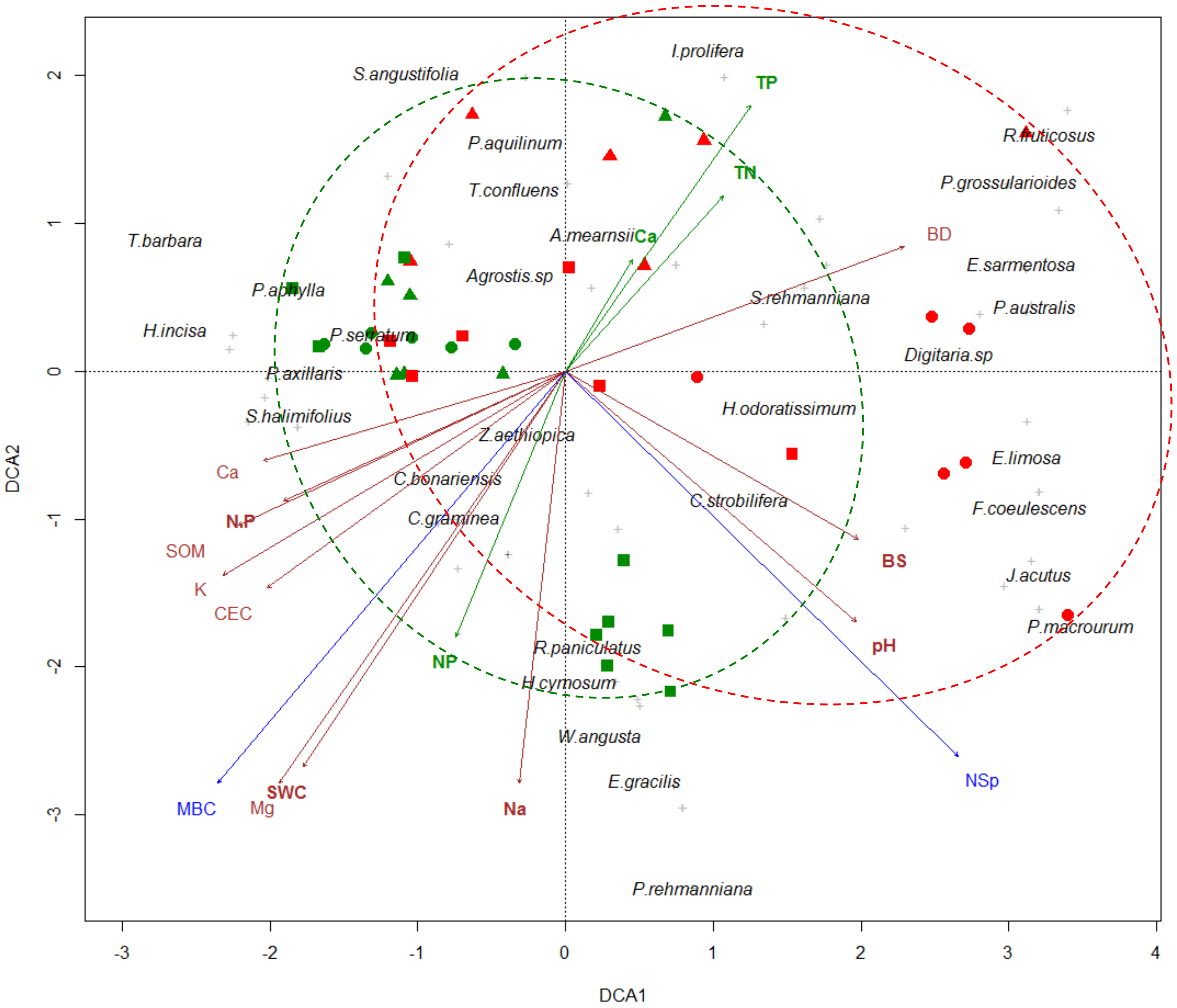

Figure A1. Detrended Correspondence Analysis (DCA) of the vegetation communities on pristine and degraded wetland fragments of three palmiet wetlands, South Africa sampled in March 2015. Degraded sites are indicated in red, pristine in green. Symbols: ▲ Theewaterskloof, ■ Goukou, ● Kromme. Species names are given in black, and + indicates species with a lower abundance that would have been masked by other labels. Abiotic parameters that were interesting or significantly different (bold) between pristine and degraded wetland fragments were overlain and are indicated by the arrows. Soil parameters are in brown, vegetation composition in green. Stippled circles encompass sites from pristine and degraded wetland fragments. For full species names see **Supplementary Material**.

5

Vegetation patterns in wetlands dominated by the ecosystem engineer Palmiet (*Prionium serratum*)

Rebelo, A.J., Sieben, E., Meire, P., and Esler, K.J.

Palmiet wetlands filling the bottom of the valley of the Kromme catchment, Eastern Cape, South Africa. The light green colour in the valley-bottom is agriculture (also on the alluvial fans) but within the wetland itself there are patches of different colours, representing different vegetation communities.

Abstract

Wetlands are ecosystems subjected to high stress, disturbance and competition. It is thought that pH and mechanical disturbance, in addition to light, nutrients, water and space, may drive plant community assembly in wetlands. South African palmiet wetlands are patchy in appearance, supporting plant communities that are dominated by the super-competitor Palmiet, and other, more functionally diverse communities. It is not well understood what drives this patchiness. We ask which environmental parameters drive dominance of Palmiet, and which plant functional traits account for its super-dominance. We also seek to understand whether this is the result of alternate stable states, or succession. In 21 plots from three palmiet wetlands situated approximately 200 km apart, key soil, groundwater and vegetation parameters, as well as vegetation community composition were measured. Twenty-two dominant species were selected and 13 plant functional traits were measured on 10 individuals from each species. We calculated the community weighted means for each trait as well as functional diversity indices for each plot. Soil pH and relative groundwater depth were found to be the main environmental parameters related to plant community assembly in palmiet wetlands. However long-term monitoring is needed to better understand the relationship between relative groundwater depth and plant community assembly in palmiet wetlands. Palmiet communities were characterized by higher community weighted means for stem diameter, leaf length-width ratio, leaf area as well as cellulose and lignin concentration. These suggest adaptations to fire (thicker stems) and floods (long, thin leaves and flexible shoots). We speculate that palmiet communities are the climax community of palmiet wetlands, and that the fynbos communities are made up of pioneers.

5.1 Introduction

Wetlands are ecosystems subjected to high stress (e.g. water inundation), high disturbance (i.e. floods or fires) as well as high levels of competition (Moor et al., 2017; Sieben et al., 2017). Competition can be defined as neighboring plants having similar ability to use light, nutrients, water and space (Grime, 1973). As a result of these three factors, wetlands differ from terrestrial ecosystems by their different conditions (e.g. anoxia), processes (e.g. peat accumulation, denitrification) and therefore plant adaptations (e.g. aerenchyma, clonality, tussock formation) (Moor et al., 2017). Wetlands have been said to represent complex stress gradients beyond the scope of commonly studied gradients (e.g. water availability, light, nutrients, salinity, disturbance such as grazing or fire etc) (Moor et al., 2017; Reich, 2014; Sieben et al., 2017). There are also thought to be key drivers which are important to wetland communities, but which are not included in the typical plant economic spectrum (Díaz et al., 2015), such as pH and mechanical disturbance (e.g. flood damage) (Reich, 2014). Wetlands are thought to be situated at the extremes of stress gradients (Reich, 2014), which makes wetland community ecology ideal to study from a trait perspective.

The extreme water-stress characteristic of wetland ecosystems, has led to the evolution of specific plant functional traits in wetland species (Moor et al., 2017; Sieben et al., 2017). Moor et al. (2017) summarizes trait responses to soil saturation, water table fluctuations and flooding in wetlands. Soil saturation, resulting in either temporary or permanent anoxia in the root zone, is the first major challenge to wetland plants and produces key adaptations which distinguish obligate and facultative wetland species. Under temporary anoxic conditions, certain plants are able to use anaerobic respiration in the root zone (Sieben et al., 2017). However obligate wetland species have developed tissue (aerenchyma) to carry oxygen to the root zone (Sieben et al., 2017). Additionally higher wetness favours higher leaf dry matter content, lower specific leaf area and leaf nitrogen content, resulting in a more conservative habit (Moor et al., 2017).

Water table fluctuations and flooding in wetlands is the second major challenge to wetland plants and has two main consequences: submergence as well as mechanical disturbance (Moor et al., 2017). It has been proposed that there are two major strategies to overcome submergence: tolerance or escape (Colmer and Voesenek, 2009). Tolerance involves the cessation of growth during short-term submergence, whereas escape means an increase of growth after a re-orientation of growth direction, as well as the preservation or development of additional aerenchyma (Colmer and Voesenek, 2009; Moor et al., 2017; Sieben et al., 2017). Adaptation to mechanical disturbance on the other hand, involves high root biomass allocation, extensive rhizomes, high stem flexibility and narrow leaves (Catford and Jansson, 2014; Colmer and Voesenek, 2009). Specific leaf area is a useful plant functional traits to measure for wetland communities, as its inverse (leaf mass area) was found to be correlated with three components of leaf mechanical resistance: work to shear, force to punch and force-to- tear (Onoda et al., 2011). Sclerophylly is also common in wetland vegetation which may represent an adaptation to mechanical stress as well as being a syndrome of nutrient conservation (Moor et al., 2017).

Despite the challenges faced by wetlands, they are still highly productive environments, so species that are able to adapt have a great deal to gain (Sieben, 2012). This results in strong competition amongst obligate wetland plants despite the challenge of seed germination in submerged soil being a barrier to dispersal (Sieben and le Roux, 2017). Obligate wetland plants tend to be clonal species, dispersing by their rhizomes, that are very effective competitors for habitat space. This is the case for South African valley-bottom palmiet wetlands which are dominated by a single mono-dominant species, *Prionium serratum* (Palmiet), which is a unique competitor and has even been suggested to be an ecosystem engineer (Sieben, 2012; Sieben et al., 2017). This species was found to be the most functionally divergent of all palmiet wetland species in a study of the Goukou wetland (Sieben, 2012).

South African valley-bottom palmiet wetlands are peatlands which are relatively rare and understudied (Job, 2014; Rebelo, 2012). Palmiet wetlands are subject to extreme water stress: soil saturation, water table fluctuations, floods as well as droughts and fires. Although palmiet wetlands are dominated by Palmiet, there are patches of other communities in these wetlands. It is not well understood what drives these different communities, and whether this is a case of succession, or alternate stable states (Suding et al., 2004). We aim to compare homogeneous, species-poor communities of Palmiet with more functionally diverse communities (including Palmiet) in palmiet wetlands. We ask which environmental parameters drive dominance of Palmiet, and which plant functional traits account for its super-dominance? Finally we investigate whether this is the result of alternate stable states (one species rich, the other poor) or whether these are different successional stages.

5.2 Methods

Study region & wetlands

The Cape Floristic Region has a mediterranean-type climate characterised by summer droughts and winter rainfall resulting from the passage of cold fronts (Midgley et al., 2003). The soils of the Cape Floristic Region are mainly highly leached dystrophic lithosols associated with the sandstone mountains of the Cape Supergroup (Midgley et al., 2003). Three palmiet wetlands were selected as study sites within the Cape Floristic Region: the Theewaterskloof and Goukou wetlands (Western Cape) and the Kromme wetland (Eastern Cape) (**Table 1**). Despite being situated as much as 470 km apart, these wetlands are remarkably similar in vegetation composition. They tend to occur at altitudes of around 400 m; mean annual precipitation is highly variable, highest in the Theewaterskloof catchment and lowest in the Goukou catchment. Mean annual runoff is also highest in the Theewaterskloof catchment but lowest in the Kromme catchment. In the case of the Kromme and Goukou, most of this runoff occurs over a short period of time, during flood events (Job, 2014; Rebelo et al., 2015). All three wetlands have accumulated peat layers that are between 0.5 and 10 m deep (**Table 1**).

Table 1. Site information for the three study wetlands. MAP: mean annual precipitation, MAR: mean annual runoff (Job, 2014; Kotze, 2015; Middleton and Bailey, 2008; Nsor, 2007; Sieben, 2012).

Catchment	Theewaterskloof	Goukou	Kromme
Co-ordinates	33°57'40.32"S, 19°10'10.00"E	34° 0'30.46"S, 21°24'59.97"E	33°52'24.69"S, 24° 2'24.13"E
Altitude (m)	362.4	180.7	353.6
MAP (mm)	1241	645	745
Winter 2014 (mm)	644	316	197
Summer 2015 (mm)	107	351	148
MAR (mcm)	149.8	52.3	25.4
Rainfall Region/Pattern	Winter	winter	bimodal
Peat Depth (m)	0.5-2	3-10	0.5-2.8

Study design

Each wetland was sampled twice: once in September 2014, which was just after winter, and once in March/April 2015, which was just after the summer. The purpose of this design was to capture seasonal variation in wetland properties and processes. Rainfall for the six months preceding the first fieldtrip was average for all sites (approximating 50% of the MAP); however rainfall for the six months preceding the second fieldtrip was far lower for Theewaterskloof and the Kromme (**Table 1**). Therefore for Theewaterskloof and the Kromme, the second campaign represents a drier season, whereas there is no such difference for the Goukou wetland. At each wetland undisturbed (pristine) stretches were sampled, yielding a total of three sites. It should be noted that all wetlands are transformed to some degree, with channelization occurring upstream or downstream of pristine fragments. At each of the three sites, cross-sectional transects (100-200 m) were made across the wetland, with six plots (3x3 m) placed between 20-50 m apart, yielding a total of 18 plots (**Fig. 1**). Transects and plots were chosen in the field to ensure adequate representation of the two plant communities, which we term: palmiet and fynbos. To this end we included one extra site in the Goukou wetland, with only three plots, yielding a final sum of 21 plots. Piezometers (3 m, PVC) were placed adjacent to every second plot, yielding a total of 12 piezometers (**Fig. 1**).

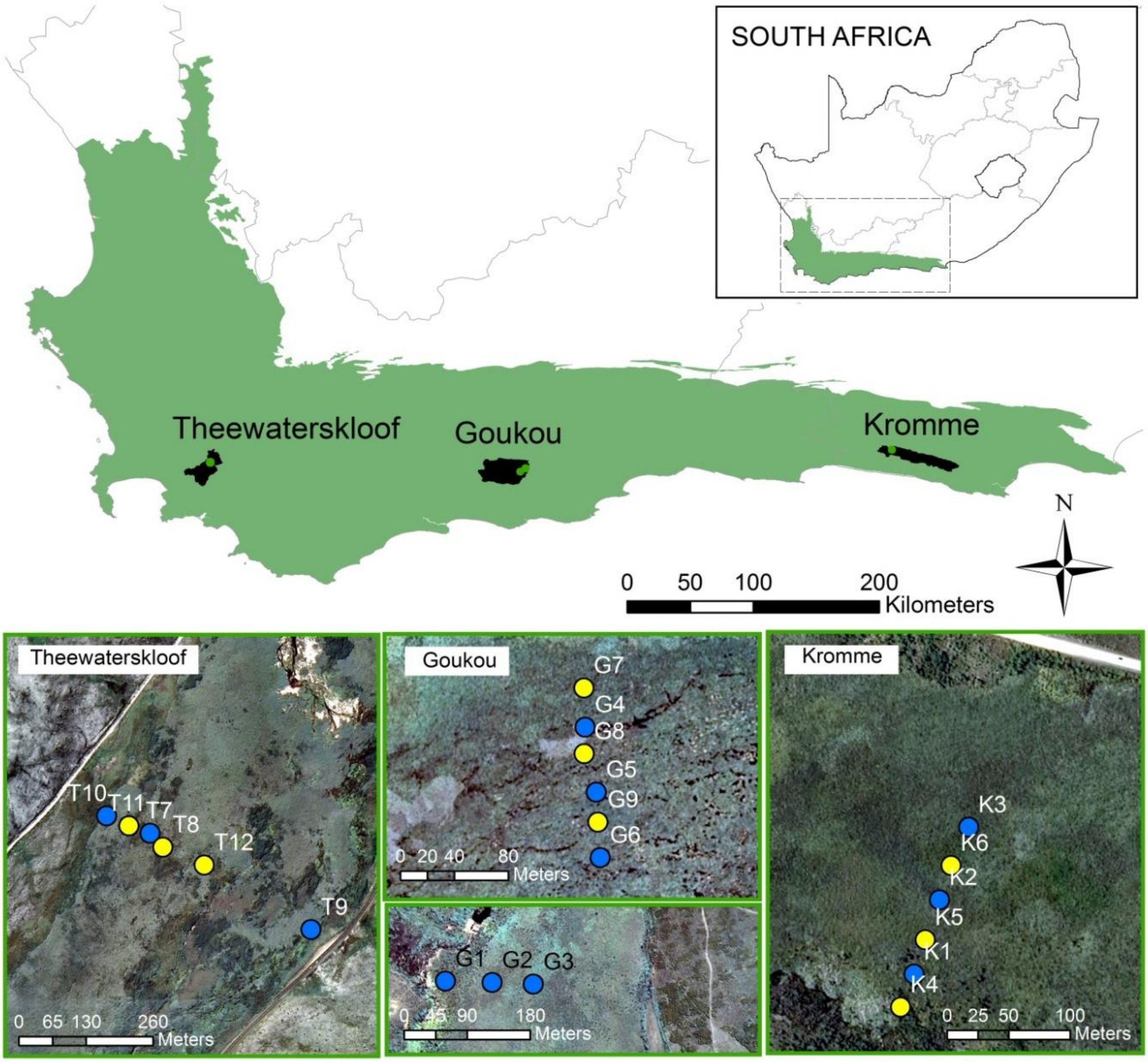

Figure 1. The location of the 21 study plots and three study wetlands within the Cape Floristic Region (green) of South Africa. Blue shaded circles indicate the location of piezometers within the wetlands.

Sampling

a) Plant community composition and vegetation analysis

In each plot, all plants were identified to species level where possible and percentage cover was estimated for each species using the Braun-Blanquet Scale (Mueller-Dombois and Ellenberg, 1974). Vegetation was sampled from three small, randomly selected subplots of 0.28x0.28 m within each plot. This above-ground biomass was dried for 48 hours at 70°C, weighed and then ground and homogenised using a mill. Plant total nitrogen and total phosphorus were determined using acid digestion and were measured with a continuous -flow analyzer (CFA) (SKALAR: SAN++) (Walinga et al., 1989). Potassium, calcium, and magnesium were analyzed by Inductively Coupled Plasma-emission spectrometry (ICP-OES) (Walinga et al., 1989) after acid digestion of ±0.3 g of dried and finely ground vegetation with H_2SO_4–Se-salicylic acid. Thirteen plant functional traits were collected for the 22 dominant wetland species. All methods were based on the standardised protocol of Pérez-Harguindeguy et al. (2013), see **Table A1** for details.

b) Soil sampling and chemical analyses

In each plot one composite soil sample was taken from 10 points throughout the plot at a depth of 1-10 cm using a hand held auger of 1 cm in diameter. Soil pH-H_2O was measured after adding distilled water to a 10 g soil sample and shaking it for an hour. Additionally in each plot one undisturbed soil sample was taken of the topsoil using a 100 cm^3 metal Kopecky ring to measure bulk density. Samples were weighed after oven drying for 48 hours at 70°C and values are expressed as g/cm^3.Soil water content was calculated gravimetrically by weighing ±20 g of fresh soil before and after drying for 24 hours at 105°C. Soil organic matter content was determined by loss on ignition (4h at 550°C). Total phosphorus and nitrogen were analyzed on a CFA. Soft extractions were done on fresh soil to determine NO_3^-, NH_4^+ and PO_4^{3-}. Samples were extracted and preserved for later analysis on a CFA using AA-EDTA (ammonium acetate – ethylenediaminetetraacetic acid) for PO_4^{3-} and AA-KCl (ammonium acetate - potassium chloride) for NO_3^- and NH_4^+ respectively (Houba et al., 1989). Nutrient pools were calculated by multiplying nutrient concentrations by bulk density measurements.

Cation exchange capacity was determined using the method of Brown (1943) by weighing ±8 g of soil before and after air drying in an incubator at 40°C for 48 hours. Samples were then sieved through a 2 mm sieve, 25 ml ammonium acetate solution (1M) was added to 2.5 g of soil and samples were shaken for one hour. Soil pH was measured and samples were filtered through a 0.45 µm filter before being analyzed for H, Ca, K, Mg, Na, Al, Fe, Mn ions on an ICP-OES. Potassium, calcium, and magnesium were analyzed on the ICP-OES after acid digestion of ±0.3 g of dried and finely ground soil with H_2SO_4–Se-salicylic acid (Walinga et al., 1989). Soil microbial biomass carbon was measured as a proxy for microbial activity in the soil at each site. We used the chloroform fumigation direct extraction protocol for microbial biomass carbon (Beck et al., 1997; Martens, 1995).

c) Groundwater sampling and chemical analyses

Depth to the water table was measured in each piezometer using a sounding device, and the standing water was emptied using a bailer. Once fresh water had refilled the piezometer, a sample was taken for a pH, and conductivity reading. Six water samples were taken and filtered (0.45 µm) to test for water quality parameters. The concentration of phosphate (PO_4^{3-}-P), ammonium (NH_4^+-N), total phosphorus (P-tot), and total Kjeldahl nitrogen were measured on a CFA. Concentrations of sodium, magnesium and calcium were measured on the ICP-OES.

Data analysis

We performed an analysis of similarity (ANOSIM) to determine whether palmiet and fynbos vegetation were in fact distinct, using the Bray–Curtis dissimilarity index. Next we performed a similarity percentage analysis (SIMPER) to determine which species characterised palmiet and fynbos communities. We used the 'Vegan' package for community ecology in R for these two analyses (Warton et al., 2012) as well as to calculate functional diversity indices & community weighted means.

To test the relationship between plant community, wetland (Theewaterskloof, Goukou, Kromme) and soil, groundwater, vegetation tissue chemistry and functional diversity parameters, we fitted linear mixed models taking season into account (winter 2014, summer 2015). Plots were entered as a random effect to account for the dependence between observations from within the same plot. Wetland, plant community, season and the interaction between wetland and plant community were entered as fixed effects. First, the significance of the interaction was tested by comparing the fit of this model to a reduced model with only the three main effects. Where the interaction term was significant, we split the dataset by wetland and tested for the effect of plant community in all three wetlands separately. Where the interaction term was not significant, we excluded it from the model and tested the significance of the main effect: plant community. Significance was tested using an F-test with Kenward-Roger correction for degrees of freedom, as implemented in the "pbKRtest" package of R. All variables, besides pH and ratios, were log(x+1) transformed prior to analysis to satisfy the assumptions of normality and homoscedasticity of the linear mixed models.

Lastly a Detrended Correspondence Analysis (DCA) was performed on species abundance data, using the "vegan" package in R. Each season was analyzed separately (2014, 2015). Soil and vegetation parameters that differed significantly between palmiet and fynbos communities were correlated to the first and second axes, and overlain on the plot.

5.3 Results

Abiotic parameters driving palmiet and fynbos communities

The only measured soil property that differed between fynbos and palmiet communities was pH, where it was marginally higher in fynbos communities (**Table 3**). Nutrients, nutrient pools and soil buffering capacities showed no significant differences nor interesting trends. Relative groundwater depth was significantly different between the two communities, tending to be closer to the surface but more variable for fynbos communities, and deeper below the ground for palmiet communities (**Table 4**). There was significantly higher Kjeldahl nitrogen in the groundwater of palmiet compared to fynbos communities in the Goukou wetland, however these trends were not observed for other wetlands.

Table 3. The difference in soil parameters between fynbos and palmiet communities of three South African palmiet wetlands. The significance of the difference between fynbos and palmiet communities within each wetland is displayed: * $p<0.05$. CEC stands for cation exchange capacity. For all parameters the effect of wetland was non-significant.

		Theewaterskloof			Goukou			Kromme
		Palmiet	Fynbos		Palmiet	Fynbos		Palmiet
Physical properties	pH	4.5±0.12	4.6±0.50	*	4.0±0.09	4.9±0.35	*	5.3±0.18
	Bulk Density (g/cm^3)	0.3±0.15	0.3±0.11		0.2±0.04	0.3±0.10		0.3±0.12
	Soil Water Content (%)	42.2±22.79	50.8±17.76		58.7±3.66	62.0±5.28		70.6±6.06
	Soil Organic Matter (%)	24.0±14.43	23.0±11.67		34.6±4.46	30.1±6.49		18.3±3.60
Nutrients	N/P Ratio	12.8±3.47	15.9±5.49		15.9±0.62	16.3±1.69		12.1±2.38
	P_{tot} (mg/kg)	363.0±192.95	313.7±147.34		436.3±67.12	472.3±124.47		242.1±61.27
	PO_4-P (mg/kg)	5.0±2.58	5.1±3.58		7.0±3.51	4.0±1.97		2.3±1.10
	N_{tot} (mg/kg)	4920.2±3143.93	4777.3±2379.75		6919.0±851.32	7681.7±2042.59		3008.4±953.82
	NH_4-N (mg/kg)	2.9±2.07	5.2±5.98		4.8±2.33	6.3±2.77		11.0±21.30
	NO_3-N (mg/kg)	0.7±0.58	0.6±0.55		0.1±0.06	0.9±0.77		0.5±0.66
Nutrient pools	P pool (mg/L)	99.6±26.25	100.9±63.80		105.0±28.71	140.9±56.19		64.0±23.54
	PO_4 Pool (mg/L)	1.5±0.94	1.7±1.49		1.7±0.91	1.3±1.17		0.6±0.41
	N pool (mg/L)	1309.9±535.51	1442.2±779.41		1658.3±409.94	2270.7±806.22		764.6±278.91
	NH_4 Pool (mg/L)	0.8±0.41	1.8±2.15		1.1±0.39	1.8±0.72		2.5±4.40
	NO_3 Pool (mg/L)	0.2±0.19	0.2±0.17		0.0±0.01	0.3±0.24		0.1±0.15
Buffering capacity	CEC (meq/100g)	14.7±8.44	17.5±5.31		25.4±3.41	24.9±2.14		21.5±3.10
	Base Saturation (%)	10.2±4.12	9.1±3.72		12.1±1.41	15.8±3.91		29.2±3.52
	Na (meq/100g)	0.2±0.06	0.2±0.17		0.5±0.18	0.6±0.14		0.8±0.19
	Ca (mg/kg)	434.3±468.30	308.8±171.88		434.8±61.15	442.1±129.08		758.6±215.45
	Mg (mg/kg)	552.2±347.30	527.0±261.28		928.0±147.85	1864.1±589.98		1216.3±165.98
	K (mg/kg)	4220.2±2936.51	4243.8±2246.99		3933.3±527.58	5555.9±1503.44		3186.2±487.17
Biological	Microbial Biomass	0.3±0.15	0.4±0.36		1.5±0.61	0.8±0.27		0.5±0.22

** Statistics for pH: F=5.16, ndf=1, ddf=12, p=0.04.*

Table 4. The difference in groundwater parameters between fynbos and palmiet communities in South African palmiet wetlands. Significance is displayed: * p<0.05. Parameters in bold are those where the effect was the same regardless of location (wetland effect not significant).

		Theewaterskloof			Goukou			Kromme
		Palmiet	Fynbos		Palmiet	Fynbos		Palmiet
Physical	**pH**	**5.3±0.44**	**5.8±0.73**		**5.6±0.33**	**5.7±0.23**		5.8±0.33
	Conductivity (uS/cm)	**44.5±10.61**	**76.3±16.74**		**128.0±53.25**	**134.5±13.55**		149.4±34.17
	Relative Groundwater Depth (m)	**0.7±0.01**	**0.7±0.98**	*	**1.5±1.10**	**0.2±0.37**	*	1.0±1.14
Nutrients	Kjeldahl Nitrogen (mg/l)	1.1±0.33	2.6±1.23		4.1±2.85	1.0±0.13	*	3.6±5.14
	NH_4-N (mg/l)	**0.0±0.04**	**0.3±0.32**		**0.1±0.08**	**0.1±0.07**		0.1±0.06
	P_{tot} (mg/l)	**0.1±0.10**	**0.2±0.09**		**0.2±0.18**	**0.1±0.07**		0.3±0.38
	PO_4-P (mg/l)	**0.0±0.02**	**0.0±0.02**		**0.0±0.02**	**0.0±0.02**		0.0±0.02
Ions	**Na (mg/l)**	**2.8±0.57**	**4.9±0.23**		**14.2±5.62**	**13.4±0.84**		17.6±2.05
	Ca (mg/l)	**0.4±0.01**	**1.7±1.67**		**5.2±1.55**	**4.8±3.17**		4.2±2.76
	Mg (mg/l)	**0.4±0.09**	**0.8±0.23**		**1.4±1.09**	**1.8±0.12**		2.6±0.41

** Statistics for RGD: F=0.68, ndf=1, ddf=6, p=0.02; KjN: F=16.59, ndf=1, ddf=4, p=0.02.*

Biotic factors driving palmiet and fynbos communities

Although there was no significant difference in soil or groundwater K and Mg, there was a significantly higher concentration of these cations in palmiet vegetation compared to fynbos (**Table 5**). Nutrient concentrations in plant tissues did not differ significantly between communities. Palmiet communities tend to be dominated by one species: Palmiet (P*rionium serratum*), making up on average 80-98% of cover (**Table 6**). As a consequence, the number of species differed between communities, fynbos communities being more diverse than palmiet communities, significantly so in the Goukou wetland. However there was no significant difference in the number of functional types for the two communities. None of the diversity indices differed significantly between communities, however various community weighted means did. Stem diameter, leaf length-width ratio, leaf area as well as cellulose and lignin concentration in the leaves were significantly higher in palmiet communities relative to fynbos communities. Conversely, the community weighted mean for percentage of plant DSi was higher in fynbos than palmiet communities.

Table 5. The difference in vegetation parameters between fynbos and palmiet communities in three South African palmiet wetlands. The significance of the difference between fynbos and palmiet wetland communities is displayed: * p<0.05, ** p<0.01. Parameters in bold are those where the effect was the same regardless of location (wetland effect not significant). For all parameters the effect of wetland was non-significant.

	Theewaterskloof			Goukou			Kromme
	Palmiet	Fynbos		Palmiet	Fynbos		Palmiet
N/P ratio	18.7±2.15	24.3±10.28		17.9±3.7	30.6±10.59		22.3±5.65
Ptot (mg/kg)	366.7±121.58	359.5±271.63		408.9±129.8	217.3±90.02		378.5±254.16
Ntot (mg/kg)	6836.7±2364.66	6741.8±2026.69		7079.6±1467.41	6013±1357.84		7478.9±4245.99
K (mg/kg)	5406.8±2790.54	3015.8±1662.88	**	6887±3390.71	3312.4±1432.24	**	10070.9±4701.28
Ca (mg/kg)	2965.3±1758.7	1427±591.15		2375.8±864.54	2021.6±1173.54		2643.8±1200.94
Mg (mg/kg)	1715±398.18	996.9±254.89	**	1469.8±497.69	1008.5±302.37	**	1483.1±377.77

** Statistics for K: F=10.00, ndf=1, ddf=12, p=0.008; Mg: F=12.07, ndf=1, ddf=12, p=0.004.*

Table 6. Composition of fynbos and palmiet communities in three South African palmiet wetlands, including functional diversity indices and community weighted means. The significance of the difference between fynbos and palmiet communities is displayed: * p<0.05, ** p<0.01; F and p values are given in **Table A2.** Parameters in bold are those where the effect was the same regardless of location (wetland effect not significant).

		Theewaterskloof			Goukou			Kromme
		Palmiet	Fynbos		Palmiet	Fynbos		Palmiet
General	Number of species	5.7±1.37	8.0±1.26		3.0±0.00	8.4±2.28	***	4.3±1.06
	Number of functional types	**4.2±1.17**	**4.2±0.75**		**3.0±0.00**	**3.9±1.17**		**2.4±0.84**
	% Cover by dominant	**85.0±9.49**	**59.2±22.00**		**80.0±17.80**	**64.6±18.96**		**97.5±3.54**
Diversity Indices	**Functional richness**	**6.9±2.71**	**7.3±2.64**		**1.3±0.25**	**-**		**-**
	Functional evenness	**0.7±0.24**	**0.6±0.20**		**0.9±0.11**	**-**		**-**
	Functional diversity	**0.9±0.06**	**0.8±0.06**		**0.8±0.08**	**-**		**-**
	Functional dispersion	**3.4±0.53**	**3.7±1.03**		**4.2±0.26**	**3.2±1.28**		**2.0±1.51**
	Rao's entropy	**14.1±2.36**	**16.3±5.04**		**19.0±2.22**	**13.6±6.74**		**8.0±5.88**
Community Weighted Means	**Shoot length (mm)**	**1662.2±72.40**	**1295.8±537.18**		**1471.6±90.58**	**1319.1±213.99**		**1450.8±307.91**
	Stem diameter (mm)	**55.1±6.65**	**28.5±16.70**	**	**49.9±3.16**	**19.3±16.37**	**	**70.9±10.69**
	Total biomass (g)	**896.5±134.39**	**443.5±273.06**	*	**5199.0±2215.49**	**709.3±1545.10**	*	**1151.7±269.82**
	Leaf length-width ratio	**19.9±2.56**	**9.9±5.99**	*	**19.2±1.25**	**6.4±6.48**	*	**23.1±4.31**
	Leaf mass (mg)	**10358.7±1938.03**	**8705.7±4546.80**		**6064.6±448.05**	**10626.4±5336.56**		**8306.8±1691.15**
	Leaf area (mm^2)	**11884.4±1969.51**	**6463.8±3676.64**	*	**9202.4±675.86**	**4355.3±3021.99**	*	**12680.7±2510.67**
	Specific leaf area (mm^2/mg)	**1.5±0.27**	**1.4±0.47**		**1.7±0.23.00**	**3.7±3.10**		**3.7±1.84**
	Si concentration (%)	**833.2±355.77**	**4842.7±5179.11**	*	**734.3±23.80**	**5270.6±3679.17**	*	**844.4±321.60**
	Cellulose per leaf (mg)	**2958.2±397.18**	**1435.8±872.81**	*	**2440.4±181.16**	**625.0±954.89**	*	**3352.1±683.38**
	Lignin per leaf (mg)	**352.7±42.20**	**188.5±99.73**	*	**298.3±21.50**	**83.7±112.74**	*	**404.0±81.78**
	Aerenchym (score: 1-3)	**1.9±0.23**	**1.6±0.32**		**1.6±0.04**	**1.6±0.24**		**1.8±0.16**
	Woodiness (score: 1-3)	**2.0±0.17**	**1.8±0.43**		**2.0±0.00**	**2.1±0.26**		**2.1±0.20**
	Hollowness (score: 1-3)	**1.1±0.09**	**1.1±0.17**		**1.1±0.15**	**1.0±0.03**		**1.0±0.00**

A comparison of palmiet and fynbos communities

The results of the ANOSIM revealed 62-72% dissimilarity between fynbos and palmiet plant communities. Additionally, palmiet communities tended to be characterized by mainly: *Prionium serratum* (Palmiet, 87-94%) and additionally *Cliffortia odorata*, and ferns: *Todea barbara* and *Pteridium aquilinum* (**Table A3**). On the other hand, fynbos communities were predominantly distinguished by: *Restio paniculatus* (43-44%), *Cliffortia strobilifera* (17-23%), as well as to a lesser extent two graminoids: *Epischoenus gracilis* and *Isolepis prolifera* (**Table A3**). The results of the DCA, based on plant community structure from September 2014, confirm the observation that fynbos communities tend to be more diverse than palmiet ones (**Fig. 2**). Fynbos plots cluster to the right of the plot and palmiet communities to the left. Two fynbos plots cluster closer to the palmiet communities. These two plots were both within palmiet communities, though were classified as non-palmiet communities as the cover of palmiet was less than 50%. However it is clear retrospectively that these are not from the same community as the other fynbos plots. The results from 2015 showed similar trends and are displayed in **Fig. A1**.

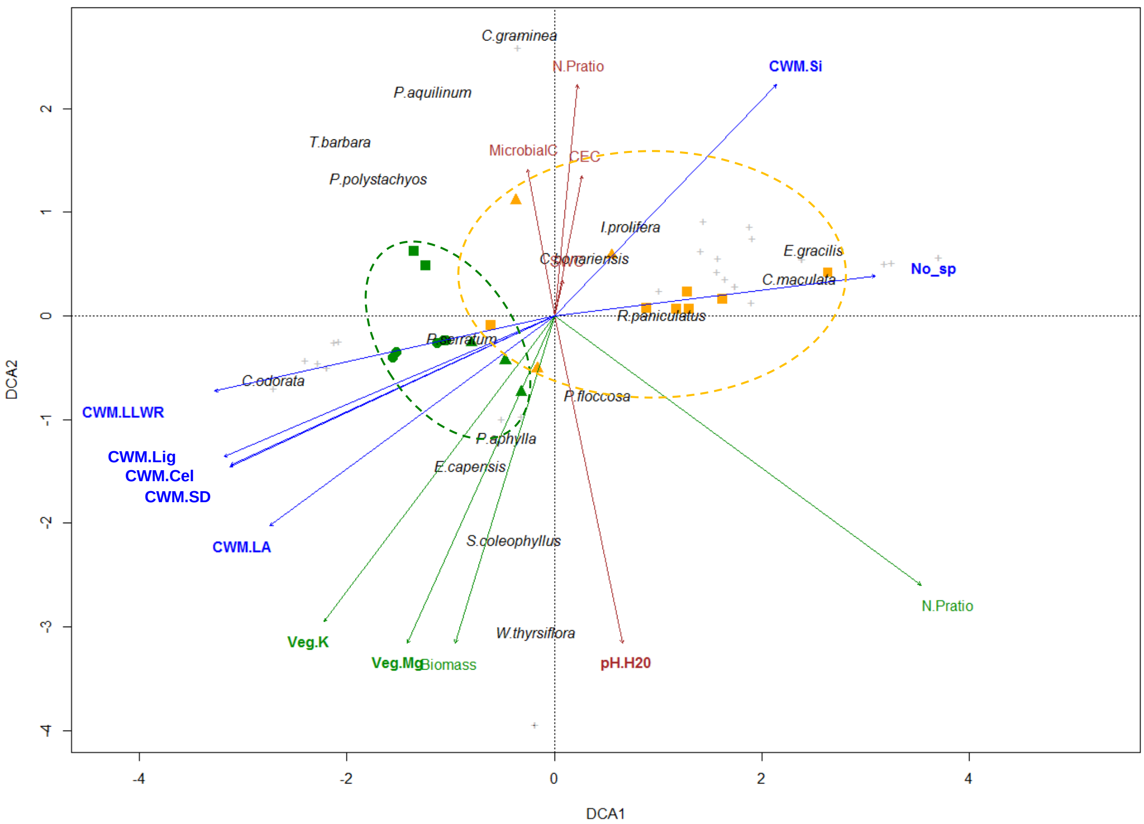

Figure 2. Detrended Correspondence Analysis (DCA) of the plant communities in fynbos and palmiet patches in three South African palmiet wetlands sampled in September 2014. Fynbos sites are in orange, palmiet in green. Symbols: ▲ Theewaterskloof, ■ Goukou, ● Kromme. Species names are given in black, and + indicates species with a lower abundance that are masked by other labels. Parameters that were interesting or significantly different (bold) between pristine and degraded wetland fragments were overlain and are indicated by the arrows. Soil parameters are in brown, vegetation composition in green, functional diversity indices in blue. Stippled circles encompass sites from fynbos and palmiet communities. For full species names see supplementary material.

5.4 Discussion

Which environmental parameters explain patchiness in palmiet wetlands?

Only two abiotic variables differed significantly between fynbos and palmiet patches in palmiet wetlands. These were soil pH, which was slightly higher in fynbos communities, and relative groundwater depth, which tended to be closer to the surface but more variable for fynbos communities. In a study on the Kromme palmiet wetland, Nsor (2007) also found soil pH to be a key environmental variable influencing community assembly. Additionally a study on riparian zones in South Africa confirmed that flow regimes were the key variable determining four different zones of differing plant communities (Reinecke, 2013). There is no doubt that hydrological regime will play an important role in shaping wetland plant communities, however in the case of palmiet wetlands, longer term monitoring of water table depth is needed to yield more insight. It is also possible that the vegetation itself determines the local groundwater depth through transpiration (Rebelo et al., 2015).

Though not explicitly quantified in this study, competition and disturbances may also play a role in shaping plant community assembly. Palmiet wetlands experience severe drought (Job, 2014), fires (Nsor, 2007), floods (Rebelo et al., 2015) and challenges to recruitment (Sieben, 2012). We hypothesize that palmiet communities are the climax community of palmiet wetlands and that fynbos communities represent the pioneers of the ecosystem. We further hypothesize that community assembly in palmiet wetlands is a result of a combination of water inundation extremes as well as fire and flooding which create local erosion, allowing for other species (fynbos community) to establish (Grenfell et al., 2009). Fires are known to burn riparian areas and wetlands with relative frequency across the world (Dwire and Kauffman, 2003). The super-dominant Palmiet, according to literature, is fire adapted (Boucher and Withers, 2004). Their thick stems are not killed and they develop side-shoots after fire events (Boucher and Withers, 2004). Additionally fire is necessary for their seeds to germinate (Boucher and Withers, 2004). However it is possible that palmiet communities are fire retardants and not fire promoters like fynbos communities (Rebelo, 2001), therefore relying on fire in some aspects (e.g. germination of seeds), but discouraging increased intensity or its spread through the entire wetland.

Can plant functional traits shed light on the hypotheses about palmiet wetland community assembly?

It is clear from the results that there are two distinct plant communities: palmiet-dominated communities, and somewhat more diverse fynbos communities. A study on wetland plants in the United States suggest that there are three basic functional wetland types: dominant matrix species, interstitial species, and annuals (Boutin and Keddy, 1993). This is the case to some extent with palmiet communities: *P. serratum* acting as the dominant matrix species, *Cliffortia odorata*, ferns *Todea barbara* and *Pteridium aquilinum* as well as various *Psoralea sp*. (depending on the region) acting as the interstitial species. Vegetation potassium and magnesium concentration was significantly higher in the palmiet communities relative to the fynbos, however these differences are not reflected in the soil or groundwater, therefore it is not clear why this difference should occur. This accumulation of K could be the result of high transpiration rates (Brag, 1972). Another possibility is that it is indicative of palmiet communities being older than the fynbos ones, and these tissue concentrations reflecting longer term uptake from soil and groundwater. Additionally, at low pH, Mg becomes more soluble and therefore may be more available for plant uptake (Jackman and Black, 1951; Lucas and Davis, 1961).

Interestingly, fynbos communities had more plant species than palmiet communities, however no difference in the number of functional types. This suggests that although palmiet communities are more species poor, the suite of species is optimal for taking advantage of the niche space provided by the wetland. Community weighted means for stem diameter, leaf length-width ratio, leaf area as well as cellulose and lignin concentration in the leaves were significantly higher in palmiet communities relative to fynbos communities. The community weighted mean values in palmiet communities were highly influenced by the dominant species: Palmiet. The palmiet community's overall large stem diameter than that of the fynbos may be confirmation of the community being fire retardants as opposed to promoters (Rebelo, 2001). The significantly higher leaf length-width ratio (long strap-like leaves) may be an adaptation to the mechanical disturbance of floods (Catford and Jansson, 2014; Colmer and Voesenek, 2009). Additionally, the higher cellulose and lignin concentration of the leaves, but lower biogenic silica concentration may indicate high stem flexibility (Schoelynck et al., 2010), representing an adaptation to flood events (Catford and Jansson, 2014; Colmer and Voesenek, 2009). We did not measure below ground traits in this study, however another study on palmiet wetland communities has shown that rhizome internode length (a measure for clonality) was important in explaining vegetation spatial patterns (Sieben, 2012).

5.5 Conclusion

Soil pH and relative groundwater depth were two key environmental parameters correlated with plant community assembly in palmiet wetlands. Long-term monitoring is needed to understand the relationship between relative groundwater depth and plant community assembly in palmiet wetlands. Palmiet communities were characterized by higher community weighted means for stem diameter, leaf length-width ratio, leaf area as well as cellulose and lignin concentration. These suggest adaptations to fire (thicker stems – fire retardants) and floods (long, thin leaves and flexible shoots). We suggest that palmiet communities are the climax community of palmiet wetlands, and that the fynbos communities represent pioneers.

5.6 Acknowledgements

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5.8 Appendix

Table A1. The 13 functional traits collected for the 22 dominant wetland species. All methods were based on the standardised protocol of Pérez-Harguindeguy et al. (2013). For categorical traits the codes assigned are shown in brackets.

	Trait	Measurement method used	Unit	Scale
Morphological/ Anatomical Traits	Shoot Length	Average shoot length of 10 mature plants	mm	Ratio
	Stem Diameter	Average diameter of 10 stems at base level	mm	Ratio
	Total Biomass	Average value of total biomass divided by number of mature shoots (in case of a tuft or rhizome)	g	Ratio
	Leaf Length/Width Ratio (LLWR)	Ratio between the length and the width of a leaf based on an average of 10 leaves	mm/mm	Ratio
	Leaf Dry Mass	Average leaf mass after being oven dried at 60°C for 72 hours (10 leaves)	mg	Ratio
	Leaf Area	Area of a single surface of a leaf based on an average of 10 leaves	mm^2	Ratio
	Specific Leaf Area (SLA)	The total surface area of a leaf divided by its dry mass (based on an average of 10 leaves)	mm^2/mg	Ratio
	Presence of Aerenchym	Scale of 1 to 3 (1 = no aerenchym, 2 = less than 50% aerenchym, 3 = predominantly aerenchym)	Class	Ordinal
	Woodiness of Stem	Scale of 1 to 3 (1 = no woody tissue, 2 = less than 50% woody tissue, 3 = predominantly woody tissue)	Class	Ordinal
	Hollowness of Stem	Scale of 1 to 3 (1 = stem not hollow, 2 = hollow space less than 50%, 3 = hollow space more than 50%)	Class	Ordinal
Biochemical Traits	Si Content	Biogenic silica was extracted from 25 mg dry plant (leaf and stem) material from 10 plants and analysed using ICP-OES	%	Ratio
	Absolute amount of Cellulose per leaf	Cellulose content (%) multiplied by average dry leaf mass to get an amount of Si per leaf	mg	Ratio
	Absolute amount of Lignin per leaf	Lignin content (%) multiplied by average dry leaf mass to get an amount of Si per leaf	mg	Ratio

Table A2: Statistical results of the linear mixed models for community parameters. Parameters in bold indicate no significant effect of wetland. NS indicates not significant.

		Theewaterskloof		Goukou	
		Palmiet	Fynbos	Palmiet	Fynbos
General	Number of species	NS		**F=33.65, ndf=1, ddf=12, p=0.000**	
	Number of functional types	**NS**			
	% Cover by dominant	**NS**			
Diversity Indices	**Functional richness**	**NS**			
	Functional evenness	**NS**			
	Functional diversity	**NS**			
	Functional dispersion	**NS**			
	Rao's entropy	**NS**			
Community Weighted Means	**Shoot length (mm)**	**NS**			
	Stem diameter (mm)	**F=9.41, ndf=1, ddf=12, p=0.010**			
	Total biomass (g)	**F=7.26, ndf=1, ddf=12, p=0.020**			
	Leaf length-width ratio	**F=8.20, ndf=1, ddf=12, p=0.014**			
	Leaf mass (mg)	**NS**			
	Leaf area (mm^2)	**F=6.79, ndf=1, ddf=12, p=0.023**			
	Specific leaf area (mm^2/mg)	**NS**			
	Si concentration (%)	**F=4.88, ndf=1, ddf=12, p=0.050**			
	Cellulose per leaf (mg)	**F=5.29, ndf=1, ddf=12, p=0.040**			
	Lignin per leaf (mg)	**F=6.32, ndf=1, ddf=12, p=0.027**			
	Aerenchym (score: 1-3)	**NS**			
	Woodiness (score: 1-3)	**NS**			
	Hollowness (score: 1-3)	**NS**			

Table A3: Results of the SIMPER analysis comparing palmiet and fynbos communities in palmiet wetlands for 2014 and 2015.

Year	Species	Average contribution	Standard deviation	Cumulative sum of most influential species	Fynbos sites (%)	Palmiet sites (%)
2014	*Prionium serratum*	0.24	0.099	0.31	23.5	87.0
	Restio paniculatus	0.15	0.117	0.51	43.5	4.5
	Cliffortia strobilifera	0.07	0.068	0.60	19.5	0.6
	Epischoenus gracilis	0.04	0.056	0.65	10.8	0.0
	Cliffortia odorata	0.03	0.069	0.69	0.0	10.0
	Todea barbara	0.03	0.058	0.73	1.5	7.0
2015	*Prionium serratum*	0.28	0.087	0.33	15.9	93.5
	Restio paniculatus	0.15	0.111	0.51	42.8	2.4
	Cliffortia strobilifera	0.06	0.064	0.57	16.6	0.3
	Pteridium aquilinum	0.05	0.068	0.63	6.2	11.6
	Epischoenus gracilis	0.05	0.072	0.69	13.6	0.0
	Isolepis prolifera	0.04	0.109	0.73	9.5	0.0

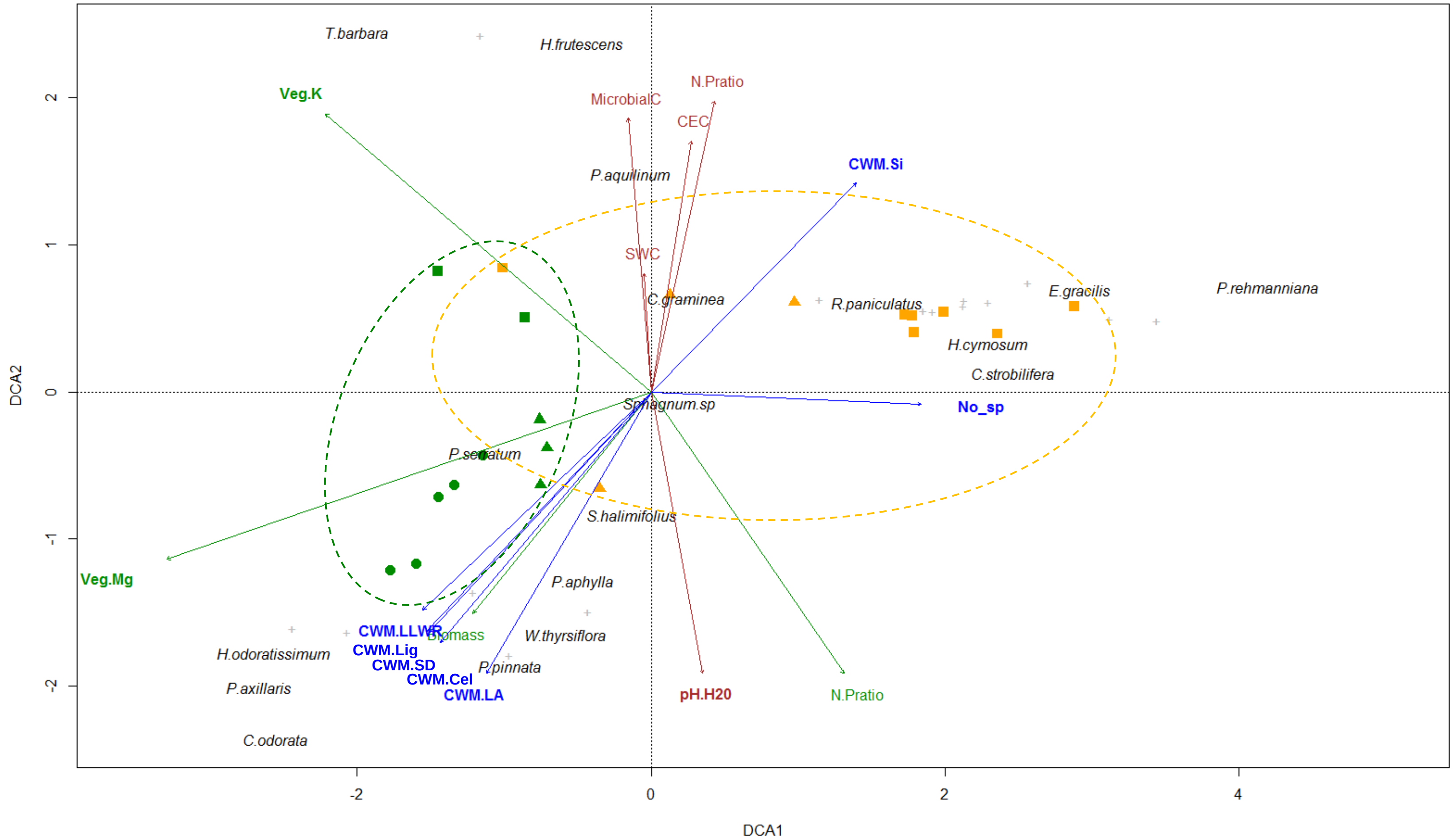

Figure A1. Detrended Correspondence Analysis (DCA) of the plant communities in fynbos and palmiet patches in three South African palmiet wetlands sampled in March 2015. Fynbos sites are in orange, palmiet in green. Symbols: ▲ Theewaterskloof, ■ Goukou, ● Kromme. Species names are given in black, and + indicates species with a lower abundance that are masked by other labels. Parameters that were interesting or significantly different (bold) between pristine and degraded wetland fragments were overlain and are indicated by the arrows. Stippled circles encompass sites from fynbos and palmiet communities. Soil parameters are in brown, vegetation composition in green, functional diversity indices in blue. For full species names see supplementary material.

6

Relationships between functional diversity and ecosystem properties for three key wetland ecosystem services

Rebelo, A.J

The Goukou wetland nestled in a valley that emerges from the Langeberg Mountains near Riversdale in South Africa. Beneath the unremarkable looking wetland vegetation lies several meters of peat, which is rather significant for a region which experiences such low rainfall, and such high evaporation rates.

Abstract

Wetlands are known to provide important ecosystem services to society, though it is not well understood which ecosystem properties underpin the ecosystem processes supporting these services. Are abiotic parameters the key drivers or does biodiversity play a role? If biodiversity does play a role, through which mechanisms does it affect ecosystem service provision? According to the mass ratio hypothesis, one would expect the functional diversity of dominant species, or the community weighted means of their relevant plant functional traits to be important. I used the formal step-wise procedure of Díaz et al. (2007) to investigate these questions in South African palmiet wetlands. I found that abiotic variables were slightly more important in underpinning ecosystem processes than biotic variables. However community weighted trait means were also important in influencing final models, whereas trait distribution was unimportant. Results were not highly consistent between the two seasons studied, and therefore it is concluded that either the relationships between ecosystem processes and functional diversity in wetlands are more complicated than those of other ecosystems (such as the frequently studied sub-alpine grasslands), or this method is not robust enough to model ecosystem processes, as multiple input variables can confuse the output models.

6.1 Introduction

Ecosystem processes may be defined as intrinsic processes or fluxes of an ecosystem whereby properties of the ecosystem interact in time and space (Díaz et al., 2006; MEA, 2005). These ecosystem processes include: decomposition, nutrient cycling and primary productivity, amongst others. Ecosystem properties, such as biomass, soil organic carbon and soil nitrogen content, underpin these processes. Although the connection is not well understood, ecosystem processes, and by inference also ecosystem properties, are thought to approximate ecosystem service provision (Díaz et al., 2007). Additionally it is widely accepted that plant functional traits at the community level underpin ecosystem properties and therefore ecosystem service provision (Díaz et al., 2006, Dias et al., 2013). One relevant theory is the mass ratio hypothesis, which states that ecosystem properties are determined by the plant functional traits and functional diversity of the dominant species in the community, and relatively insensitive to those species that either occur in low numbers, or low biomass, or both. Therefore implying that ecosystem properties have little or no link to species richness (Díaz et al., 2004). According to this hypothesis, it should be possible to approximate ecosystem properties by quantifying the community weighted means of plant functional traits with demonstrable links to those ecosystem properties (Díaz et al., 2007). It has been suggested that where the relationship between community weighted means and ecosystem properties is weak, functional diversity may have a strong influence (Díaz et al., 2007).

Not many studies have investigated the relative importance of community weighted means and functional diversity effects on ecosystem properties (Dias et al., 2013). Additionally there has been very little research on relationships between plant functional traits and ecosystem properties in wetland ecosystems (Moor et al., 2017). To this end, I investigated whether ecosystem service provision in South African palmiet wetlands could be explained by abiotic factors, community weighted mean trait values, trait value distribution or a combination of these. I used the formal step-wise procedure of Díaz et al. (2007) to identify the key abiotic and biotic (community weighted means and functional diversity) factors affecting ecosystem properties as well as to construct useful predictive models for each ecosystem property. I considered the three important ecosystem service complexes in wetlands: water regulation, water purification and carbon sequestration (Moor et al., 2017). They are called ‘complexes’ because they are sometimes made up of more than one ecosystem service, which may trade-off with each other, or be mutually exclusive (Moor et al., 2017).

South African palmiet wetlands are valley-bottom wetlands dominated by a species which is endemic to southern Africa: Palmiet (*Prionium serratum*). These wetlands have been shown to provide many important ecosystem services to society (Rebelo et al., 2015, **Chapter 9**). Despite their value, these wetlands are highly threatened (Nel et al., 2007, **Chapter 3**). There is a need to understand which factors (abiotic or functional diversity modifications) are key in influencing ecosystem properties and therefore ecosystem service provision of these wetlands. This method could provide a cost-effective way to monitor the effects of climate change and land-use/land-cover change on ecosystem properties and therefore ecosystem services in palmiet wetlands (Díaz et al., 2007).

6.2 Methods

Study site and field measurements

Palmiet wetlands occur in valley-bottoms of the Cape Floristic Region of South Africa. Climate is mediterranean and soils are mainly highly leached dystrophic lithosols associated with the sandstone mountains of the Cape Supergroup (Midgley et al., 2003). Much of these wetlands have been transformed into agricultural lands, with few intact wetlands remaining (**Chapter 3**). Three of these were selected as study sites: the Theewaterskloof wetland (33° 57' 36.3" S, 19° 10' 11.77" E), Goukou wetland (34° 1' 41.27" S, 21° 23' 21.91" E) and the Kromme wetland (33° 52' 25.44" S, 24° 2' 29.66" E). Data were collected from the three study wetlands on two sampling occasions representing two seasons: September 2014 (after winter), and March/April 2015 (after summer). Both degraded and reference stretches of each of the three wetlands were sampled. Degraded stretches were characterized by some form of erosion with subsequent drainage, often accompanied by alien tree or weed invasion. Six to nine 3x3 m plots spaced 20-50 m apart on 100-200 m cross-sectional transects through the wetlands (39 total) were surveyed for floristic composition (relative abundance), ecosystem properties relating to three wetland ecosystem service complexes, soil properties and plant functional traits at the population level (**Chapters 4, 5**).

Ecosystem service complexes

Each ecosystem service was estimated by means of one or more proxy ecosystem properties. The ecosystem service complex water flow regulation is made up two different services (or components, cf.: Boerema et al., 2017): water storage and flood attenuation, only the latter of which was considered in this study. I used the cellulose, lignin and dissolved biogenic silica (DSi) concentration of the vegetation (related to vegetation stiffness and flexibility) as well as its biomass as a proxy of the flood attenuation capacity of the wetland. The climate regulation service is made up of energy exchange, carbon sequestration and greenhouse gas emissions. Only carbon sequestration was considered in this study. Ecosystem properties related to carbon sequestration were: vegetation biomass, soil organic carbon, and total topsoil organic carbon. The ecosystem service complex water quality regulation includes the retention or removal of excess nutrients and sediments from runoff, as well as biogeochemical transformations. Here I consider the removal of excess nutrients from runoff. Ecosystem properties used as proxies for this service were a measure for microbial activity of the soil (microbial biomass index), soil cation exchange capacity, bulk density, base saturation, as well as vegetation bioconcentration factors and nutrient uptake capacity (Schachtschneider et al., 2017). The first four ecosystem properties are either measures of soil health or fertility and therefore cation/nutrient retention capacity, or the capacity to protect groundwater and surface water from cation/nutrient contamination. The last two ecosystem properties are indications of the ability of vegetation to assimilate nutrients, ultimately decreasing the load in the soil and eventually in the water (Schachtschneider et al., 2017).

Ecosystem properties

A total of 25 ecosystem properties were measured. Standing vegetation biomass was sampled in three small subplots of 0.28x0.28 m within each plot. Vegetation was weighed before and after oven drying for 48 hours at 70°C, ground and homogenised using a mill. Plant tissue silica (biogenic silica - DSi) was extracted using the procedure of Schoelynck et al. (2010). Plant lignin and cellulose content were measured using the Van Soest method (Van Soest, 1963). DSi, cellulose and lignin content were expressed both as percentages and weighted by biomass (g/m^2). Total plant nitrogen and total phosphorus were determined using acid digestion and were measured with a continuous -flow analyzer (CFA) from SKALAR (Type: SAN++) (Walinga et al., 1989). Soil organic matter was determined by loss on ignition. Total carbon (C_{tot}) was determined by total combustion of dried and finely ground soil on a Flash 2000 CN-analyzer (Thermo Fisher Scientific). Soil organic carbon was calculated as the quotient of soil organic matter and a conversion factor of 1.72, which is based on the assumption that organic matter contains 58% organic carbon. Total organic carbon was calculated by multiplying soil organic carbon with bulk density in the top 10 cm of the soil). In each plot one bulk density sample was taken of the topsoil using a 100 cm^3 metal Kopecky ring. Samples were weighed before and after oven drying for 48 hours at 70°C and expressed as g/cm^3. Soil microbial biomass carbon was measured as a proxy for microbial activity in the soil at each site. I used the chloroform fumigation direct extraction protocol for microbial biomass carbon (Beck et al., 1997; Martens, 1995). Cation exchange capacity and base saturation were determined using the method of Brown (1943). Bioconcentration factors are the ratio of nutrient concentrations in the soil to those in vegetation (Schachtschneider et al., 2017). Nutrient uptake capacity is the product of total plant nutrient concentration by its biomass (Schachtschneider et al., 2017). Bioconcentration factors and nutrient uptake capacities for TN, TP, Ca, Mg and K were calculated.

Soil properties

Composite soil samples were taken from 10 points within each plot at a depth of 1-10 cm using a hand held auger of 1 cm in diameter. Soft extractions were done to determine soil bioavailable nutrients (NO_3^-, NH_4^+ and PO_4^{3-}) (Houba et al., 1989) and the pH (KCl) was measured. Soil water content was calculated gravimetrically by weighing soil before and after drying for 24 hours at 105°C. Cation exchange capacity, base saturation, bulk density, soil organic matter, total carbon and soil organic carbon were quantified as outlined in the previous section. Total phosphorus (TP) and nitrogen (TN) were analyzed on a CFA; potassium, calcium, magnesium, and sodium were quantified using the acid digestion method (Walinga et al., 1989). Ratios N/P and C/N were calculated. Nutrient pools were calculated by multiplying nutrient concentrations (TN, TP and bioavailable nutrients) by bulk density measurements.

Quantification of functional diversity

I measured 17 plant functional traits from the 22 dominant species which may be related to the ecosystem properties and ecosystem services considered in this study (**Table A1, A2**): shoot length, stem diameter, total biomass, leaf length-width-ratio, dry leaf mass, leaf area, specific leaf area, and C/N ratio. Tissue Si, cellulose and lignin content were all expressed both as percentages and as a concentration per leaf mass (mg). Lastly aerenchym, woodiness and hollowness were scored from 1-3. The definition and methods used for each of the plant functional traits are given in **Table A1**. For all commonly measured plant functional traits, I used the standardized protocol for measurements (Pérez-Harguindeguy et al., 2013). Functional diversity indices, functional richness, evenness, divergence, dispersion and Rao's entropy, were calculated for each plot. Community weighted mean trait values were calculated for each plot by multiplying plant functional traits values of dominant species with their relative abundance. Summary statistics are shown for each of the continuous plant functional traits in **Table A3**.

Data analysis

I used the six-step general linear model approach of (Díaz et al., 2007) to test relationships between functional diversity and ecosystem properties in R. The approach is divided into two stages: the first composed of the first four steps, the second of two. In the first stage, the effects of abiotic variables on each ecosystem property is considered (step 1), followed by the effects of community weighted means (step 2), functional diversity (step 3) and finally idiosyncratic species effects (step 4). In the first stage each step was completed sequentially and all significant terms were conserved for stage two. In the second stage (step 5), all significant terms ($p < 0.01$) from steps 1-4 were combined in a step-wise ascending procedure and the best model was selected using Akaike criterion (Díaz et al., 2007). If none of the linear models from step 1 were satisfactory, data were reexamined for discontinuities (step 6). All ecosystem properties were tested for normality using the Shapiro-Wilk test in R, and any non-normal variables transformed using log(x+1) and retested. Any non-normal ecosystem properties were excluded from further analysis. All final models were examined to ensure that assumptions were met: the distribution of the residuals were checked for normality, as well as plotted against fitted values to ensure homoscedasticity.

6.3 Results

I used the formal step-wise procedure of Díaz et al., (2007) to identify the key abiotic and biotic factors affecting ecosystem properties as well as to construct useful predictive models for each ecosystem property. For 2014, 13 of the 25 ecosystem properties were normally distributed and therefore modelled (**Table 1a**). For the ecosystem service flood attenuation; five ecosystem properties were relevant, and abiotic variables and community weighted means were most important in underpinning them. Vegetation cellulose content (%) was underpinned by soil bulk density and the community weighted mean of the woodiness of the vegetation, whereas total cellulose (g/m^2) was influenced by soil Ca, and community weighted mean of leaf area and leaf mass. Likewise vegetation DSi content (%) was underpinned by DSi in the soil and stem diameter, whereas total DSi (g/m^2) was determined largely by the amount of Na in the soil, however the variance explained by these two models was not high (22-28%). Lignin content was described by a complex model including various soil parameters, functional dispersion as well as the idiosyncratic effects of *Searsia angustifolia*. Vegetation biomass was well explained (63%) by Ca in the soil as well as the community weighted mean of leaf area and Aerenchym. For the ecosystem service water quality regulation, five ecosystem properties were relevant and normally distributed, and abiotic parameters were the most important variables underpinning them. Microbial biomass was underpinned solely by abiotic variables: soil organic matter, TP, pH and soil Mg and K. Likewise soil base saturation was determined by soil pH, TP and K. Nutrient uptake capacity was usually underpinned by a combination of the community weighted mean of leaf area and one of the soil cations (Ca or Mg), except in the case of Mg uptake, which was also influenced by cellulose (mg). Variances were high for microbial biomass index and base saturation, but lower for nutrient uptake capacities. For the last ecosystem service, carbon sequestration, three ecosystem properties were relevant and normally distributed and again abiotic variables seemed to be most important in underpinning these ecosystem services. Both soil organic carbon and total organic carbon were underpinned by soil cation exchange capacity and various nutrients (N/P ratio, TP, N/P, N_{pool}) as well as a few other abiotic variables for soil organic carbon. Rather complex models, the variance explained for both these parameters was high.

Table 1a. Summary of significant results (P < 0.01) for general linear models of ecosystem properties from palmiet wetlands sampled in 2014 following steps 1–6 of the framework of Díaz et al. (2007). (*) indicates log transformed variables. SOC: soil organic carbon, TOC: total organic carbon, CEC: cation exchange capacity, BD: bulk density, SOM: soil organic matter, BS: base saturation, SWC: soil water content, SL: shoot length, SD: stem diameter, TB: total biomass, LLWR: leaf length-width-ratio, LM: dry leaf mass, LA: leaf area, SLA: specific leaf area, FRich: functional richness, FEve: functional evenness, FDiv: functional divergence, FDis: functional dispersion and RaoQ: Rao's entropy.

		Stage I: Individual effects of abiotic and biotic factors								Stage II: Combining significant effects into the best predictive model (Step 5: Final model)	
		Step 1: Abiotic factors		Step 2: Community weighted mean traits		Step 3: Trait distribution		Step 4: Idiosyncratic species effects			
Ecosystem Services	Ecosystem Properties	Variable	*P* value	Variable	*P* value	Variable	*P* value	Variable	*P* value	Model	% var
Water Regulation: Flood Attenuation	Cellulose Content (%)	BD, CEC, N/P, TN, TP	0.001, 0.003, 0.003, 0.006, 0.007	Woodiness	0.001					Cellulose Content = -6.14 BD + 5.55 Woodiness + 24.04	45
	Cellulose in Vegetation (g/m^2) *	Ca, Mg, Na, K	0.002, 0.002, 0.004, 0.009	LA, LM, Cellulose (mg), Aerenchym, Lignin (mg), Lignin (%)	0.000, 0.001, 0.001, 0.002, 0.002, 0.007			*Prionium serratum*, *Isolepis prolifera*	0.001, 0.002	Cellulose Content = 0.31 Ca + 0.000025 LA + 0.000036 LM + 1.75	47
	Lignin Content (%)	pH_{KCl}, PO_4 Pool, Na	0.002, 0.002, 0.006			FDis, RaoQ	0.002, 0.008	*Searsia angustifolia*	0.007	Lignin Content = -5.02 pH_{KCl} + 1.74 PO_4 Pool - 6.45 Na + 1.63 FDis + 0.25 *Searsia angustifolia*	63
	DSi Content (mg/kg) *			DSi (mg/kg), SD, Woodiness	0.005, 0.006, 0.009					DSi Content = 0.00002 DSi - 0.002 SD + 3.6	28
	DSi in Vegetation (g/m^2) *	Na	0.003							DSi Content = 0.60 Na + 0.47	22
	Vegetation Biomass Index (g) *	Ca, Mg, Na	0.003, 0.004, 0.004	LA, Cellulose (mg), Aerenchym, Lignin (mg), LM, Lignin (%)	0.000, 0.001, 0.001, 0.001, 0.002, 0.009			*Prionium serratum*, *Isolepis prolifera*	0.000, 0.003	Biomass Index = 0.35 Ca + 0.000014 LA + 0.56 Aerenchym + 0.53	47

*Table 1a continued

	Microbial Biomass Index *	SOM, C_{tot}, TN, CEC, BD, SWC, N/P, TP, pH_{KCl}, Mg, Na, Ca, K, N_{pool}	0.000, 0.000, 0.000, 0.000, 0.000, 0.000, 0.000, 0.000, 0.000, 0.000, 0.000, 0.000, 0.000, 0.000, 0.000, 0.001, 0.002	LM	0.004		*Todea barbara*	0.001	Microbial Biomass Index = 0.0058 SOM - 0.00014 TP - 0.083 pH_{KCl} + 0.015 Mg + 0.29 K + 0.35	88
Water Purification: Water Quality Regulation	Soil Base Saturation (%)	pH_{KCl}, BD, TP, PO_4-P, K, C_{tot}, TN, SOM	0.000, 0.000, 0.001, 0.001, 0.001, 0.002, 0.003, 0.004	LLWR	0.001				Soil Base Saturation = 10.92 pH_{KCl} - 0.04 TP + 54.55 K -20.97	67
	Veg. TP Uptake Capacity (mg/m^2)*	Ca	0.004	LA, Cellulose (mg), Lignin (mg)	0.003, 0.006, 0.008		*Prionium serratum*	0.003	Veg. P Uptake Capacity = 0.33 Ca + 0.000041 LA + 1.97	31
	Veg. K Uptake Capacity (mg/m^2)*	Mg, Na, Ca, K	0.001, 0.002, 0.003, 0.004	LA, Cellulose (mg), Lignin (mg), Aerenchym, Lignin (%)	0.000, 0.000, 0.000, 0.001, 0.009		*Prionium serratum*	0.000	Veg. K Uptake Capacity = 0.22 Mg + 0.000071 LA + 2.67	49
	Veg. Mg Uptake Capacity (mg/m^2)*	Ca	0.004	Cellulose (mg), LA, Lignin (mg), Aerenchym	0.000, 0.001, 0.002, 0.005		*Prionium serratum, Isolepis prolifera*	0.001, 0.003	Veg. Mg Uptake = 0.33 Ca - 0.00028 Cellulose + 0.0013 LA + 2.32	40

**Table 1a continued*

	Soil Organic Carbon (%)*	CEC, BD, SWC, TN, TP, N/P, K, pH_{KCl}, Mg, N_{pool}, Na, Ca, BS, PO_4-P	0.000, 0.000, 0.000, 0.000, 0.000, 0.000, 0.000, 0.000, 0.000, 0.000, 0.001, 0.001, 0.002, 0.002	LM, SLA, Hollowness, DSi (mg)	0.002, 0.003, 0.005, 0.007			Soil Organic Carbon = 0.012 CEC - 0.29 BD - 0.00000051 TN + 0.00079 TP + 0.012 N/P + 0.027 Mg - 0.0017 DSi + 0.49	98
Climate Regulation: Carbon Sequestration	Total Topsoil Organic Carbon (t/ha)	N_{pool}, TN, TP, CEC, K, SWC, Mg, P_{pool}, N/P, pH_{KCl}, PO_4-P	0.000, 0.000, 0.000, 0.000, 0.000, 0.000, 0.000, 0.000, 0.000, 0.002, 0.008	SLA	0.007			Total Topsoil Organic Carbon = 0.014 N_{pool} - 0.001 TN + 0.93 CEC + 1.80	83
	Vegetation Biomass Index (g)*	Ca, Mg, Na	0.003, 0.004, 0.004	LA, Cellulose (mg), Aerenchym, Lignin (mg), LM, Lignin (%)	0.000, 0.001, 0.001, 0.001, 0.002, 0.009	*Prionium serratum,* *Isolepis prolifera*	0.000, 0.003	Biomass Index = 0.35 Ca + 0.000014 LA + 0.56 Aerenchym + 0.53	47

The results from 2015 differed slightly, firstly in that 14 of the 25 ecosystem properties were normally distributed (**Table 1b**). Differences included the addition of total lignin (g/m^2) for flood attenuation, the loss of microbial biomass, the addition of Ca uptake capacity and K bioconcentration factor for water quality regulation and the loss of soil organic carbon for carbon sequestration. For the ecosystem service flood attenuation, community weighted means were the most important variables underpinning ecosystem properties, followed by abiotic variables with some idiosyncratic species effects. Cellulose content was mainly influenced by the community weighted mean cellulose (%), and when weighted by biomass was additionally related to soil bulk density. *Pteridium aquilinum* underpinned both ecosystem properties lignin content (%) and lignin weighted by biomass, but whereas the former was also related to community weighted mean lignin (%) the latter was also influenced by soil bulk density. Similarly to 2014, ecosystem properties DSi (%) and DSi weighted by biomass had low explained variance (26-40%). The former was underpinned largely by community weighted means for woodiness and SD, where the latter was determined by soil bulk density. Lastly, the ecosystem property vegetation biomass was underpinned by soil bulk density and the idiosyncratic species effects of *Prionium serratum*. Variables underpinning the ecosystem service water quality regulation were mainly abiotic with some idiosyncratic species effects. Soil base saturation was well explained (87%) by five different abiotic variables as well as the community weighted mean of vegetation hollowness. The ecosystem property K Bioconcentration Factor was underpinned by soil TN and TP and base saturation. Vegetation TP and Ca uptake capacity were not significantly influenced by any of the variables measured in this study. The presence of *Prionium serratum* influenced both K and Mg uptake capacity, though the former was additionally influenced by soil Ca and the community weighted mean specific leaf area. The ecosystem service carbon sequestration was mainly underpinned by abiotic variables. The ecosystem property total organic carbon was well explained (98%) by four abiotic variables and the community weighted mean for DSi.

Table 1b. Summary of significant results (P < 0.01) for general linear models of ecosystem properties from palmiet wetlands sampled in 2015 following steps 1–6 of the framework of Díaz et al. (2007). (*) indicates log transformed variables. SOC: soil organic carbon, TOC: total organic carbon, CEC: cation exchange capacity, BD: bulk density, SOM: soil organic matter, BS: base saturation, SWC: soil water content, SL: shoot length, SD: stem diameter, TB: total biomass, LLWR: leaf length-width-ratio, LM: dry leaf mass, LA: leaf area, SLA: specific leaf area, FEve: functional evenness, FDis: functional dispersion and RaoQ: Rao's entropy.

		Stage I: Individual effects of abiotic and biotic factors								Stage II: Combining significant effects into the best predictive model (Step 5: Final model)	
		Step 1: Abiotic factors		Step 2: Community weighted mean traits		Step 3: Trait distribution		Step 4: Idiosyncratic species effects			
Ecosystem Services	Ecosystem Properties	Variable	*P* value	Variable	*P* value	Variable	*P* value	Variable	*P* value	Model	% var
Water Regulation: Flood Attenuation	Cellulose Content (%)	BD, Ca, SWC	0.000, 0.005, 0.005	Cellulose (%), Cellulose (mg), Lignin (mg), LA, Lignin (%), C/N Ratio	0.000, 0.003, 0.004, 0.005, 0.006, 0.007			*Prionium serratum*	0.003	Cellulose Content = 0.67 Cellulose (%) + 15.38	45
	Cellulose in Vegetation (g/m^2)			Cellulose (%), Cellulose (mg), Lignin (mg), Lignin (%), LA, SLA	0.000, 0.000, 0.000, 0.000, 0.001, 0.001, 0.002			*Prionium serratum*	0.000	Cellulose in Vegetation = -577.05 BD + 41.79 Cellulose (%) - 204.42	57
	Lignin Content (%)*			Lignin (%), C/N Ratio, LLWR, Cellulose (%), LA, Cellulose (mg), Lignin (mg), Aerenchym	0.000, 0.001, 0.001, 0.001, 0.001, 0.002, 0.008, 0.009	FDis	0.004	*Pteridium aquilinum,* *Prionium serratum*	0.005, 0.006	Lignin Content = 0.02 Lignin (%) + 0.003 *Pteridium aquilinum* + 0.90	46
	Lignin in Vegetation (g/m^2)*	BD, N/P Ratio, pH_{KCl}, BS, C_{tot}, SOM, TN, CEC, Ca	0.000, 0.000, 0.000, 0.000, 0.001, 0.001, 0.005, 0.008, 0.009	SLA	0.002	FEve	0.003	*Pteridium aquilinum*	0.005	Lignin in Vegetation = -0.58 BD + 0.008 *Pteridium aquilinum* + 2.62	56
	DSi Content (mg/kg)*			Woodiness, DSi (mg/kg), SD	0.000, 0.002, 0.005					DSi Content = -0.43 Woodiness - 0.002 SD + 4.54	40

*Table 1b continued

Water Regulation: Flood Attenuation	DSi in Vegetation (g/m^2)*	BD, C_{tot}, SOM, pH_{KCl}, N/P Ratio, TN	0.001, 0.002, 0.003, 0.004, 0.004, 0.007			FEve	0.007			DSi in Vegetation = -0.45 BD + 1.20	26
	Vegetation Biomass Index (g)	BD, Ca, SWC	0.000, 0.004, 0.009	Cellulose (%), Cellulose (mg), Lignin (%), Lignin (mg), SLA, LA	0.000, 0.001, 0.001, 0.002, 0.002, 0.002			*Prionium serratum*	0.000	Vegetation Biomass Index (g) = -111.00 BD + 0.88 *Prionium serratum* + 189.50	53
Water Purification: Water Quality Regulation	Soil Base Saturation (%)	C_{tot}, TP, TN, pH_{KCl}, BD, K, N_{pool}, N/P Ratio, NH_4-N, PO_4-P, CEC, P_{pool}, C/N Ratio	0.000, 0.000, 0.000, 0.000, 0.000, 0.000, 0.000, 0.000, 0.000, 0.000, 0.001, 0.003, 0.005	SLA, LLWR, Hollowness	0.001, 0.005, 0.008					Soil Base Saturation = -0.01 C_{tot} - 0.0006 TP + 0.21 pH_{KCl} -0.04 NH_4-N + 0.02 CEC + 0.23 Hollowness + 0.43	87
	K Bioconcentration Factor *	TN, TP, C_{tot}, SOM, BS, N_{pool}, BD, C/N Ratio, pH_{KCl}, N/P Ratio, CEC, Ppool, Mg, NH_4-N	0.000, 0.000, 0.000, 0.000, 0.000, 0.000, 0.000, 0.000, 0.000, 0.001, 0.001, 0.002, 0.002, 0.002	DSi (mg), LLWR	0.001, 0.002			*Restio paniculatus*	0.007	K Bioconcentration Factor = 0.00002 TN + 0.0002 TP - 0.003 BaseSat + 0.19	71
	Veg. TP Uptake Capacity (mg/m^2)*									-	
	Veg. Ca Uptake Capacity (mg/m^2)*									-	
	Veg. K Uptake Capacity (mg/m^2)*	Ca, Mg, BD, SWC, K	0.000, 0.001, 0.002, 0.003, 0.003	Cellulose (mg), LA, Lignin (mg), Cellulose (%),SLA, Lignin (%),	0.000, 0.000, 0.000, 0.000, 0.000, 0.001			*Prionium serratum*	0.000	Veg. K Uptake Capacity = 0.004 *Prionium serratum* - 0.03 SLA + 0.30 Ca + 3.66	64

** Table 1b continued*

Water Purification: Water Quality Regulation	Veg. Mg Uptake Capacity (mg/m^2)			Cellulose (mg), Lignin (mg), LA, Cellulose (%)	0.001, 0.001, 0.003, 0.006			*Prionium serratum*	0.000	Veg. Mg Uptake Capacity = 27.81 *Prionium serratum* + 2202.03	36
Climate Regulation: Carbon Sequestration	Total Topsoil Organic Carbon (t/ha)*	N_{pool}, TN, C_{tot}, TP, BS, pH_{KCl}, K, N/P Ratio, BD, CEC, P_{pool}, C/N Ratio, Mg, Ca, NH_4-N, SWC	0.000, 0.000, 0.000, 0.000, 0.000, 0.000, 0.000, 0.000, 0.000, 0.000, 0.000, 0.000, 0.000, 0.006, 0.007, 0.008	DSi (mg), SLA, LLWR, LM	0.000, 0.000, 0.004, 0.005			*Restio paniculatus*	0.000	Total Topsoil Organic Carbon = 0.02 N_{pool} - 0.007 TN + 3.04 C_{tot} + 0.07 DSi (mg) - 0.02 P_{pool} + 2.13	98
	Vegetation Biomass Index (g)	BD, Ca, SWC	0.000, 0.004, 0.009	Cellulose (%), Cellulose (mg), Lignin (%), Lignin (mg), SLA, LA	0.000, 0.001, 0.001, 0.002, 0.002, 0.002			*Prionium serratum*	0.000	Vegetation Biomass Index (g) = -111.00 BD + 0.88 *Prionium serratum* + 189.50	53

6.4 Discussion

In terms of the final model results, soil variables seemed to be the most important in underpinning ecosystem properties, which makes ecological sense. However, biodiversity played an almost equally important role through influencing ecosystem properties by means of community weighted mean variables. Trait distribution (functional diversity indices) seemed to be of lesser importance, with only one index (functional dispersion) making it into any final general linear model. It has been postulated that where the relationship between ecosystem properties and community weighted means is poor, that other components of functional diversity may exert stronger relationships (Díaz et al., 2007). That seems to be the case in this study on palmiet wetlands. In most cases where significant relationships existed between functional diversity indices and ecosystem properties, there were poor relationships with community weighted means (e.g. lignin content (2014), lignin in vegetation (2015), DSi in vegetation (2015)) with the notable exception of lignin content in 2015. In that case there was a significant relationship with functional dispersion as well as eight community weighted mean variables. The most important functional diversity indices proved to be functional dispersion, as well as functional evenness. Some species played an important role in underpinning ecosystem properties, including *Searsia angustifolia* (for the ecosystem property lignin content, 2014), *Pteridium aquilinum* (lignin content and lignin in vegetation, 2015) and, most commonly, the wetlands namesake: *Prionium serratum* (vegetation biomass index, K and Mg uptake capacities, 2015). The comparison of results from two seasons showed relatively low consistency of the relationships between ecosystem properties and the various predictor variables. On the one hand, the types of variables explaining each ecosystem property did not differ substantially. For instance, DSi content weighted by biomass, was explained by the community weighted mean woodiness and stem diameter in 2014, compared to the community weighted mean DSi and stem diameter in 2015. All three community weighted means were related to the hardness and stem diameter of the vegetation in the community. Likewise, total organic carbon was mostly explained by abiotic variables for both years. On the other hand, some variables underpinning ecosystem properties changed type completely between the two seasons, such as the ecosystem property percentage of lignin content, which was mainly underpinned by soil variables in 2014 and conversely by one community weighted mean and one idiosyncratic species in 2015. Overall there was not a high level of agreement of variables underpinning ecosystem properties between years.

This finding raises questions as to how useful these relationships are. What amount of data per variable, and how many variables are necessary to quantify these relationships? One of the shortcomings of this study is that it may be that the variables necessary to explain each ecosystem property may not all have been measured. An additional shortcoming of this method may be that the link between ecosystem properties and ecosystem services are weak, and that ecosystem processes would be better to use in the future. A key example is that of the ecosystem service carbon sequestration. It would be far better to get a measurement of the flow (change over time) as opposed to the stock (vegetation biomass or soil organic carbon). Overall this lack of consistency between the two study seasons has implications for the usefulness of this method. There have been few studies to test this method, and the case study it was tested on was a sub-alpine grassland (Lavorel et al., 2011). It is possible that the relationships in wetlands may prove significantly more complicated to untangle.

6.5 Conclusion

For South African palmiet wetlands it appears that abiotic variables are slightly more important in underpinning ecosystem properties than biotic variables. However community weighted mean variables were almost as important in influencing final general linear models, whereas functional diversity indices seemed comparatively unimportant. Results were not highly consistent between the two seasons studied, and therefore it is concluded that either the relationships between ecosystem properties and functional diversity in wetland are more complicated than those of other ecosystems, or this method is not robust enough to estimate ecosystem properties, as multiple input variables can confuse the output models.

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6.8 Appendix

Table A1. The 17 plant functional traits collected for the 22 dominant wetland species. All methods were based on the standardised protocol of Pérez-Harguindeguy et al. (2013). For categorical traits the codes assigned are shown in brackets.

	Trait	Measurement method used	Unit	Scale
Morphological/ Anatomical Traits	Shoot Length	Average shoot length of 10 mature plants	mm	Ratio
	Stem Diameter	Average diameter of 10 stems at base level	mm	Ratio
	Total Biomass	Average value of total biomass divided by number of mature shoots (in case of a tuft or rhizome)	g	Ratio
	Leaf Length/Width Ratio (LLWR)	Ratio between the length and the width of a leaf based on an average of 10 leaves	mm/mm	Ratio
	Leaf Dry Mass	Average leaf mass after being oven dried at 60°C for 72 hours (10 leaves)	mg	Ratio
	Leaf Area	Area of a single surface of a leaf based on an average of 10 leaves	mm^2	Ratio
	Specific Leaf Area (SLA)	The total surface area of a leaf divided by its dry mass (based on an average of 10 leaves)	mm^2/mg	Ratio
	Presence of Aerenchym	Scale of 1 to 3 (1 = no aerenchym, 2 = less than 50% aerenchym, 3 = predominantly aerenchym)	Class	Ordinal
	Woodiness of Stem	Scale of 1 to 3 (1 = no woody tissue, 2 = less than 50% woody tissue, 3 = predominantly woody tissue)	Class	Ordinal
	Hollowness of Stem	Scale of 1 to 3 (1 = stem not hollow, 2 = hollow space less than 50%, 3 = hollow space more than 50%)	Class	Ordinal
Biochemical Traits	Leaf C/N Ratio	Mass ratio of carbon versus nitrogen	g/g	Ratio
	DSi Content	Biogenic silica was extracted from 25 mg dry plant (leaf and stem) material from 10 plants and analysed using ICP-OES	mg/kg	Ratio
	Absolute amount of DSi per leaf	DSi concentration multiplied by average dry leaf mass to get an amount of DSi per leaf	mg	Ratio
	Cellulose Content	Cellulose was measured by removing protein from 0.5-1 g of dry plant material from 10 plants, and by calculating mass before and after treatment with 72% sulfuric acid (Van Soest method)	%	Ratio
	Absolute amount of Cellulose per leaf	Cellulose content (%) multiplied by average dry leaf mass to get an amount of cellulose per leaf	mg	Ratio
	Lignin Content	Lignin was measured by taking the results of the sulfuric acid digestion and weighing it before and after ashing at 550°C (Van Soest method)	%	Ratio
	Absolute amount of Lignin per leaf	Lignin content (%) multiplied by average dry leaf mass to get an amount of lignin per leaf	mg	Ratio

Table A2. Hypotheses of how the selected plant functional traits would be expected to link to the three Ecosystem Service complexes. ↑ symbolizes a possible positive correlation, ↓ a negative correlation, → a non-directional relationship, and – signifies no relationship. *Italicized traits are categorical.* Relationships are taken from (Moor et al., 2017).

	Trait	Water quality regulation	Flood attenuation	Carbon sequestration	Total number of Ecosystem Services
Morphological/ Anatomical Traits	Shoot Length	-	↑	↑	2
	Stem Diameter	-	↑	↑	2
	Total Biomass	↑	↑	↑	3
	Leaf Length/Width Ratio	→	↑	-	2
	Leaf Dry Mass	→	↑	-	2
	Leaf Area	↑	↑	-	2
	Specific Leaf Area (SLA)	-	↓	-	1
	Presence of Aerenchym	-	↓	-	1
	Woodiness of Stem	-	→	-	1
	Hollowness of Stem	-	↓	-	1
Biochemical Traits	Leaf C/N Concentration	-		↑	1
	Si Concentration	-	↑	-	1
	Absolute amount of DSi per leaf	-	↑	-	1
	Cellulose Content	-	↑	↑	2
	Absolute amount of Cellulose per leaf	-	↑	↑	2
	Lignin Content	-	↑	↑	2
	Absolute amount of Lignin per leaf	-	↑	↑	2

Table A3. Summary statistics for each of the continuous plant functional traits derived from 22 dominant plant species in South African palmiet wetlands

	Plant Functional Trait	Mean	Min	Max	Median
Morphological/ Anatomical Traits	Shoot Length (mm)	1513.90	78.30	10500.00	1061.35
	Stem Diameter (mm)	38.76	0.13	450.00	11.13
	Total Biomass (g)	1280.86	0.20	15271.63	57.42
	Leaf Length/Width Ratio	12.97	0.00	88.40	2.80
	Leaf Dry Mass (mg)	2835.27	1.53	20430.00	146.14
	Leaf Area (mm^2)	3420.28	31.70	16032.50	507.55
	Specific Leaf Area (SLA) (mm^2/mg)	8.81	0.10	34.24	7.52
Biochemical Traits	Leaf C/N Ratio	42.71	16.61	85.86	40.29
	Si Content (mg/kg)	5045.75	80.00	31750.96	1328.03
	Absolute amount of DSi per leaf (mg)	7.99	0.00	87.03	0.37
	Cellulose Content (%)	29.60	15.67	44.91	29.01
	Absolute amount of Cellulose per leaf (mg)	505.39	0.35	4165.15	39.80
	Lignin Content (%)	14.41	1.33	45.24	11.83
	Absolute amount of Lignin per leaf (mg)	83.44	0.36	499.05	21.10

7

Can wetland plant functional groups be spectrally discriminated?

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Submitted

A fynbos community in the Goukou palmiet wetland, Western Cape, South Africa, illustrating some of the diversity in plant form. The spectacular orange *Watsonia angusta* is pictured in the foreground.

Abstract

Plant functional traits underpin ecosystem processes and therefore ecosystem service provision. If plant functional traits are possible to detect and discriminate spectrally, then it may be possible to use remote sensing applications to map ecosystem processes or services within and across landscapes. As a first step towards this application, we explored whether functional groups of 22 dominant South African wetland species were spectrally separable based on their plant functional traits. We measured 23 plant functional traits, both biochemical and morphological, and we collected reflectance spectra from 350-2349 nm using a handheld spectroradiometer. First, we evaluated the possibility of accurately predicting morphological and biochemical plant functional traits from reflectance spectra using three approaches: spectrum averaging, redundancy analysis, and partial least squares regression. Second, we established whether functional groups and species were spectrally distinguishable. We found leaf area, but not specific leaf area, to be a key plant functional trait in all three approaches. Leaf area correlated positively with reflectance spectra across the entire spectrum (r^2 = 0.41). Structural components, like lignin (r^2 = 0.54) and cellulose (r^2 = 0.49) content, were found to be important in at least two of the analyses, corresponding especially with the near-infrared portion of the spectrum. Four other plant functional traits were important in at least one of the analyses: leaf mass (r^2 = 0.41, RMSE -root mean square error- = 0.92), leaf length/width ratio (r^2 = 0.31, RMSE = 0.50), lignin concentration (%) (r^2 = 0.42, RMSE = 0.26) and the C/N ratio (r^2 = 0.62, RMSE = 0.13). Redundancy analysis suggests that there is a large percentage (52%) of the spectrum not explained by the plant functional traits measured in this study. Promisingly, however, functional groups, and even species, appeared to be spectrally distinguishable, mostly in the ultraviolet part of the spectrum. This has interesting applications for mapping plant functional traits using remote sensing techniques, and therefore for estimating related ecosystem processes and services.

7.1 Introduction

Plant functional traits are those characteristics of a plant that may both respond to (response traits), and shape (effect traits) their environment (de Bello et al., 2010; Tilman, 2001). It has been suggested that plant functional traits are the key ecological attributes by which organisms and communities affect ecosystem processes and functioning (Díaz et al., 2007; Lavorel et al., 2007). For example, plant functional traits such as leaf dry matter content and specific leaf area underpin soil fertility amongst others, whereas canopy size and architecture underpin climate and water regulation (Díaz et al., 2007). Since ecosystem processes are known to underpin ecosystem service provision, it is potentially possible to use plant functional traits to understand ecosystem service supply in ecosystems. Therefore mapping functional groups, species clustered according to plant functional traits, could potentially be used in mapping ecosystem services. Plant functional traits also determine the optical properties of plants, which can have important implications for remote-sensing applications.

Canopy reflectance is determined by leaf, stem, and litter optical properties as well as attributes of canopy structure (Ali et al., 2015; Asner, 1998; Ross, 1981). There has been much research on trees at each of these scales, both deciduous (Asner and Martin, 2008; Baltzer and Thomas, 2005) and coniferous (Marín et al., 2016), and less research on herbaceous species (Roelofsen et al., 2014). Herbaceous/under-storey vegetation presents an interesting case due to lower coherence of chemistry-reflectance relationships as a result of often not being in direct sunlight (Roelofsen et al., 2014). There is a need for more research on the link between plant functional traits and reflectance spectra for other ecosystem types, such as shrublands, grasslands and wetlands.

Leaves are optically interesting since plant species have differentially evolved unique properties to both optimise energy capture from the sun while minimizing sun damage and water loss. Leaf traits can influence their optical properties and the importance of specific traits in doing so varies within a species (Poona and Ismail, 2013), among growth forms (Klančnik et al., 2012) and between species (Katja Klančnik et al., 2014; Marín et al., 2016). Different plant functional traits also affect different regions of the spectrum, for example the cuticle affects reflection and absorption in the visible and ultraviolet ranges (Krauss et al., 1997), whereas leaf thickness affects reflection and transmittance in the near-infrared range (Knapp and Carter, 1998). Leaf pigments have been shown to affect the visible part of the spectrum (Asner and Martin, 2008; Klančnik et al., 2015a; Zhang et al., 2008).

There has been much research on the use of leaf reflectance to predict plant functional traits, both biochemical (Carter and Spiering, 2002; Castro and Sanchez-Azofeifa, 2008; Klančnik et al., 2015b; Marín et al., 2016; Roelofsen et al., 2014; Serbin et al., 2014; Zhang et al., 2008) and anatomical/morphological (Klančnik et al., 2015b; Marín et al., 2016). At the leaf scale, specific leaf area, an index of leaf density, has been shown to be highly correlated (r = 0.90) with the near infra-red and short-wave infrared part of the leaf spectrum for tropical forests (Asner and Martin, 2008), and coniferous trees (Lukeš et al., 2013), but poorly related ($r^2 = 0.26$) for herbaceous species (Roelofsen et al., 2014). Leaf dry matter content is well correlated with reflectance ($r^2 = 0.67$), even for herbaceous species (Roelofsen et al., 2014). Other studies have found biochemical plant functional traits to be more important for explaining spectral variation in aquatic plants, and morphological plant functional traits more important for terrestrial plants (Klančnik and Gaberšcik, 2016). Specifically trichome density and the thickness of the epidermis were most important in influencing the reflectance spectra of wetland species (Klančnik et al., 2015b). For aquatic plants, chlorophyll a and b and specific leaf area cumulatively explained 60% of the reflectance spectra (Klančnik et al., 2015b). More plastic plant functional traits, such as nutrients in plant tissues also affect reflectance (Asner and Martin, 2008; Baltzer and Thomas, 2005; Lukeš et al., 2013; Roelofsen et al., 2014; Serbin et al., 2014), as does tissue water content (Asner and Martin, 2008). It is important to establish the key plant functional traits influencing reflectance at various scales in different ecosystems.

We analysed plant functional traits and spectra of dominant species in a South African palmiet wetland system to determine whether any relationships could be used to map functional groups. Wetlands are key ecosystems where understanding ecosystem function, and quantifying ecosystem services, are important for society (Rebelo et al., 2015). Wetlands are also extreme environments that have distinct community patterns, such as monospecific dominance in patches, making them interesting and important case study systems (Sieben, 2012). We ask two main research questions: can plant (or canopy)-level reflectance be used to predict morphological and biochemical plant functional traits in wetland vegetation? and; are wetland communities spectrally distinguishable (by functional groups, species)? If clear relationships exist between plant functional traits and spectra of these wetland species, then it may be possible to use hyperspectral methods to map ecosystem service hotspots in these wetlands.

7.2 Methods

Study wetlands

South African palmiet wetlands are small valley-bottom systems underlain by 0.5 to 10 m of peat and occurring throughout the Cape Floristic Region of South Africa, a biodiversity hotspot (Job, 2014; Nsor, 2007). Due to their position in important strategic water-providing catchments in South Africa (Nel et al., 2011), and their peat accumulation, they are thought to provide important ecosystem services to society (Rebelo et al., 2015). Palmiet wetlands are so named after the species that dominates them: *Prionium serratum*, or Palmiet, thought to be an ecosystem engineer (Sieben, 2012). However other plant communities occur within these wetlands, giving them a patchy appearance that may be possible to classify using hyperspectral remote-sensing techniques. In this study, dominant species were determined from vegetation surveys in three palmiet wetlands: Theewaterskloof, Goukou and Kromme (**Fig. 1**). In places the wetlands have become invaded by alien weeds, such as Bramble (*Rubus fruticosus*), as well as trees such as Black Wattle (*Acacia mearnsii*). These palmiet wetlands typically occur at elevations of 100-400 masl, with mean annual precipitation ranging from ±614 mm (Kromme) to ±600-1000 mm (Goukou) to ±1600-2000 mm (Theewaterskloof) (Job, 2014; Midgley et al., 1994; Rebelo et al., 2006).

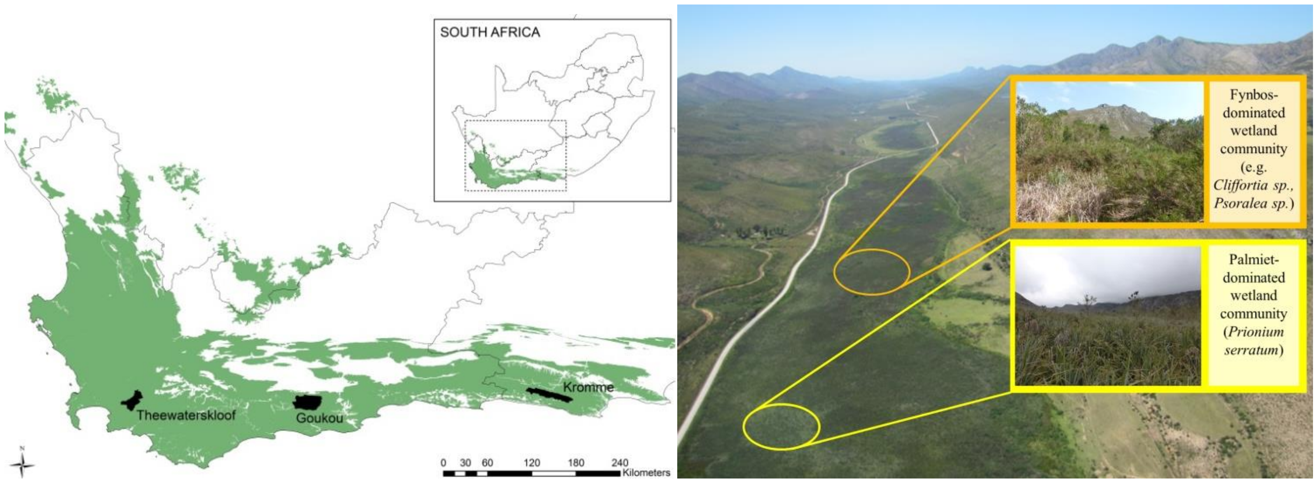

Figure 1. (Left) The catchments of the three study palmiet wetlands, located within the Cape Floristic Region of South Africa (shown in green). (Right) The Kromme Palmiet wetland, showing the patchy nature of the vegetation communities (light gray and dark green), with the two main plant communities indicated and described.

Study design

Species composition data were obtained from 39 plots in the three different palmiet wetlands. Plots were arranged on transects (100-200 m) along cross sections through the wetlands, with six plots (3x3 m) placed between 20-50 m apart, yielding a total of 36 plots. In the Goukou wetland, three extra plots were added to fully capture variation in plant communities. Species and their relative abundances were recorded in each plot, using the Braun-Blanquet Scale (Mueller-Dombois and Ellenberg, 1974). Dominant species were defined as those making up more than 25% cover in any plot. The resultant 22 species are listed in **Table A1**, and shown in **Plate A1**. Ten mature specimens from each dominant species were collected from their wetland of origin for measurement of plant functional traits at the respective field station or in the lab (depending on the trait). Traits were collected once for each species from random specimens in the field (maximum abundance approach, Carmona et al. 2015). Extra specimens were collected from one of the three sites for each species (**Table A1**).

Plant functional traits

We measured 23 plant functional traits, each selected as they were predicted to have a link to at least one wetland ecosystem service (**Table A2**). Definitions and methods for the measurements of each plant functional trait are given in **Table A3**; and for all commonly used plant functional traits we used the standardized protocol for measurements (Pérez-Harguindeguy et al., 2013). Of the plant functional traits measured, 16 were morphological/anatomical, and seven were biochemical in nature (**Table A3**). For biochemical plant functional traits, samples were cleaned, dried at 70°C for 48 hours, ground and homogenised using a mill to 0.5 mm particles. Total carbon and total nitrogen were determined by total combustion of 5 mg of each sample on a Flash 2000 CN-analyzer (Thermo Fisher Scientific). To determine plant silicon content, we used a procedure for extracting biogenic silica (Schoelynck et al. 2010), which involved incubating a 25 mg sample of dried plant material in a 0.1 m Na_2CO_3 mixture which was placed in a water bath at 80°C for 4 hours. This dissolved biogenic silica was then spectrophotometrically analysed on a Thermo IRIS inductively coupled plasmaspectrophotometer (ICP; Thermo Fisher, Franklin, MA, USA). Plant lignin and cellulose content were measured using the Van Soest method (Van Soest, 1963). Summary statistics are shown for each of the continuous plant functional traits in **Table A4**.

Reflectance measurements

Plant canopy spectra were measured in the field in November 2015 under clear sky conditions within two hours of local solar noon. All reflectance measurements were taken with a portable ASD Fieldspec Pro (ASD Inc., Boulder, USA). The probe was held at a constant distance of 60 cm above the surface (25° FOV; diameter 26.59cm), keeping the sensor perpendicular to the angle of the sun. Live (wet) specimens from each species were arranged on a large matt black (non-reflective: uniform<5% reflectance across the 350-2500 nm range) surface (1.5x2 m), with leaves facing upwards (adaxial surface up) where possible. This measurement set-up allowed us to measure the reflectance of individual plant species without background contamination originating from soil or other plant species. This set-up thus allowed us to make a one-on-one comparison between reflectance and plant functional traits. It is acknowledged that the spectral effects of 3D canopy structure (i.e. volume scattering effects) were not fully captured with this set-up. Since this study focussed primarily on leaf traits, this is not expected to present any problems.

Twenty spectral signatures were collected for each species. There were two cases where data had to be excluded due to equipment problems (see **Table A1** for details). Between readings for each species, the ASD was optimised using a spectralon (Spectralon®, Labsphere, North Sutton, USA) and white reference measurements were captured. Spectra were collected over the range of 350-2500 nm with 1 nm intervals. ASD binary files were first converted to ASCII reflectance files using ViewSpecPro and subsequently post-processed to remove data in the water absorption bands at 1350-1460 nm and 1790-2000 nm as well as noise at 2350-2500 nm.

Analysis

Analysis was carried out in two stages; first, plant-level reflectance was assessed for use in predicting morphological and biochemical plant functional traits, and second, wetland communities were assessed to determine whether they are spectrally distinguishable, and to what level (functional groups, species).

(i) Predicting morphological and biochemical traits from reflectance

To determine whether it was possible to predict morphological and biochemical plant functional traits from plant reflectance spectra, we first used an approach similar to that of Knapp & Carter (1998) to relate spectra to plant functional traits by reducing the spectrum to four average reflectance values: visible (400-700 nm), near infra-red (700-1000 nm), short-wave infrared (1000-2349 nm), and the total measured spectra (350-2349 nm). Simple regression analyses in R were used to determine the relationships between the averaged spectra and plant functional traits. Second, we performed a redundancy analysis using the 'Vegan' package in R to determine whether the reflectance spectra (response variables) could be explained by various plant functional traits (explanatory variables). For this analysis, the reflectance spectra were divided into 11 categories and averaged: the four categories listed above (visible, near infra-red, short-wave infrared and total) as well as ultraviolet (320-399 nm), violet (400-424 nm), blue (425-491 nm), green (492-575 nm), yellow (576-585 nm), orange (586-647 nm), and red (648-699 nm). All variables were standardised for the analysis, and categorical plant functional trait data were excluded. Forward selection of explanatory variables was used to avoid co-linearity between variables (threshold: $r^2 > 0.7$). Variable inflation factors of greater than 10 were used to exclude other collinear variables to obtain the most parsimonious redundancy analysis. The significance of the redundancy analysis was assessed using an ANOVA-like permutation test for redundancy analysis in R, with 1000 permutations (Legendre et al., 2011).

Lastly we performed a partial least squares regression using the 'pls' package (Mevik and Wehrens, 2007) and 'autopls' code (Feilhauer et al., 2010) in R to determine which plant functional traits could be predicted from the reflectance spectra. The advantage of partial least squares regression over other types of regression is its ability to deal with a high number of predictors (in this case spectral bands) relative to a low number of observations (i.e. each plant functional trait) as well as handle collinearity of these predictors. We averaged reflectance spectra to obtain 5 nm intervals over the measured range from 350-2349 nm, yielding a total of 336 predictors. We performed partial least squares regression for each of the 14 measured continuous plant functional traits, which were log transformed. Collinearity of spectral bands is dealt with by transferring information content to independent latent variables which are optimised to represent the response variable. In each model, the number of latent variables was chosen so as to minimise the root mean square error using leave-one-out cross-validation. Each ordination axis was modelled separately (calibrated) and then validated, and regression coefficients were calculated in each case, and predictors are left out iteratively until an optimum was reached. Backward selection of predictors was used to further optimise the model by a combination of removing correlated bands and jack-knifing. All other settings were left at the default, following the method of Feilhauer et al. (2010). Model accuracy is expressed by both the root mean square error and the coefficient of determination r^2 which compares observed and predicted values for the calibration and validation phases.

(ii) Discriminating wetland communities

To determine at what level wetland communities are spectrally distinguishable, we compared the effectiveness of discriminating individual species with that of discriminating functional groups. We determined functional and spectral groups of the 22 dominant species using two-step cluster analysis in SPSS (SPSS, 2001), which is able to handle both categorical and continuous data. All variables were standardised and the log-likelihood distance measure was applied for plant functional traits, and the Euclidean distance measure for spectra (**Table A6**). The threshold for number of functional and spectral groups was determined using a K-means partitions comparison and Calinski criterion, as well as a Scree plot in R. The importance of various plant functional traits in influencing the functional groups was assessed using a predictor analysis in SPSS. To assess how well functional groups and species could be discriminated, we used two approaches.

Firstly we compared functional groups and species to spectral groups generated using reflectance spectra, in a confusion matrix and assessed coherence. We did this by estimating 'spread' of functional groups throughout the spectral groups. If each functional group corresponded with its distinct spectral group, we would expect to see low spread in the confusion matrix, i.e. only 6 out of the 36 blocks in the grid would be occupied (6 blocks occupied is the minimum). However a poor agreement (high spread), could mean that 22 of the 36 blocks were occupied (22 species is the maximum). Therefore discrimination accuracy was calculated by expressing the number of occupied blocks scaled between 0 and 16 (n) as a percentage, and inverting it; i.e: discrimination accuracy = 100-(100n/16). Secondly the spectral separability between each functional group and among species was calculated using the M-Statistic for four parts of the spectrum: visible (400-700 nm), near infra-red (700-1000 nm), short-wave infrared (1000-2349 nm), and the total measured spectra (350-2349 nm). The M-Statistic is calculated by dividing the difference of the means of spectra of the two species or functional groups being compared, by the sum of their standard deviations (Kaufman and Remer, 2002). In the case of species, each species was compared with an average of all other species. A value of M<1 signifies that the distributions significantly overlap and the ability to discriminate the two groups is poor, whereas a value of M>1 signifies that there is little overlap and the ability to discriminate the two groups is good.

7.3 Results

Predicting morphological and biochemical plant functional traits from spectral reflectance

Only four plant functional traits showed reasonably strong relationships with various parts of the spectrum. Biochemical plant functional traits such as cellulose content and lignin content were reasonably well correlated with the near infra-red part of the spectrum (**Fig. 2; Table A5**). Morphological plant functional traits, such as leaf area and mass, on the other hand correlated more weakly with the total reflectance spectrum.

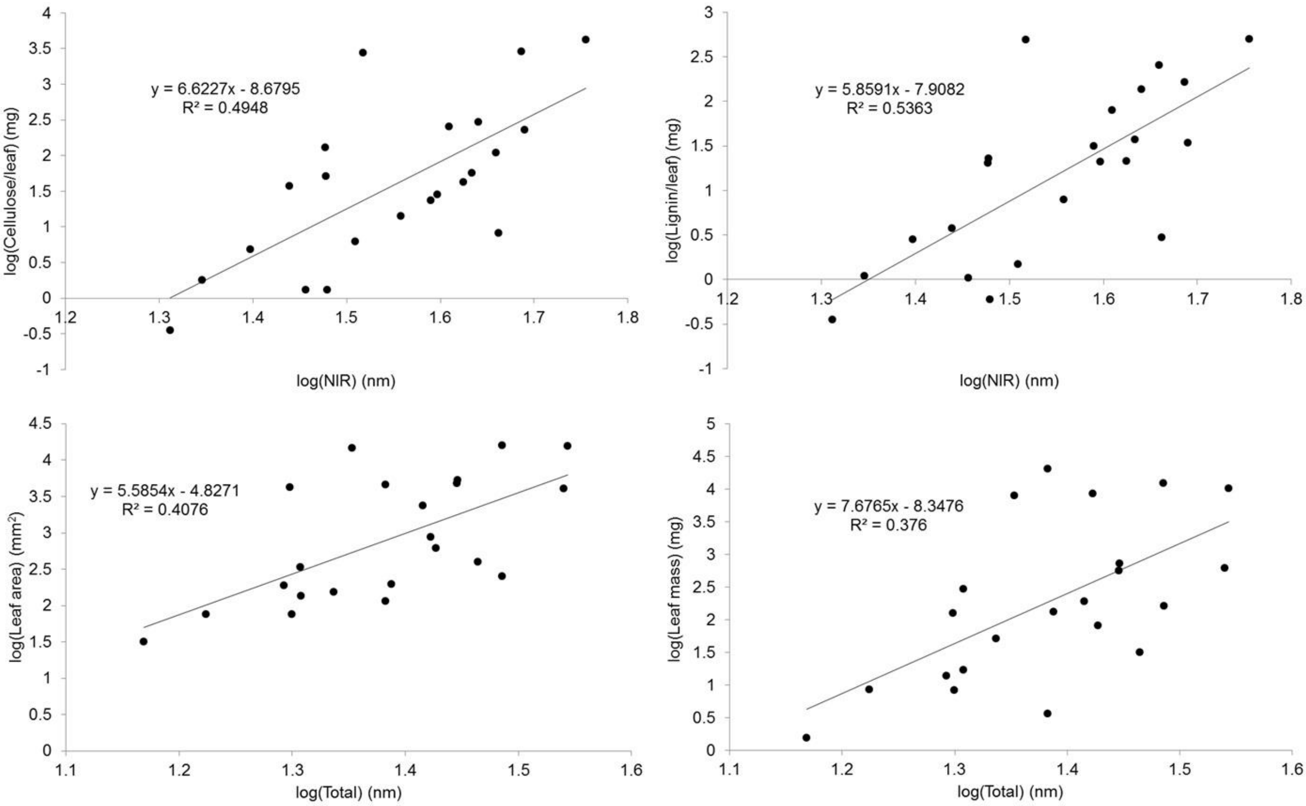

Figure 2. The relationship between the log of four key morphological (leaf area, leaf mass) and biochemical (cellulose content, lignin content) plant functional traits and the log of averaged sections of the reflectance spectra (near infra-red: 700-1000 nm, Total: 350-2349 nm) for 22 South African wetland species.

A redundancy analysis suggested that four plant functional traits were most important in explaining reflectance spectra of the 22 dominant wetland species investigated: leaf area, the leaf length/width ratio, specific leaf area and lignin concentration (**Fig. 3**). Together these plant functional traits explained 48% of the variation in the spectra. Of these plant functional traits, only one was biochemical, suggesting that of the plant functional traits measured, morphological plant functional traits exerted more influence on the reflectance spectra. Leaf area and leaf length/width ratio were strongly positively correlated with reflectance, whereas specific leaf area and lignin concentration were weakly negatively correlated.

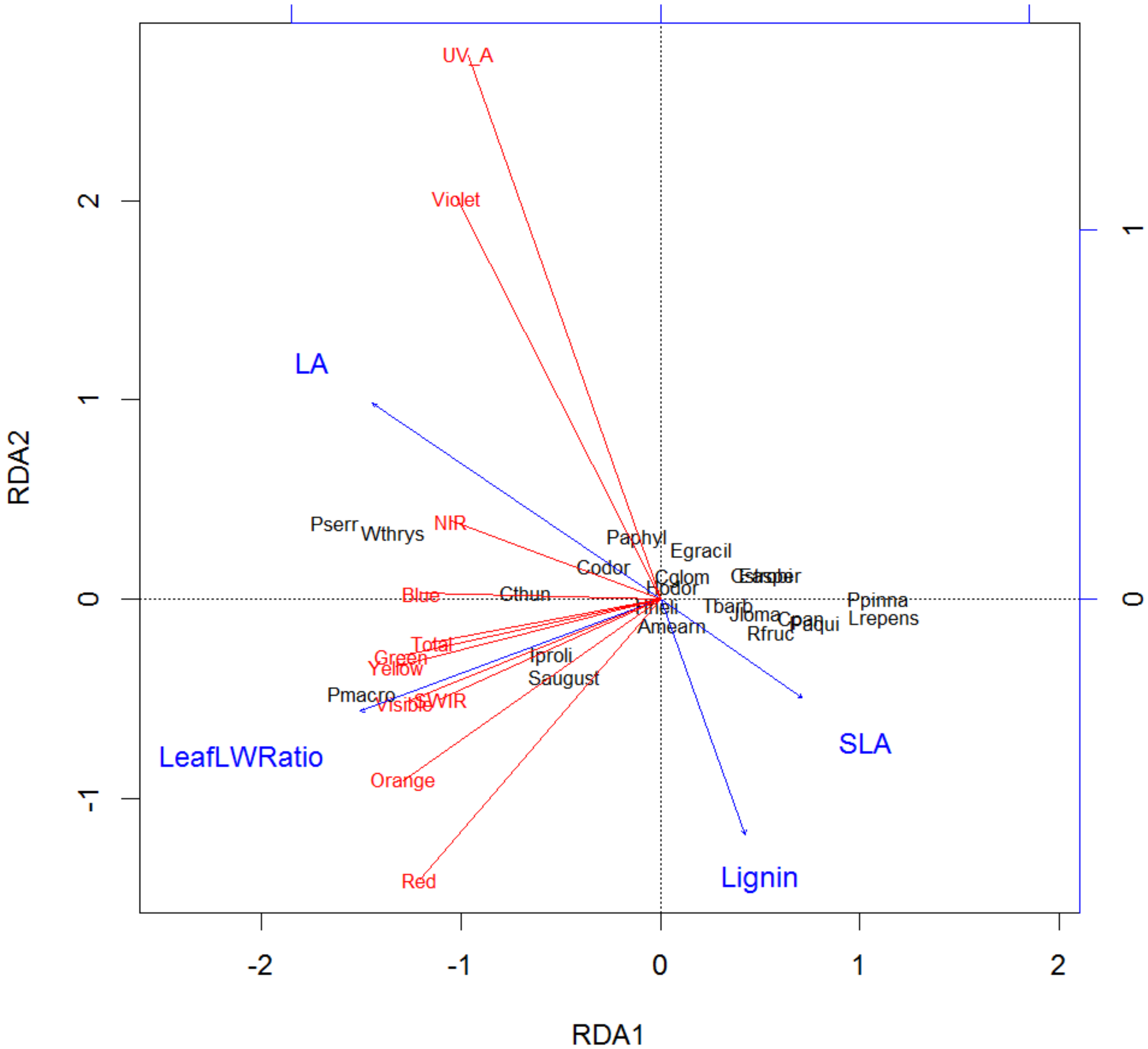

Figure 3. The redundancy analysis plot presenting the strength of associations between anatomical and biochemical parameters and different regions of the reflectance spectra for 22 South African wetland species. Eigenvalues for the first two axes were 4.77 and 0.41 respectively, and only the first axis was significant. Species abbreviations are given in black (see Table A1 for full names). The various regions of the spectrum are given in red. Abbreviations for the most important plant functional traits influencing the model are given in blue: LA: leaf area (mm^2), SLA: specific leaf area (mm^2/mg), LeafLWRatio: leaf length-width ratio and Lignin: lignin concentration (%).

Only one of the 14 continuous plant functional traits investigated using partial least squares regression was predicted from the reflectance spectra with high accuracy, and this was cellulose content (r^2_{cal} = 0.88) (**Table 1, Fig. 4**). However this model also had the highest number of latent variables (7), suggesting a complex, non-linear relationship (high information content). Leaf C/N ratio was predicted with average accuracy (r^2_{cal} = 0.62), and two other plant functional traits (lignin content and leaf area) were weakly predictable from the reflectance spectra (r^2_{cal} = 0.52, and r^2_{cal} = 0.42 respectively).

Table 1. Model performance parameters for partial least squares regression of predicting plant functional traits from reflectance spectra of 22 South African wetland species. Abbreviations: nlv is the number of latent variables, r^2, the coefficient of determination, is given for model calibration (cal) and validation (val), as is RMSE: the root mean square error.

	Plant Functional Traits	nlv	r^2_{cal}	r^2_{val}	$RMSE_{cal}$	$RMSE_{val}$
Morphological Traits	Shoot Length	2	0.15	-0.40	0.47	0.60
	Stem Diameter	2	0.16	-0.08	0.66	0.75
	Total Biomass	2	0.16	-0.06	1.26	1.41
	Leaf Length/Width Ratio	2	0.31	0.01	0.50	0.60
	Leaf Dry Mass	2	0.41	0.13	0.92	1.11
	Leaf Area	2	0.42	0.19	0.63	0.75
	Specific Leaf Area	2	0.19	-0.22	0.57	0.70
Biochemical Traits	Leaf C/N Ratio	5	0.62	0.38	0.13	0.17
	Si Concentration	2	0.25	-0.04	0.61	0.72
	Si Content	2	0.36	-0.30	1.09	1.56
	Cellulose Concentration	2	0.39	0.21	0.09	0.10
	Cellulose Content	7	0.88	0.68	0.37	0.62
	Lignin Concentration	2	0.42	0.18	0.26	0.31
	Lignin Content	2	0.52	0.36	0.64	0.74

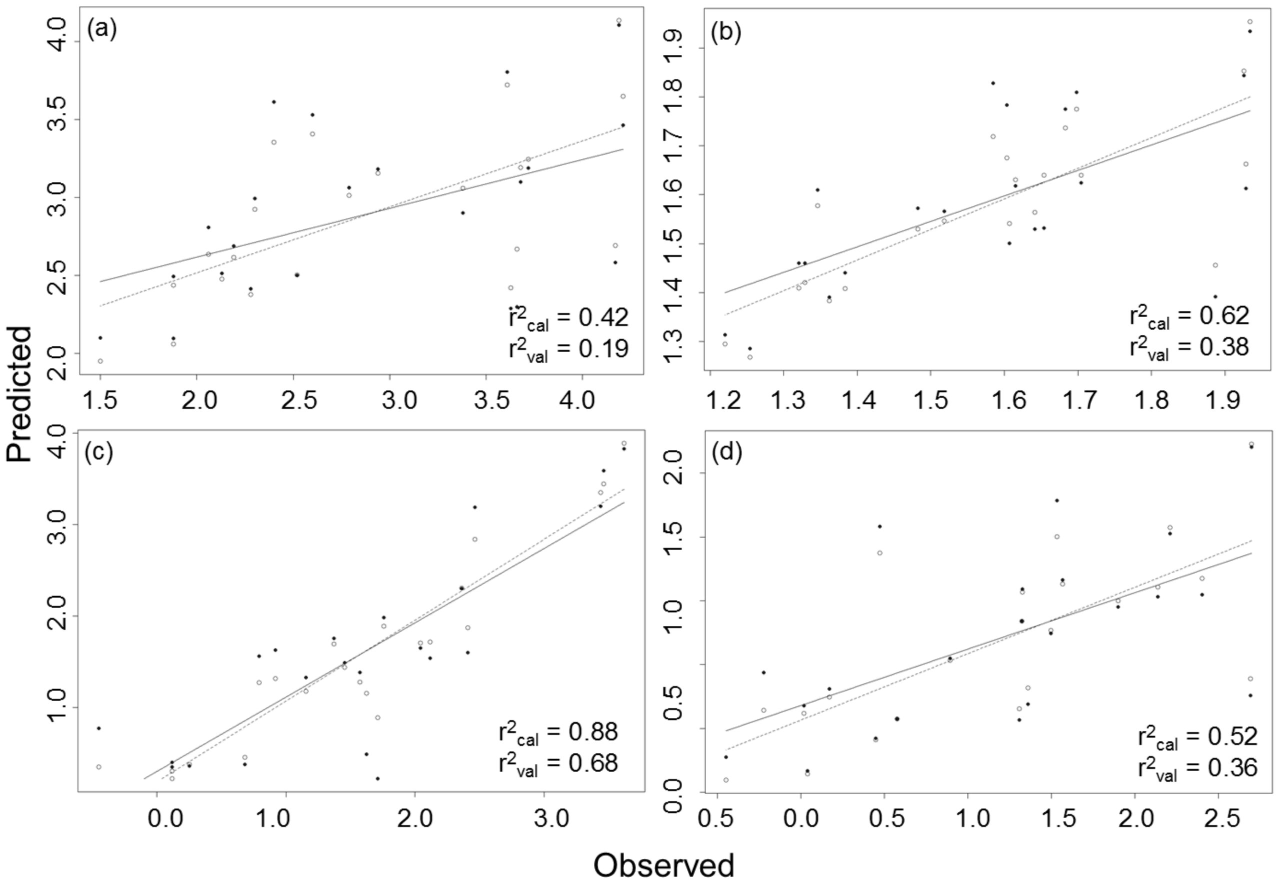

Figure 4. Observed and predicted plant functional trait values from reflectance spectra using partial least squares regression for 22 South African wetland species. The coefficient of determination (r^2) is given for both model calibration (○) and validation (●). Plant functional traits (all log transformed) are: (a) leaf area, (b) C/N ratio, (c) cellulose content, and (d) lignin content.

Overall, the results suggest that there are eight plant functional traits of those measured that influence optical properties to some degree: four morphological plant functional traits (leaf area, leaf mass, specific leaf area, leaf length-width ratio) and four biochemical plant functional traits (lignin concentration, cellulose content, lignin content, C/N ratio).

Discriminating wetland communities

For both functional and spectral groups, K-means partitions and scree plots indicated that the optimal number of groupings was six. For functional groups, species were relatively well spread, with an average of four (±1.3) species per group (**Table A6**). Spectral groups were less well spread, with one large group containing nine species (**Table A7**). The ten most important plant functional traits driving functional groups were (in decreasing order of importance): cellulose content, leaf area, leaf orientation, leaf type, leaf length-width ratio, lignin content, C/N ratio, rooting type, woodiness and clonal strategy. Functional groups seem to make sense ecologically, and the six groups can be broadly described as: (1) woody species with small simple leaves with medium surface area and medium cellulose content, (2) woody species with larger simple leaves with smaller surface area and low cellulose content, (3) ferns; with pinnatifid leaves (low leaf area), and low cellulose content, (4) less woody species with no true leaves, and medium cellulose content, (5), herbaceous species (non-woody) with long broad leaves (high area) but low cellulose content, and (6) herbaceous species (non-woody) with long broad leaves (high area) but high cellulose content. The two most important plant functional traits: cellulose content and leaf area, correspond well with those shown to be predictable from the reflectance spectrum.

The ten most important reflectance spectra driving spectral groupings were all in the range 530-615 nm, the visible (green, yellow, orange) part of the electromagnetic spectrum, suggesting that photosynthetic pigments are the most important plant functional traits determining spectral separability of species. Interestingly spectral group 5 corresponds well to functional group 6, containing two species in common: the ecosystem engineer *Prionium serratum* and *Wachendorfia thyrsiflora* (both broad-leaved species).

A confusion matrix comparing functional and spectral groups suggests that there is not high coherence between functional groups and spectral groups, with 37.5% overall discrimination accuracy (**Table 2**). The large spectral group (1), for example, is composed of 6 different functional groups. Specific functional groups (3 and 6) are marginally distinguishable spectrally (functional groups split into only two spectral groups in each case).

Table 2. Confusion matrix displaying the spectral separability of functional groups. The numbers in the matrix represent number of species.

		Spectral Group 1	2	3	4	5	6
Functional Group	1	2	2				
	2	2	2	1			1
	3	1	1				
	4	2		1			1
	5	1			1		1
	6	1				2	

According to the calculated spectral separability index (M-Statistic), most of the functional groups are best discriminable in the ultraviolet part of the spectrum (**Table 3**). The only exception is functional group 3 (ferns) and 6 (broad-leaved species) which are additionally separable using the visible part of the spectrum. Only two of the functional groups were problematic to separate, and these were functional groups 1 and 4. Sixteen out of the 22 species were highly spectrally distinguishable, mainly in the ultraviolet part of the spectrum (**Table 4**). Only three species were a challenge to discriminate from the rest: *Cliffortia strobilifera*, *Elegia asperiflora*, and *Helichrysum helianthemifolium*. *Laurembergia repens* was additionally spectrally distinct from the other species in the near infra-red part of the spectrum, and *Psoralea pinnata* in the visible.

Table 3. The M-Statistic for five sections of the spectrum for comparisons between each of the six functional groups of South African wetland species. A value of M<1 signifies that the histograms significantly overlap and the ability to discriminate the two regions is poor, whereas a value of M>1 (highlighted in table) signifies that there is little overlap and the ability to discriminate the two regions is good.

Functional Group	Ultraviolet (350-400 nm)	Visible (400-700 nm)	Near Infra-red (700-1000 nm)	Short-wave Infrared (1000-2349 nm)	Total (350-2349 nm)
FG1-2	0.61	0.32	0.07	0.04	0.02
FG2-3	1.70	0.47	0.21	0.04	0.01
FG3-4	2.20	0.33	0.21	0.07	0.02
FG4-5	0.91	0.63	0.30	0.13	0.12
FG5-6	3.10	0.12	0.37	0.02	0.05
FG1-3	2.30	0.18	0.14	0.00	0.01
FG1-4	0.09	0.17	0.07	0.07	0.04
FG1-5	1.05	0.82	0.22	0.20	0.15
FG1-6	4.50	0.96	0.56	0.21	0.20
FG2-4	0.65	0.14	0.01	0.03	0.01
FG2-5	1.56	0.53	0.30	0.16	0.13
FG2-6	5.00	0.66	0.65	0.17	0.18
FG3-5	2.96	0.92	0.06	0.19	0.13
FG3-6	6.28	1.06	0.40	0.20	0.18
FG4-6	4.17	0.77	0.65	0.15	0.17

Table 4. The M-Statistic for five sections of the spectrum for comparisons between each of the 22 South African wetland species. A value of M<1 signifies that the histograms significantly overlap and the ability to discriminate the species is poor, whereas a value of M>1 (highlighted in table) signifies that there is little overlap and the ability to discriminate species is good. In each case the species listed was compared with all other species together.

Species	Ultraviolet (350-400 nm)	Visible (400-700 nm)	Near Infra-red (700-1000 nm)	Short-wave Infrared (1000-2349 nm)	Total (350-2349 nm)
Acacia mearnsii	2.40	0.16	0.44	0.10	0.10
Carpha glomerata	0.83	0.07	0.24	0.09	0.08
Cliffortia odorata	1.25	0.04	0.45	0.14	0.13
Cliffortia strobilifera	0.19	0.45	0.50	0.20	0.17
Cyperus thunbergii	1.58	0.50	0.22	0.13	0.11
Elegia asperiflora	0.48	0.52	0.27	0.21	0.15
Epischoenus gracilis	1.46	0.13	0.44	0.21	0.17
H. helianthemifolium	0.03	0.07	0.42	0.04	0.02
H. odoratissimum	1.14	0.15	0.81	0.22	0.20
Isolepis prolifera	0.60	0.31	0.35	0.26	0.18
Juncus lomatophyllus	1.37	0.29	0.61	0.19	0.18
Laurembergia repens	4.67	0.86	1.11	0.43	0.38
Psoralea aphylla	2.25	0.07	0.34	0.03	0.05
Pteridium aquilinum	4.42	0.75	0.04	0.14	0.10
Pennisetum macrourum	0.78	0.90	0.63	0.39	0.30
Psoralea pinnata	3.44	1.09	0.96	0.33	0.31
Prionium serratum	6.20	0.97	0.93	0.29	0.28
Restio paniculatus	3.15	0.85	0.38	0.07	0.02
Rubus fruticosus	3.99	0.68	0.27	0.04	0.04
Searsia augustifolia	2.17	0.52	0.12	0.08	0.07
Todea barbara	1.43	0.37	-0.15	0.03	0.01
Wachendorfia thyrsiflora	4.70	0.78	0.63	0.17	0.18

7.4 Discussion

Clear relationships were established between wet-material reflectance spectra and certain plant functional traits of 22 dominant South African wetland species, both herbaceous and woody. These relationships are relatively strong considering that reflectance spectra and plant functional traits were measured on different specimens, suggesting that using reflectance spectra to characterise plant functional traits in these systems is feasible. This presents significant opportunities for plant functional trait prediction or mapping in these wetland systems, using imaging spectroscopy or hyperspectral remote sensing techniques.

Relationships between leaf traits and spectra

There was some commonality between the results of the three approaches used to explore plant functional trait/reflectance relationships: regressions, redundancy analysis and partial least squares regression. For example, leaf area was consistently found to be a key plant functional trait, in all three analyses. Leaf area was strongly, positively correlated with reflectance spectra, though according to the regression results the entire spectrum was important – no particular region stood out. Interestingly, specific leaf area was only found to be an important plant functional trait by the redundancy analysis, and showed a weak negative relationship with reflectance spectra, especially in the near infra-red region. This is in contrast with other studies, for example on aquatic and wetland plants, where specific leaf area was found to be strongly positively correlated with reflectance spectra (Klančnik et al. 2014, Klančnik et al. 2015). One possible reason for this weak relationship between specific leaf area and reflectance spectra in the near infra-red region could be the loss of 3D information as a result of our measurement set-up (Ali et al., 2015; Ross, 1981). On the other hand, other studies have successfully found relationships between specific leaf area and leaf dry matter content using only leaf level spectra, without any information on plant architecture/canopy structure (Ali et al., 2015).

Structural components, lignin and cellulose content, were shown to be important by two analyses (the regressions and the partial least squares regression), corresponding especially with the near infra-red portion of the spectrum. A study on northern temperate and boreal tree species identified lignin and cellulose to be plant functional traits that scale well in reflectance-trait models (leaf to canopy scale (Serbin et al., 2014)). Four other plant functional traits were found to be important by only one of the three analyses: leaf mass, leaf length/width ratio, lignin concentration and the C/N ratio. Overall the redundancy analysis suggests that there is a large fraction (over half) of the variation in the spectra not explained by the plant functional traits measured in this study. This has implications for future ecological studies with remote-sensing application: important plant functional traits to measure may include photosynthetic pigments, or correlates, such as leaf thickness. There have been several studies investigating the importance of biochemical leaf traits in explaining reflectance spectra specifically. These studies suggest that chlorophyll a and b, together with specific leaf area account for most of the spectral variability in aquatic plants (Klančnik et al. 2014), as well as trichome length, leaf mass and anthocyanin content per dry mass (Klančnik et al., 2012). For wetland species, total mesophyll and spongy tissue thickness were found to be important as well as leaf prickle hair properties and epidermal thickness for monocots, and leaf thickness and specific leaf area for dicots (Klančnik and Gaberšcik, 2016). Other factors such as epiphyton and silicified structures were also shown to affect reflectance spectra in macrophytes (Katja Klančnik et al., 2014; Klančnik et al., 2015a).

Predicting leaf traits from spectra

Overall biochemical plant functional traits were more successfully predicted from reflectance spectra than morphological plant functional traits. Expressing biochemical parameters per leaf mass (content rather than concentration) improved its predictive ability from the reflectance spectrum, similar to findings of another study with expressing foliar nutrients per leaf area (Roelofsen et al., 2014). Measuring only leaf spectra, they found weak relationships between morphological properties of herbaceous species, such as specific leaf area, but stronger relationships for particular biochemical plant functional traits, such as leaf nitrogen content. In contrast, leaf dry matter content, which we did not measure, was found to be well predicted from reflectance and transmittance spectra (Roelofsen et al., 2014). Since our study as well as Roelofsen et al. (2014) also only measured leaf/stem spectra, the lack of 3D information in our spectral measurements may be a cause for the weak relationships found between spectra (particularly in the near infra-red region) and certain morphological plant functional traits relating to plant size or growth form, such as biomass, stem diameter and plant height (Ali et al., 2015; Ross, 1981).

Leaf reflectance for forest (top of canopy) species however, were strongly related to morphological plant functional traits. For example specific leaf area, or its inverse (leaf mass per area), were well predicted by reflectance spectra for forest species, with the correlation co-efficient ranging from 0.79 to 0.91 (Asner et al., 2011; Asner and Martin, 2009, 2008; Serbin et al., 2014). For carbon containing compounds, such as cellulose, lignin and photosynthetic pigments, Asner et al., (2011) were able to successfully project leaf spectra to the canopy level. This suggests that it may well be possible to map these plant functional traits at an ecosystem scale using remote-sensing techniques. This study investigated relatively few plant species (22) relative to previous studies (e.g. 35 in Roelofsen et al. (2014) and hundreds of samples in other studies (Asner et al., 2011; Serbin et al., 2014)). The reason for this low number of species is the high level of monospecific dominance in these wetland communities. A low number of species limits the power of the partial least squares regression models, therefore in more diverse systems including more species may reveal more clear relationships. Overall our results suggest that it may be possible to use spectroscopic methods to quantify certain plant functional traits, including certain morphological plant functional traits (leaf area), structural components (lignin, cellulose) and nutrients (C/N ratio) in South African wetlands, based on information from dominant species. However it is also possible that species, or functional groups, should be distinguishable within wetland communities, based on the findings that certain plant functional traits are related to reflectance spectra, despite intra-specific variation.

Applications for using plant functional traits-reflectance spectra relationships to map ecosystem service hotspots

It appears feasible to discriminate dominant South African wetland species using reflectance spectra. It appears equally possible to discriminate functional groups, which has interesting implications for mapping plant functional traits, as well as related ecosystem functions and services (Díaz et al., 2007; Lavorel et al., 2011). It has been noted that the way functional groups are defined influences discrimination success (Harris et al., 2015). Therefore if plant functional traits that explain more of the variation in the spectra are measured (i.e. optical traits; Ustin and Gamon, (2010)), functional groups may be different, and more easily discriminable. In this study, the key predictors driving functional groups in South African wetlands were morphological (e.g. leaf area) and biochemical (e.g. cellulose content) and even included root traits (e.g. root type). These plant functional traits relate to decomposition, flood attenuation/water regulation, soil quality, soil retention (erosion prevention) as well as climate regulation (**Table A2**). Some of the discrimination power was found to be in the visible part of the reflectance spectrum, suggesting that spectral differences between functional groups/species are due to their photosynthetic machinery (Ren et al., 2010). This suggests that photosynthetic pigments are important to measure for studies aiming to link plant functional traits or functional groups to reflectance (Klančnik et al., 2012; Marín et al., 2016). Specifically for ecosystem service mapping in wetlands using remote sensing techniques, the plant functional traits typically measured in the field in standard ecological studies should be reviewed.

7.5 Conclusion

This research on 22 dominant South African wetland species demonstrates that it is possible to discriminate functional groups, and even species, based on their reflectance spectra, with reasonable accuracy. This provides an opportunity for further research to build upon these findings to attempt to use such functional groups to map ecosystem processes, or even services, in wetlands.

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7.7 References

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7.8 Appendix

Table A1: Species list of the 22 dominant plant species in South African palmiet wetlands and the wetlands they were recorded as being dominant in (from data recorded in plots) as well as the wetland the specimens for the reflectance measurements were collected from. Letters correspond to the photographs in **Plate A1.** * 34° 3' 14.72" S; 18° 51' 32.52" E

	Species name	Growth form	Wetland dominant in	Wetland collected from	Number of spectra collected
a	*Acacia mearnsii* (alien)	Tree	All	Goukou	20
b	*Carpha glomerata*	Graminoid	Theewaterskloof	Theewaterskloof	20
c	*Cliffortia odorata*	Shrub	Kromme	Somersetwest*	20
e	*Cliffortia strobilifera*	Shrub	All	Theewaterskloof	20
f	*Cyperus thunbergii*	Graminoid	Theewaterskloof, Kromme	Theewaterskloof	20
g	*Elegia asperiflora*	Graminoid	Goukou	Goukou	20
h	*Epischoenus gracilis*	Graminoid	Goukou	Goukou	16
i	*Helichrysum helianthimifolium*	Shrub	Goukou	Goukou	19
j	*Helichrysum odoratissimum*	Shrub	Kromme	Theewaterskloof	20
k	*Isolepis prolifera*	Graminoid	Theewaterskloof, Kromme	Theewaterskloof	20
l	*Juncus lomatophyllus*	Graminoid	Kromme	Theewaterskloof	20
m	*Laurembergia repens*	Annual	Theewaterskloof	Theewaterskloof	20
p	*Pennisetum macrourum*	Graminoid	Kromme	Theewaterskloof	20
r	*Prionium serratum*	Shrub	All	Theewaterskloof	20
n	*Psoralea aphylla*	Shrub	Theewaterskloof	Theewaterskloof	20
q	*Psoralea pinnata*	Shrub	Theewaterskloof	Theewaterskloof	20
o	*Pteridium aquilinum*	Shrub	Theewaterskloof	Theewaterskloof	20
d	*Restio paniculatus*	Graminoid	All	Theewaterskloof	20
s	*Rubus fruticosus* (alien)	Annual	Theewaterskloof, Kromme	Theewaterskloof	20
t	*Searsia augustifolia*	Tree	Theewaterskloof	Theewaterskloof	20
u	*Todea barbara*	Annual	Goukou	Goukou	20
v	*Wachendorfia thyrsiflora*	Forb	Theewaterskloof, Goukou	Theewaterskloof	20

Table A2: Hypotheses of how the selected plant functional traits would be expected to link to Ecosystem Service provision (based on expert opinion). ↑ symbolizes a possible positive correlation, ↓ a negative correlation, → a non-directional relationship, and – signifies no relationship. *Italicized traits are categorical.*

		Provisioning Ecosystem Services							**Regulating Ecosystem Services**									**Cultural Ecosystem Services**					
	Trait	Food Production	Water Provision	Materials & Fibre	Energy & Fuel	Genetic Resources	Medicinal Resources	Ornamental Resources	Water Purification	Water Regulation	Air Quality	Soil Quality	Soil Retention	Climate Regulation	Pollination	Biological Control	Life Cycle Maintenance	Recreation & Tourism	Scientific & Educational	Heritage, Cultural, Bequest	Aesthetic Services	Symbolic, Sacred, Spiritual	Total no. of Eco. Services
Morphological/ Anatomical Traits	Shoot Length	-	↓	↑	↑	-	-	-	-	↓	↑	↑	-	↑	-	-	-	↑	-	↑	↑	↑	11
	Stem Diameter	-	↓	↑	↑	-	-	-	-	↓	↑	↑	-	↑	-	-	-	-	-	-	-	-	7
	Total Biomass	-	↓	↑	↑	-	-	-	↑	↓	↑	↑	↑	↑	-	-	-	-	-	-	-	-	9
	Leaf Length/Width Ratio	-	→	-	-	-	-	-	→	→	→	→	-	-	-	-	-	-	-	-	-	-	5
	Leaf Dry Mass	-	→	-	-	-	-	-	→	→	→	→	-	-	-	-	-	-	-	-	-	-	5
	Leaf Area	-	↓	-	-	-	-	-	↑	↓	↑	-	-	-	-	-	-	-	-	-	-	-	4
	Specific Leaf Area	↑	↓	-	-	-	-	-	-	↓	-	↑	-	-	-	-	-	-	-	-	-	-	4
	Presence of Aerenchym	-	-	↓	↓	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
	Woodiness of Stem	↓	↓	↑	↑	-	-	-	-	↓	-	↓	-	-	-	-	-	-	-	-	-	-	6
	Hollowness of Stem	-	-	↓	↓	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
	Rooting Type	→	-	→	→	-	→	-	→	→	-	→	→	-	-	-	-	-	-	-	-	→	9
	Growth Form	→	→	→	→	-	→	→	→	→	→	→	→	→	→	-	-	→	→	→	→	→	18
	Clonal Strategy	→	-	-	-	-	-	-	→	→	-	→	→	-	-	-	-	-	-	-	-	-	5
	Metabolism	-	-	-	-	-	-	-	-	-	-	-	-	→	-	-	-	-	-	-	-	-	1
	Leaf Orientation	-	-	-	-	-	-	-	→	-	→	-	-	-	-	-	-	-	-	-	-	-	2
	Leaf Type	-	-	-	-	-	-	-	→	-	→	-	-	-	-	-	-	-	-	-	-	-	2
Biochemical Traits	Leaf C/N Concentration	↑	-	↑	↑	-	-	-	-	↑	-	↓	-	↑	-	-	-	-	-	-	-	-	6
	Si Concentration	↓	-	↑	-	-	-	-	-	↑	-	↓	-	-	-	-	-	-	-	-	-	-	4
	Si Content	↓	-	↑	-	-	-	-	-	↑	-	↓	-	-	-	-	-	-	-	-	-	-	4
	Cellulose Concentration	↓	-	↑	↑	-	-	-	-	↑	-	↓	-	↑	-	-	-	-	-	-	-	-	6
	Cellulose Content	↓	-	↑	↑	-	-	-	-	↑	-	↓	-	↑	-	-	-	-	-	-	-	-	6
	Lignin Concentration	↓	-	↑	↑	-	-	-	-	↑	-	↓	-	↑	-	-	-	-	-	-	-	-	6
	Lignin Content	↓	-	↑	↑	-	-	-	-	↑	-	↓	-	↑	-	-	-	-	-	-	-	-	6

Table A3. The 23 functional traits collected for the 22 species used in this study. All methods were based on the standardised protocol of Pérez-Harguindeguy et al., (2013). For categorical traits the codes assigned are shown in brackets.

	Trait	Measurement method used	Unit	Scale
Morphological/ Anatomical Traits	Shoot Length	Average shoot length of 10 mature plants	mm	Ratio
	Stem Diameter	Average diameter of 10 stems at base level	mm	Ratio
	Total Biomass	Average value of total biomass divided by number of mature shoots (in case of a tuft or rhizome)	g	Ratio
	Leaf Length/Width Ratio (LLWR)	Ratio between the length and the width of a leaf based on an average of 10 leaves	mm/mm	Ratio
	Leaf Dry Mass	Average leaf mass after being oven dried at 60°C for 72 hours (10 leaves)	mg	Ratio
	Leaf Area	Area of a single surface of a leaf based on an average of 10 leaves	mm^2	Ratio
	Specific Leaf Area	The total surface area of a leaf divided by its dry mass (based on an average of 10 leaves)	mm^2/mg	Ratio
	Presence of Aerenchym	Scale of 1 to 3 (1 = no aerenchym, 2 = less than 50% aerenchym, 3 = predominantly aerenchym)	Class	Ordinal
	Woodiness of Stem	Scale of 1 to 3 (1 = no woody tissue, 2 = less than 50% woody tissue, 3 = predominantly woody tissue)	Class	Ordinal
	Hollowness of Stem	Scale of 1 to 3 (1 = stem not hollow, 2 = hollow space less than 50%, 3 = hollow space more than 50%)	Class	Ordinal
	Rooting Type	Adventitious (1), Taproot (2), Fine mesh (3), Annual (4), Tuft (tussock) (5), Rhizome (6), Stolon (7), Suffrutex (8)	Class	Nominal
	Growth Form	Geophyte (1), Forb (2), Annual (3), Graminoid (4), Shrub (5), Tree (6)	Class	Nominal
	Clonal Strategy	Tuft (1), Guerilla (2), Phalanx (3), Vegetative (4), None (0)	Class	Nominal
	Metabolism	C_3(1), C_4 (2), Parasitism (3), Carnivorous (4), CAM (5)	Class	Nominal
	Leaf Orientation	Plane (1), Stem (2), Base (3), Top (4), Leafless (0)	Class	Nominal
	Leaf Type	None (0), Simple -small narrow (1), Simple -larger round/narrow (2), Grass-like (3), Scale-like (4), Lobate (5), Palmate (6), Pinnate (7), Bipinnate (8), Pinnatifid (9), Long-leaf (10)	Class	Nominal
Biochemical Traits	Leaf C/N Ratio	Mass ratio of carbon versus nitrogen	g/g	Ratio
	Si Concentration	Biogenic silica was extracted from 25 mg dry plant (leaf and stem) material from 10 plants and analysed with ICP	mg/kg	Ratio
	Si Content	Si concentration multiplied by average dry leaf mass to get an amount of Si per leaf	mg	Ratio
	Cellulose Concentration	Cellulose was measured by removing protein from 0.5-1 g of dry plant material from 10 plants, and by calculating mass before and after treatment with 72% sulfuric acid (Van Soest method)	%	Ratio
	Cellulose Content	Cellulose content (%) multiplied by average dry leaf mass to get an amount of Si per leaf	mg	Ratio
	Lignin Concentration	Lignin was measured by taking the results of the sulfuric acid digestion and weighing it before and after ashing at 550°C (Van Soest method)	%	Ratio
	Lignin Content	Lignin content (%) multiplied by average dry leaf mass to get an amount of Si per leaf	mg	Ratio

Plate A1: Photographs of the 22 dominant plant species in South African palmiet wetlands. The extra three photographs in this plate (*indicated by x.2*) are either of flowers or in the case of Bracken (*Pteridium aquilinum*), its characteristic dead form. The letters link the photographs to the species names in **Table A1**.

Table A4. Summary statistics for each of the continuous plant functional traits derived from 22 dominant plant species in South African palmiet wetlands

	Plant Functional Trait	Mean	Min	Max	Median
Morphological/ Anatomical Traits	Shoot Length (mm)	1513.90	78.30	10500.00	1061.35
	Stem Diameter (mm)	38.76	0.13	450.00	11.13
	Total Biomass (g)	1280.86	0.20	15271.63	57.42
	Leaf Length/Width Ratio	12.97	0.00	88.40	2.80
	Leaf Dry Mass (mg)	2835.27	1.53	20430.00	146.14
	Leaf Area (mm^2)	3420.28	31.70	16032.50	507.55
	Specific Leaf Area (mm^2/mg)	8.81	0.10	34.24	7.52
Biochemical Traits	Leaf C/N Ratio	42.71	16.61	85.86	40.29
	Si Concentration (mg/kg)	5045.75	80.00	31750.96	1328.03
	Si Content (mg)	7.99	0.00	87.03	0.37
	Cellulose Concentration (%)	29.60	15.67	44.91	29.01
	Cellulose Content (mg)	505.39	0.35	4165.15	39.80
	Lignin Concentration (%)	14.41	1.33	45.24	11.83
	Lignin Content (mg)	83.44	0.36	499.05	21.10

Table A5. The relationship between average reflectance over the four averaged sections of the spectrum and plant functional traits for five key traits. Both variables (average reflectance) and the plant functional trait were logged in each regression.

	Visible		Near Infra-red		Short-wave Infrared		Total	
Trait	Multiple r^2	p-value	Multiple r^2	p-value	Multiple r^2	p-value	Multiple r^2	p-value
Cellulose content (mg)	0.36	<0.01	**0.49**	**<0.01**	0.40	<0.01	0.46	<0.01
Lignin content (mg)	0.28	<0.05	**0.54**	**<0.01**	0.43	<0.01	0.49	<0.01
Si content (mg)	0.18	<0.05	0.22	<0.05	**0.30**	**<0.01**	0.29	<0.01
Leaf mass (mg)	0.16	NS	0.37	<0.01	0.36	<0.01	**0.38**	**<0.01**
Leaf area (mm^2)	0.26	<0.05	0.36	<0.01	0.39	<0.01	**0.41**	**<0.01**

Table A6. Functional groups of 22 dominant South African wetland species based on cluster analysis with 23 functional traits. The top 10 predictors (traits) driving the separation of groups are shown as average values per functional group. The numbers in brackets indicate the importance of each predictor in driving the grouping. For categorical traits the number given is not an average but the mode (most common form of the trait). Corresponding categories for these codes can be found in **Table A3**.

Species	Functional Group	Cellulose Content (1.00)	Leaf Area (0.90)	Leaf Orientation (0.54)	Leaf Type (0.50)	LLWR (0.42)	Lignin Content (0.37)	C/N Ratio (0.24)	Rooting Type (0.21)	Woodiness (0.21)	Clonal Strategy (0.20)
Acacia mearnsii *Cliffortia strobilifera* *Psoralea aphylla* *Psoralea pinnata*	1	101.30	1453.76	4	1	3.23	98.01	24.33	2	3	0
Cliffortia odorata *Helichrysum helianthemifolium* *Helichrysum odoratissimum* *Laurembergia repens* *Rubus fruticosus* *Searsia augustifolia*	2	13.41	622.53	2	2	2.79	9.90	35.56	1	3	4
Pteridium aquilinum *Todea barbara*	3	21.39	175.43	1	8	5.63	14.41	23.48	1	2	0
Restio paniculatus *Elegia asperiflora* *Epischoenus gracilis* *Isolepis prolifera*	4	61.47	1329.34	0	0	0.00	20.41	62.71	6	2	1
Cyperus thunbergii *Juncus lomatophyllus* *Pennisetum macrourum*	5	174.84	4529.75	3	10	56.42	39.15	70.45	6	1	3
Carpha glomerata *Prionium serratum* *Wachendorfia thyrsiflora*	6	3273.22	15479.52	3	10	25.05	385.47	39.90	6	1	0

Table A7. Spectral groups of 22 dominant South African wetland species based on cluster analysis with 1678 individual reflectance spectra. The top 10 predictors (spectra) driving the separation of groups are shown as average values per spectral group. The numbers in brackets indicate the importance of each predictor in driving the grouping.

Species	Spectral Group	539nm (1.00)	540nm (1.00)	538nm (1.00)	541nm (1.00)	542nm (1.00)	613nm (1.00)	535nm (1.00)	536nm (1.00)	609nm (1.00)	610nm (1.00)
Carpha glomerata *Cliffortia strobilifera* *Elegia asperiflora* *Epischoenus gracilis* *Helichrysum odoratissimum* *Juncus lomatophyllus* *Laurembergia repens* *Pteridium aquilinum* *Psoralea pinnata*	1	6.05	6.13	5.96	6.21	6.27	6.06	5.68	5.78	6.09	6.08
Acacia mearnsii *Cliffortia odorata* *Psoralea aphylla* *Rubus fruticosus* *Todea barbara*	2	7.33	7.45	7.21	7.55	7.64	6.72	6.81	6.95	6.77	6.76
Restio paniculatus *Helichrysum helianthemifolium*	3	6.16	6.24	6.07	6.32	6.4	6.52	5.8	5.89	6.53	6.52
Pennisetum macrourum	4	12.92	13.07	12.76	13.2	13.33	14.61	12.26	12.42	14.59	14.6
Prionium serratum *Wachendorfia thyrsiflora*	5	13.75	13.94	13.54	14.1	14.25	12.46	12.89	13.11	12.59	12.56
Cyperus thunbergii *Isolepis prolifera* *Searsia augustifolia*	6	10.58	10.71	10.43	10.83	10.94	10.4	9.95	10.11	10.45	10.44

8

Water purification of South African Palmiet Wetlands

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Submitted

A canal illegally draining the Goukou palmie wetland, with the Langeberg mountains in the background. Water leaving palmiet wetlands is of high quality, and palmiet wetlands are found upstream of two large municipal dams in the Cape Floristic Region, testimony to the importance of these wetlands.

Abstract

Wetlands provide many important ecosystem services to society, arguably of which the most important is the service of water purification. Despite the importance of water purification, it is one of the more difficult ecosystem services to quantify, especially in wetland systems which are by nature complex. We attempted to quantify the water purification service of South African palmiet wetlands, which are valley-bottom peatlands highly threatened by agricultural development. First we performed a catchment scale mass-balance study, which compared the fate of various water quality parameters over degraded and pristine sections of palmiet wetlands. We found that pristine palmiet wetlands appeared to act as a sink for water, cations (Ca^{2+}, K^{+}, Mg^{2+}, Na^{+}), anions (Cl^{-}, SO_4^{2-}), dissolved silicon, and nutrients (total phosphorus and Kjeldahl nitrogen), though there was relatively high variation in these trends. The temporal variation of this water purification function and the full potential of these wetlands as sinks is also not known. There are important limitations to this catchment scale approach, including the fact that at this large scale there are multiple mechanisms (internal wetland processes as well as external inputs) at work which are impossible to untangle with limited data. Therefore secondly we performed a small-scale field survey of a wetland fragment to corroborate the catchment-scale results. There was a reasonable level of agreement between the results of the catchment scale study done in 2014, and a smaller-scale field survey (2015). In addition, the field survey showed a decrease in dissolved organic carbon along the stretch of the wetland. We conclude that it appears possible to estimate the water purification function of these valley-bottom wetlands using this catchment scale approach.

8.1 Introduction

Wetlands are considered to be one of the most important types of ecological infrastructure to society in terms of the ecosystem services they provide (Russi et al., 2013). The type of wetland, landscape configuration and hydrological connectivity have been cited to be important in determining the type and magnitude of ecosystem services that will be provided (Moor et al., 2017). Valley-bottom and floodplain wetlands in particular, due to a combination of their position in the landscape and their composition (alluvium, peat beds and vegetation), have been shown to attenuate flood events (Rebelo et al., 2015), mitigate water pollution (Fisher and Acreman, 2004), sequester carbon (Mitsch et al., 2013), retain sediment (Venterink et al., 2006), provide clean water and food for local communities (Schuyt, 2005) and provide a host of other cultural ecosystem services underpinned by their high biodiversity (Raymond et al., 2009). Despite their value, the complexity of wetland ecology has resulted in wetlands being the least studied system in terms of ecosystem services (de Bello et al., 2010). Water purification is noted to be one of three key ecosystem service complexes provided by wetlands (Moor et al., 2017). However it is an extremely difficult service to quantify given the internal complexity of wetland ecosystems.

Water purification, sometimes referred to as 'water quality' in ecosystem service studies, has been estimated in many different ways (**Chapter 2**). Besides rapid assessments or scores, the simplest way to attempt to quantify water purification is to measure either physical or chemical properties of a water body at one point in time, focussing on parameters of interest and known thresholds for these parameters (Aherne and Posch, 2013; Kandziora et al., 2013; **Chapter 2**). Other studies use modelling techniques: investigating nutrient retention at a catchment scale, using the InVEST model or modelling nutrient retention, export or turnover rates in vegetation or in the ecosystem itself (Bai et al., 2011; Firbank et al., 2013, **Chapter 2**). Some studies measure properties of the soil (nutrients or elements of interest), nutrient retention in vegetation or nutrient removal potential of particular land-covers (Smukler et al., 2010; Snapp et al., 2010; **Chapter 2**). Lastly, some studies quantify processes such as decomposition rates and net primary productivity, relating these to water purification (Dominati et al., 2014; Kandziora et al., 2013; **Chapter 2**). Ultimately many of these methods can be problematic because they study water quality, or impacts to water quality, rather than the water purification ability of a particular ecosystem, or are modelled estimates, often not validated (**Chapter 2**). Therefore there is a need for studies to explore possible novel techniques to estimate the water purification ability of ecosystems.

In South Africa, the value of valley-bottom/flood-plain wetlands in terms of water purification has often been overlooked in favour of their fertile soils for potential food provision. Therefore South African wetlands and associated river systems are in a critical state, with over 65% reported to be damaged, and 50% estimated to have been destroyed (Nel et al., 2007). Increasing concern over the loss of water-related ecosystem services following wetland degradation (mainly in terms of water provision, but also of water quality) has prompted conservation and restoration efforts in South Africa (e.g.

the Working for Water Programme) (Turpie et al., 2008). South African Palmiet wetlands are a type of unchannelled valley-bottom wetland with peat layers ranging between 0.5 to 10 m deep (Job, 2014; Sieben, 2012). Palmiet wetlands are so named after the plant species that dominates the system: *Prionium serratum*, which is a super-dominant ecosystem engineer (Sieben, 2012) and peat-forming species. However there has been little research done on these unique wetlands, and there is little understanding of their structure and functioning. Therefore in the face of the threats to these wetlands, there is an urgency to better understand these systems and the ecosystem services they provide. In this study, we attempt to quantify the ecosystem service of 'water purification' in South African palmiet wetlands. We investigate how water quality changes spatially in three of these wetlands subjected to agricultural pollution at a catchment-scale, as well as in a small-scale field survey. We ask the following research question: do pristine palmiet wetlands act as a sink for pollutants (nutrients and metals) linked to agricultural fertilizer application?

8.2 Methods

Study sites

Palmiet wetlands occur in valley-bottoms throughout the Cape Floristic Region of South Africa. The Cape Floristic Region is characterised by oligotrophic and acidic soils due to the highly leached dystrophic lithosols associated with the sandstone mountains of the Cape Supergroup (Midgley et al., 2003). Therefore palmiet wetlands are naturally slightly acidic systems (Davies and Day, 1998). Three palmiet wetlands were selected as study sites in three different catchments throughout the Cape Floristic Region: the Theewaterskloof and Goukou wetlands (Western Cape) and the Kromme wetland (Eastern Cape) (**Fig. 1**). The catchments are of varying sizes, the Theewaterskloof the smallest, and the Kromme the largest. All wetlands have been transformed to some degree, all with some level of channel erosion; invasion of alien trees (especially in tributaries) and the Goukou and Kromme are situated in an agricultural context, receiving runoff from liming and fertilizers (**Fig. 1**). This impact tends to intensify in a downstream direction, with the least impact upstream in the catchment, and the greatest impact/most transformed wetlands downstream.

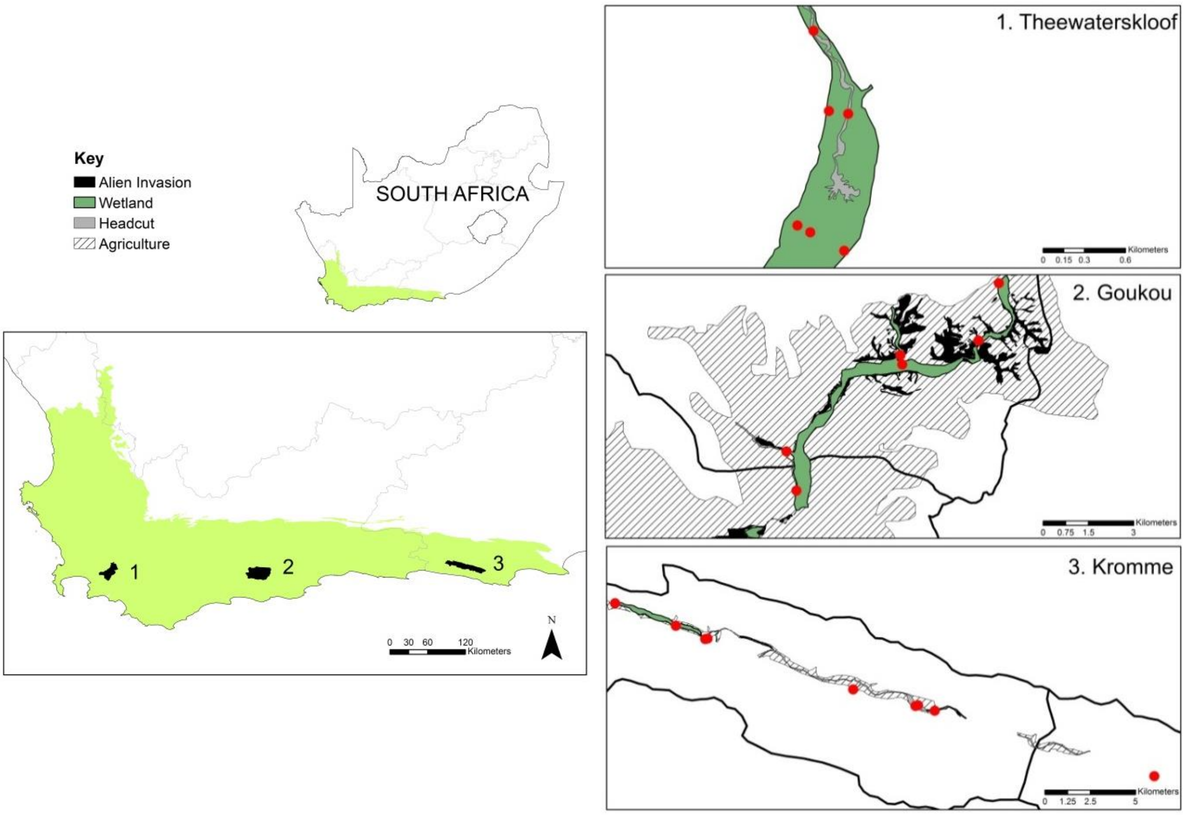

Figure 1. The three study palmiet wetlands in their respective catchments (labelled 1-3) in the Cape Floristic Region of South Africa (light green). Water quality sampling points are indicated with red points in each catchment.

Study design

We used two approaches to estimate the water purification ability of South African palmiet wetlands: firstly a catchment scale analysis of three wetlands, and secondly a small field survey. To quantify the service of water purification at a catchment scale, we compared the ability of pristine wetland sections to attenuate pollution with that of wetland sections that had lost their ecological infrastructure through degradation by channel erosion. In the field survey we attempted to follow pollutants through one wetland fragment to see whether they were exported from the wetland or whether the wetland attenuated them at this smaller scale.

a. Catchment Analysis

We collected water samples in September 2014 at various points throughout the three study catchments containing valley-bottom palmiet wetlands (**Fig. 1**). These points were opportunistically selected as locations where all the surface water moving through the wetland could be sampled. Therefore these points were either places where the wetland had become channelized and all the surface water was directed through one main channel or places where multiple small channels were evident and accessible along a cross section through the wetland. At each water quality sampling point we estimated discharge by measuring channel depth and width (to estimate river cross sectional area (m^2)) and flow velocity. Water quality parameters were selected according to their potential link to fertilizer or pesticide application by adjacent agriculture. In situ, we measured pH (water), electrical conductivity and temperature using a MultiLine F/Set-3 meter (WTW, Germany). Also in the field, we filtered (0.45 µm) and preserved samples for analysis of multiple parameters which were analysed later in the lab. The concentration of phosphate (PO_4^{3-}-P), sulphate (SO_4^{2-}-S), nitrate (NO_3^--N), ammonium (NH_4^+-N), total phosphorus (P-tot), total Kjeldahl nitrogen (Kj-N) and chloride (Cl^-) were measured on a continuous -flow analyzer (CFA) (SKALAR: SAN++). Potassium (K^+), sodium (Na^+), magnesium (Mg^{2+}), calcium (Ca^{2+}), iron (Fe), copper (Cu^+), manganese (Mn), zinc (Zn^{2+}), and aluminium (Al^{3+}) were acidified with HNO_3 and concentrations thereof -as well as dissolved silicon (DSi)- were measured on an Inductively Coupled Plasma Spectrometer using Optical Emission Spectroscopy (ICP-OES) (Thermo Scientific, type: iCAP6300 Duo). Chemical oxygen demand was measured spectrophotometrically on an ICP-OES after a 2 hour sulphuric acid - potassium dichromate digestion at 148°C in a sealed glass tube.

b. Field Survey

In April 2015 we conducted a more detailed field experiment in the Kromme Catchment to examine the effects we had seen at a catchment scale at a smaller, reach-scale. The study site included a small patch of relatively pristine wetland (approximately 300 m by 70 m of uneroded palmiet wetland vegetation) surrounded by intensive irrigated agriculture using high levels of fertilizers (**Fig. 2**). A channel entered the wetland patch from a degraded section of the wetland (all alluvium washed away) and then dispersed through the wetland (i.e. there was no more noticeable channel within the wetland as the alluvium and peatbeds were intact). The pristine palmiet wetland fragment ended at a concrete weir which was constructed to protect this remaining wetland from headcut erosion approaching from downstream. Nine water quality samples were taken in the channel entering the wetland (degraded section), another nine samples were taken 30 m apart along a transect through the relatively pristine part of the wetland and eight samples were taken at various points at the outflow (above and below the weir) (**Fig. 2**). In this field survey, the same parameters were used as from the catchment-scale analysis, but in addition dissolved organic carbon was also measured by UV/persulfate oxidation on a CFA.

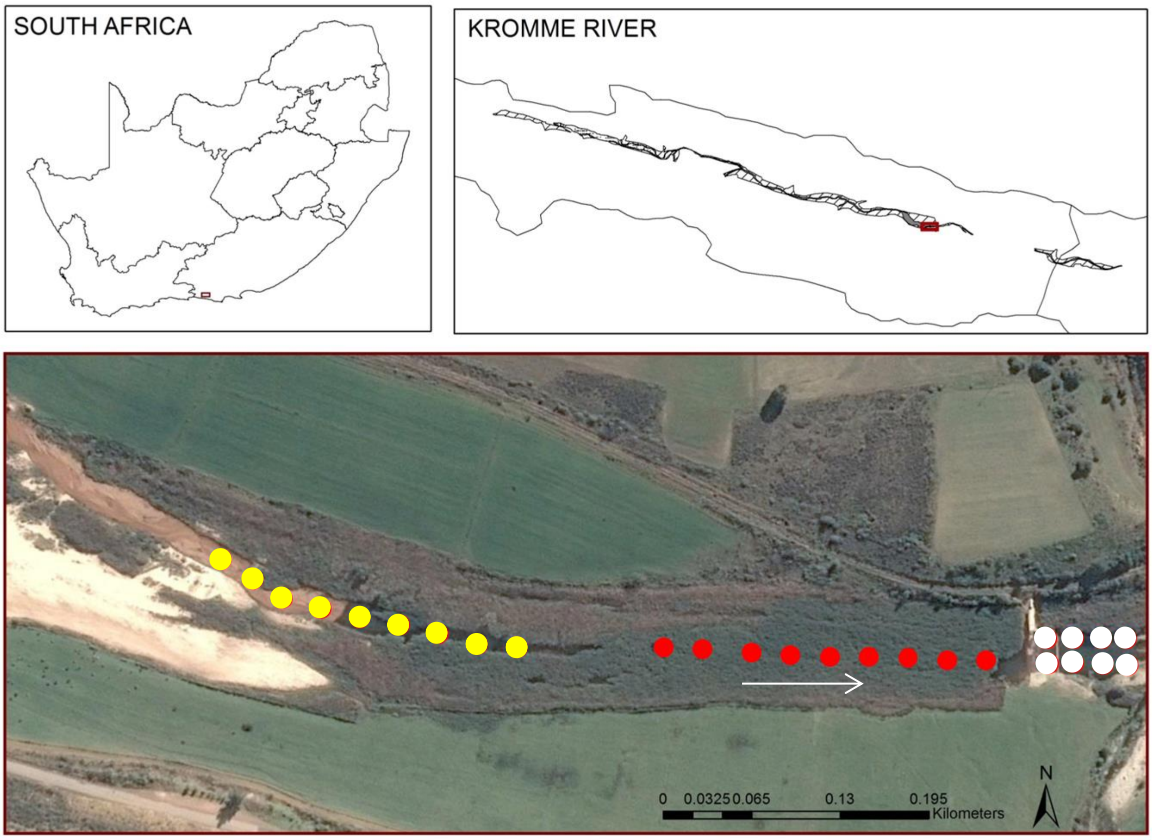

Figure 2. The transect used for the field survey in the Kromme Catchment, South Africa. Points indicate water sampling points; yellow indicate degraded and red pristine parts of the wetland, while white indicates points at the outflow of the weir. The river flows from west to east, indicated by the white arrow.

Analysis

For the catchment-scale analysis, we used a mass balance approach to estimate changes in water quality over wetland sections (sections of wetland between sampling points) (**Plate A1**). Therefore at each sampling point, the quantity (mg/s) of each water quality parameter entering the wetland was calculated by multiplying its concentration (mg/l) by the discharge (l/s). This was not done for conductivity and pH. Where there were multiple channels or tributaries, these were taken into consideration in calculations by adding these quantities to that of the water entering the wetland section via the main channel. Each wetland section was classified as either 'degraded' or 'pristine' according to one criterion: the physical condition of the wetland: whether gully or channel erosion was evident at a large scale, and whether the alluvium had been washed away. The nine wetland sections were therefore classified into six pristine sections and three degraded ones (furthest downstream): one in the Goukou and two in the Kromme (**Plate A1**). For each of these nine wetland sections, the change in water quality was calculated for each parameter by subtracting the quantity of each parameter leaving the wetland section, from the quantity entering it. If that value was positive, it indicated that the wetland section was a net sink for that parameter (either the parameter was being used by internal wetland processes, or it was being deposited). If negative, the wetland section was a net source for that parameter (exporting that parameter).

To test whether the water purification ability of wetlands differed between degraded and pristine wetland sections, we fitted linear mixed models taking wetland (site) into account. Wetland was entered as a random effect to account for the dependence between observations from within the same wetland/catchment. Degradation and the interaction between wetland and degradation were entered as fixed effects. First, the significance of the interaction was tested by comparing the fit of this model to a reduced model with only the main effect. This could not be done for the Theewaterskloof wetland, since we had no degraded sections there. Where the interaction term was significant, we could not test for the effect of degradation. Where the interaction term was not significant, we excluded it from the model and tested the significance of the main effect: degradation. Significance was tested using an F-test with Kenward-Roger correction for degrees of freedom, as implemented in the "pbKRtest" package of R.

For the field survey, we correlated each parameter against distance through the wetland fragment to see whether these parameters changed significantly passing through the pristine wetland. All nine samples entering the wetland were averaged, as well as all eight samples downstream of the wetland, yielding a sample size of 11. We used Spearman Correlations in R. If the correlation was strongly and significantly negative, the wetland fragment is acting as a sink for the parameter. If the correlation was strongly and significantly positive, the wetland fragment is acting as a source for the parameter.

8.3 Results

Catchment Analysis

On average, pristine palmiet wetlands tended to act as a sink for water, base cations (Ca^{2+}, K^+, Mg^{2+}, Na^+), anions (Cl^-, SO_4^{2-}), dissolved silicon, and nutrients (total phosphorus and Kjeldahl nitrogen), though there was relatively high variation in these trends (**Table 1, Table A1**). The pH of the water of pristine wetlands ranged from 4.3 to 7.7. Where water from agricultural runoff entered a wetland patch, pH was observed to decrease in most cases. Similarly chemical oxygen demand decreased over these pristine wetland sections. Conductivity was the only parameter that increased over the pristine sections of palmiet wetland. Degraded wetland sections behaved differently from pristine sections, though not significantly so. These sections of eroded wetland tended to export water, cations, anions, dissolved silicon, and Kjeldahl nitrogen. Additionally, pH, conductivity and chemical oxygen demand tended to increase over these wetland sections, though there was also large variation in these trends.

Table 1. Summary results for change in quantity of water quality parameters (mean ± standard deviation) across degraded and pristine sections of valley-bottom palmiet wetlands. Negative values indicate that wetlands are a net source of a parameter, and positive values indicate a net sink. For discharge, pH, conductivity and chemical oxygen demand, negative values indicate an increase and positive values a decrease. Statistics are results from linear mixed models. Significant parameters are highlighted in bold.

	Degraded	Pristine	Statistics
Discharge (l/s)	-266.7±419.39	428.6±970.08	NS
pH	-1.0±0.89	0.2±1.07	NS
Conductivity (uS/cm)	-410.9±587.24	-91.3±200.25	NS
Ca (g/s)	**-2.8±2.81**	**0.1±0.41**	F=5.76, ndf=1, ddf=6.29, p=0.05
K (g/s)	**-1.0±1.04**	**4.8±11.63**	F=5.47, ndf=1, ddf=5, p=0.07
Mg (g/s)	**-4.1±4.44**	**0.1±0.61**	F=5.57, ndf=1, ddf=6.10, p=0.06
Na (g/s)	**-32.0±35.63**	**0.8±4.96**	F=5.60, ndf=1, ddf=6.05, p=0.06
Cl (g/s)	**-53.0±57.26**	**4.7±16.02**	F=5.59, ndf=1, ddf=6.07, p=0.06
Dissolved Si (g/s)	-0.5±1.32	0.7±1.57	NS
SO_4^{2-} (g/s)	**-6.8±8.60**	**2.2±6.02**	F=5.38, ndf=1, ddf=6.25, p=0.07
Chemical Oxygen Demand (g/s)	-5.2±7.01	2.7±8.34	NS
Total P (g/s)	0.0±0.09	0.1±0.17	NS
Kjeldahl N (g/s)	-0.2±0.35	0.2±0.55	NS

Field Survey

Results show that at this point in time this Kromme wetland fragment seemed to act as a sink for K^+, dissolved organic carbon and Al^{3+} (**Table 2**). pH also decreased significantly (6.96 to 6.12) along the length of the wetland, becoming slightly more acidic (Rho=-0.72, p<0.05). However it is noteworthy that the gradients of each of these parameters are relatively flat, except for K^+ (m=-0.45). At first glance, this wetland fragment seemed to be a source of the following parameters: Ca^{2+}, Mg^{2+}, Na^+ and DSi, as all parameters have quite strong correlations (Rho = ± 0.69-0.77). However the gradients are quite flat (m<0.04), except for Na^+ which has a gradient of 0.18. Low gradients would suggest no change over the wetland fragment. Conductivity, Cl^-, Fe, SO_4^{2-}, chemical oxygen demand,

and nutrients (total phosphorus and Kjeldahl nitrogen) did not change significantly over the 300 m stretch.

Table 2. Spearmans Rho and statistics for the change in water quality parameters over distance downstream in the field survey, Kromme Wetland, South Africa. Gradient refers to the gradient of the relationship between each parameter and distance, indicating the relevance of the relationship (steeper gradient indicates more change, a gentler gradient indicates less). In this case, negative values indicate that this wetland is acting as a net sink for a parameter (decreasing); positive values indicate a net source (increasing). See **Table A3** for absolute values. Significant parameters are highlighted with bold text. DOC: dissolved organic carbon.

	Rho	Spearman Statistics	Gradient
pH	**-0.72**	S = 491.36, p-value = 0.01	**-0.07**
Conductivity (uS/cm)	-0.09	NS	-0.34
Ca (g/s)	**0.76**	S = 68.09, p-value = 0.004	**0.04**
K (g/s)	**-0.79**	S = 512.19, p-value = 0.002	**-0.45**
Mg (g/s)	**0.76**	S = 69.72, p-value = 0.004	**0.00**
Na (g/s)	**0.69**	S = 89.31, p-value = 0.01	**0.18**
Cl (g/s)	-0.07	NS	-0.13
Fe (g/s)	0.26	NS	0.01
Zn (mg Zn/l)	**0.67**	S = 95.60, p-value = 0.02	**0.00**
Al (mg Al/l)	**-0.75**	S = 500.07, p-value = 0.005	**0.00**
Dissolved Si (g/s)	**0.77**	S = 64.72, p-value = 0.003	**0.03**
SO_4^{2-} (g/s)	0.21	NS	0.05
Chemical Oxygen Demand	-0.36	NS	-0.39
Total P (g/s)	0.24	NS	0.00
Kjeldahl N (g/s)	-0.51	NS	-0.01
DOC (mg/l)	**-0.65**	S = 470.65, p-value = 0.02	**-0.08**

8.4 Discussion

Overall palmiet wetland systems are oligotrophic, therefore it is noteworthy that the absolute concentrations of each parameter are quite low (**Table A2**), and are not of concern in terms of exceeding national water quality regulations for toxicity (DWAF, 1996). Across all three catchment scales, results are similar in that pristine wetlands tended to act as sinks for most parameters, including water, mostly accompanied by a decrease in pH across the length of the wetland and an increase in conductivity. We can only speculate as to the mechanisms behind the attenuation of these parameters as these may be a complex combination of internal wetland processes and external inputs from agriculture. In terms of water (discharge) being taken up by the wetland, it may be that the wetland is facilitating percolation into aquifers, as there is thought to be high connectivity to groundwater in these wetlands (de Haan, 2016; Job, 2014). It may also be a simple effect of transpiration by wetland vegetation which is known to use relatively large amounts of water (Rebelo, 2012). Most likely it is a combination of these factors. Ultimately the fate of water in these wetlands will have a large impact on that of the various water quality parameters measured in this study.

The results of the catchment mass balance analysis show that wetlands tend to act as a sink for base cations (Ca^{2+}, Mg^{2+}, K^{+}). The field survey confirms this for K^{+}, but in this case the other two cations do not seem to change over the length of the wetland. It appears that these wetlands are acting as a sink for base cations resulting in an overall decrease in pH along the wetland section. This may possibly be linked to two conflicting mechanisms: first, liming practises from agriculture causing a spike in base cations and carbonates and a concomitant increase in pH in degraded wetland stretches (Beukes et al., 2012), and second, an increase in CO_2 in the wetland due to respiration of wetland vegetation and microbes in the soil (Trumbore, 2000), or the release of humic acids upon decomposition, causing a decrease in pH further down the wetland (Keller et al., 2009). The disappearance of nutrients (total phosphorus, potassium and Kjeldahl nitrogen), other ions, and dissolved silicon may be explained to some extent by plant uptake (Fisher and Acreman, 2004; Schachtschneider et al., 2017), microbial immobilization within the wetlands or adsorption to and retention by the soil (Fisher and Acreman, 2004).

Two of the three degraded wetlands are sources of most parameters which should be indicative of the loss of water purification function of these wetlands (**Table A1**). This may either be through excessive pollution from agricultural runoff that has saturated the water purification n ability of the wetlands, or may be indicative of peat degradation which results in the release of large quantities of dissolved substances (Bragazza et al., 2008; Evans et al., 2016; Laine et al., 2013). In the case of the third degraded wetland, which appears to be largely acting as a sink for many parameters, it is known that there is high water abstraction in this region of the catchment (Rebelo, 2012). Due to the fact that this is illegal and there are therefore no data, this is not accounted for in the mass balance and this could explain why these results seem contradictory. Overall although there are clear differences between degraded and pristine wetland sections, there are important limitations to this approach which need to be considered. Firstly, we have only one snapshot in time, and therefore have no idea of temporal variation in water purification within these wetlands. Secondly, channel structure is simplified and assumptions are made for discharge calculations, therefore affecting mass-balance results. Thirdly, results are highly sensitive to discharge and discharge has relatively high uncertainty. Additionally a large amount of discharge is in the form of subsurface water flow which was not measured in this study (de Haan, 2016). Fourthly, little is known about abstraction for irrigation, and frequency and amount of fertilizer and lime application at catchment scales. Lastly, the full extent of the water purification ability of a wetland cannot be calculated unless its capacity is exceeded by pollution, at which point its capacity would decline (Fisher and Acreman, 2004; Mitsch and Gossilink, 2000). Therefore the attempts to measure water purification of pristine wetlands are likely to be underestimates.

Due to the uncertainty present in a catchment-scale approach, we conducted a field survey to investigate the water purification function of these valley-bottom wetlands in more detail at a smaller scale. There is a good level of agreement between the findings of the catchment-scale study and the field survey. Similar results show that at the time of sampling, this wetland fragment also seemed to act as a sink for K^+, Kjeldahl nitrogen and Al^{3+}. Most significantly, pH also decreased along this stretch of wetland by almost 1 unit over only 300 m. Dissolved organic carbon was not measured in the catchment-scale study, however in this field survey it was found to decrease over the stretch of pristine wetland. Since high concentrations of dissolved organic carbon may be indicative of decomposition (Freeman et al., 2004), the fact that this wetland acts as a sink for this parameter would suggest that this wetland is not suffering drainage (Evans et al., 2016; although see Kalbitz and Geyer, 2002). Contrary to the catchment-scale study, some parameters seemed to be exported from the wetland, most notably Na. It is interesting that this wetland seems to be a source of Na^+ as this could be occurring as a result of the change in pH. Excess H^+ ions may replace certain base cations on the soil adsorption complex, thereby releasing them.

8.5 Conclusion

There was a good level of agreement between the results of the catchment scale study done in 2014, and a smaller-scale field survey done in 2015. From these results, it appears possible to estimate the water purification function of these valley-bottom wetlands. This method could be interesting for ecosystem service studies as it quantifies the ecosystem service itself rather than water quality, or impacts to water quality (a disservice). Overall these palmiet wetlands appear able to store water or aid percolation into groundwater, as well as act as a sink for many water quality parameters, although the temporal variation of this and the full potential of these wetlands as sinks is not known. This would be an interesting area for further research in light of the urgency to protect these wetlands from further degradation.

8.6 Acknowledgements

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8.7 References

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8.8 Appendix

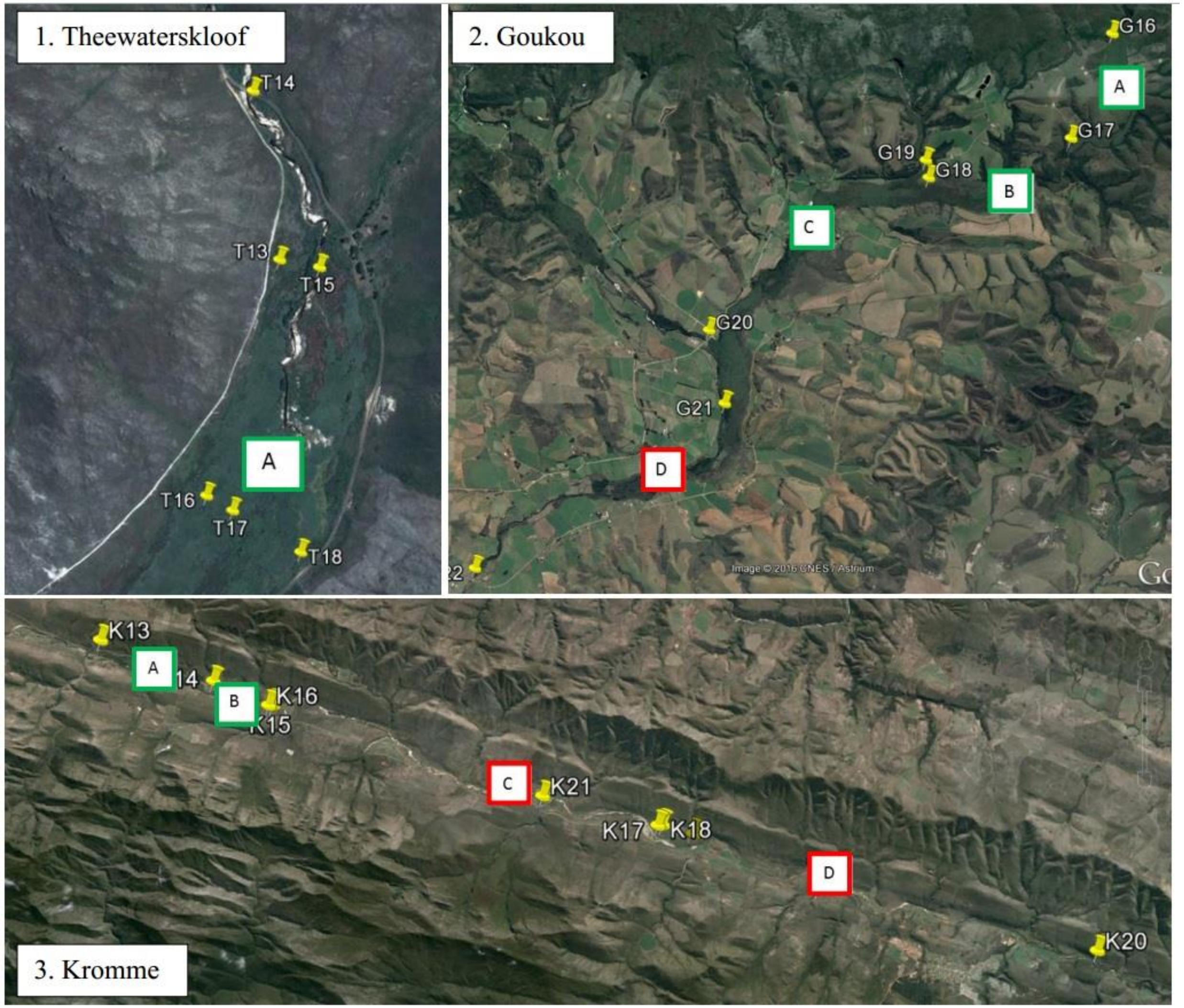

Plate A1. The three wetlands and the sections considered in this study (locations of the catchments can be seen in **Fig. 1**). Theewaterskloof wetland, 1.6km in length (1 section), the Goukou wetland, 15km in length (4 sections), and the Kromme wetland, 30 km in length (4 sections). Red boxes indicate degraded wetland sections, green boxes indicate pristine wetland sections according to the criteria of channel erosion.

Table A1. Mass balance results for three palmiet wetlands: Theewaterskloof (1 section), Goukou (4 sections), and Kromme (4 sections) wetlands. Parameters are all reported as change over the stretch of wetland, i.e. inflow – outflow, all given in g/s (parameter g/l * discharge l/s) except for pH, conductivity (uS/cm) and discharge (l/s). Negative values (red) indicate that the wetland is a source for that parameter, positive values (green) indicate that the wetland is a sink for that parameter.

		Small scale	Medium scale				Large scale			
	Unit	**Theewaterskloof**	**Goukou A**	**Goukou B**	**Goukou C**	**Goukou D**	**Kromme A**	**Kromme B**	**Kromme C**	**Kromme D**
Condition		Pristine	Pristine	Pristine	Pristine	Degraded	Pristine	Pristine	Degraded	Degraded
Discharge	l/s	2393.75	110.86	-186.73	147.70	-201.02	16.00	89.83	115.94	-715.08
pH	-	1.31	0.91	-0.185	-1.61	-1.59	0.90	-0.09	-1.47	0.00
Conductivity	uS/cm	22.33	-7.60	-16.90	-498.40	-1089.00	-31.50	-15.50	-74.25	-69.50
Ca	g/s	0.81	0.04	-0.17	-0.37	-5.06	-0.05	0.13	0.35	-3.68
K	g/s	28.50	0.21	-0.19	-0.18	-1.54	0.16	0.04	0.19	-1.69
Mg	g/s	1.13	0.10	-0.35	-0.63	-8.09	-0.09	0.28	0.70	-4.83
Fe	g/s	0.12	0.01	-0.28	0.18	0.00	0.00	0.02	0.03	-0.44
Dissolved Si	g/s	3.75	0.31	-0.71	0.67	-0.24	-0.13	0.33	0.69	-1.92
Zn	g/s	0.10	0.00	-0.01	0.01	0.00	0.00	0.00	0.00	0.00
Cu	g/s	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Al	g/s	0.24	0.00	-0.10	0.11	0.00	-0.01	0.01	0.02	-0.03
Mn	g/s	0.02	0.01	0.00	0.00	-0.01	0.00	0.00	0.00	-0.01
Na	g/s	9.65	0.79	-2.54	-4.76	-65.47	-0.41	1.79	5.46	-35.95
Cl	g/s	36.24	1.79	-4.67	-8.00	-100.22	-0.77	3.63	10.69	-69.47
SO_4^{2-}	g/s	14.29	0.33	-2.22	0.95	-15.81	0.07	-0.24	1.32	-5.87
Chemical Oxygen Demand	g/s	15.77	1.35	-8.96	7.76	-5.10	-0.42	0.83	1.76	-12.27
Total P	g/s	0.41	0.02	-0.03	0.01	-0.03	0.00	0.01	0.04	-0.14
Kjeldahl N	g/s	1.34	0.05	-0.20	0.14	-0.12	0.00	0.04	0.11	-0.57
PO4-P	g/s	0.08	0.00	-0.01	0.00	0.00	0.00	0.00	0.01	-0.02
NH4-N	g/s	0.14	0.01	-0.02	0.02	0.00	0.00	0.01	0.01	-0.04
NO3-N	g/s	-0.04	-0.01	0.01	-0.02	0.03	0.00	0.00	0.08	-0.15

Table A2. Water quality parameters for three palmiet wetlands: Theewaterskloof, Goukou, and Kromme wetlands. Acronyms: DO – dissolved oxygen, COD – chemical oxygen demand. For sampling locations see **Plate A1**.

Parameter	Units	T13	T14	T15	T16	T17	T18	G16	G17	G18	G19	G20	G21	G22
pH	-	6.5	8.1	7.1	7.0	7.7	5.8	5.5	4.5	5.1	4.3	6.2	6.4	7.9
Conductivity	μS/cm	40.0	59.0	30.0	28.0	30.0	52.0	72.1	79.7	108.0	85.2	541.0	649.0	1684.0
DO	mg/l	55.3	77.1	86.6	95.0	67.0	103.0	83.0	73.0	101.6	103.0	103.1	76.1	93.2
Ca	mg/l	0.39	0.32	0.32	0.27	0.28	0.31	0.39	0.44	0.88	0.45	3.85	6.67	18.76
K	mg/l	3.32	9.12	3.60	2.11	1.86	0.13	1.98	2.04	1.43	0.52	2.09	6.45	6.80
Mg	mg/l	0.49	0.47	0.49	0.41	0.46	0.50	0.97	1.08	1.79	1.13	9.24	11.21	30.41
Fe	mg/l	1.00	0.14	0.19	0.30	0.30	0.60	0.18	0.39	1.40	0.37	0.69	1.49	0.40
DSi	mg/l	0.99	1.63	1.73	1.90	1.74	1.82	2.82	2.84	3.79	2.36	1.90	2.26	1.51
Zn	mg/l	0.01	0.03	0.02	0.01	0.01	0.01	0.01	0.00	0.02	0.05	0.01	0.01	0.00
Cu	mg/l	0.001	0.001	0.001	0.003	0.001	0.001	0.001	0.001	0.001	0.000	0.001	0.001	0.001
Al	mg/l	0.31	0.11	0.11	0.22	0.13	0.12	0.09	0.23	0.52	0.25	0.06	0.08	0.02
Mn	mg/l	0.01	0.01	0.01	0.01	0.01	0.02	0.06	0.01	0.02	0.02	0.05	0.06	0.04
Na	mg/l	3.30	3.90	3.91	3.08	3.62	3.81	7.43	7.91	12.79	9.06	69.46	82.51	243.80
Cl	mg/l	12.30	13.70	10.60	8.40	9.10	12.80	16.90	18.30	24.40	17.80	133.70	140.90	379.40
SO_4^{2-}	mg/l	19.90	7.50	19.00	16.40	11.00	8.50	2.90	2.70	10.50	5.00	17.50	12.90	57.40
COD	mg/l	34.70	10.90	9.46	63.70	10.80	9.96	14.40	18.50	43.30	26.90	7.76	30.90	24.70
Total P	mg/l	0.20	0.17	0.17	0.22	0.17	0.17	0.14	0.13	0.15	0.15	0.17	0.39	0.20
Kjeldahl N	mg/l	1.17	0.61	0.52	1.55	0.52	0.51	0.41	0.41	0.98	0.63	0.45	1.08	0.69
PO_4-P	mg/l	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.09	0.03
NH_4-N	mg/l	0.06	0.05	0.04	0.04	0.02	0.03	0.05	0.02	0.11	0.03	0.03	0.07	0.03
NO_3-N	mg/l	0.01	0.01	0.06	0.11	0.11	0.00	0.01	0.20	0.02	0.00	0.04	0.41	0.00

Table A2 continued…

Parameter	Units	K13	K14	K15	K16	K17	K18	K19	K20	K21
pH	-	6.5	5.6	5.6	5.8	6.7	7.1	7.5	7.3	5.9
Conductivity	µS/cm	129.9	161.4	179.8	174.0	1144.0	237.0	262.0	319.0	173.6
DO	mg/l	87.0	99.0	90.4	94.0	91.2	90.6	71.0	75.0	87.5
Ca	mg/l	1.00	1.56	1.81	2.04	27.86	3.18	3.66	4.27	1.53
K	mg/l	1.68	0.58	0.70	1.13	6.67	1.37	1.82	1.97	0.80
Mg	mg/l	2.01	3.00	2.87	2.76	39.40	4.12	4.75	5.60	2.91
Fe	mg/l	0.17	0.21	0.20	0.18	3.61	0.38	0.39	0.51	0.13
DSi	mg/l	2.29	3.67	3.82	3.70	1.68	3.00	3.19	2.27	2.62
Zn	mg/l	0.01	0.04	0.01	0.05	0.01	0.07	0.04	0.01	0.02
Cu	mg/l	0.001	0.001	0.000	0.000	0.002	0.001	0.001	0.001	0.001
Al	mg/l	0.05	0.09	0.08	0.06	0.02	0.02	0.02	0.03	0.07
Mn	mg/l	0.01	0.00	0.00	0.01	0.50	0.01	0.05	0.01	0.01
Na	mg/l	15.47	20.85	23.75	23.03	124.70	30.29	32.42	41.61	22.23
Cl	mg/l	30.90	41.30	43.70	44.10	247.00	58.30	62.20	80.40	43.60
SO_4^{2-}	mg/l	2.30	2.00	1.30	27.30	7.30	6.00	4.50	6.80	3.90
COD	mg/l	5.35	9.50	10.60	10.10	99.10	6.87	8.82	14.10	6.54
Total P	mg/l	0.16	0.16	0.15	0.15	0.16	0.15	0.15	0.16	0.14
Kjeldahl N	mg/l	0.45	0.47	0.52	0.65	4.06	0.47	0.77	0.67	0.44
PO_4-P	mg/l	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03
NH_4-N	mg/l	0.03	0.05	0.02	0.03	2.18	0.08	0.13	0.05	0.05
NO_3-N	mg/l	0.00	0.02	0.00	0.02	0.02	0.28	0.03	0.17	0.33

Table A3. Absolute values for water quality parameters for the field survey, Kromme Wetland, South Africa. Points are numbered from left to right from **Fig. 2.** All parameters are given in mg/l besides pH and electrical conductivity (uS/cm). COD: chemical oxygen demand, DOC: dissolved organic carbon.

Point	Latitude	Longitude	pH	Conductivity	Ca	K	Mg	Na	Cl	Fe	Zn	Al	DSi	SO_4^{2-}	COD	Total P	Kj N	DOC
1	33°55'5.91"S	24°12'8.81"E	6.34	150	1.8	1.3	2.7	21.0	37	0.33	0.003	0.078	2.8	4	18.6	<0,02	0.82	-
2	33°55'6.39"S	24°12'10.19"E	6.77	160	1.8	4.2	2.7	20.8	40	0.32	0.003	0.085	2.8	4	19.2	<0,02	0.32	5.6
3	33°55'6.96"S	24°12'10.09"E	6.69	158	1.8	4.9	2.7	20.7	40	0.24	0.003	0.077	2.8	<4	20.9	<0,02	0.44	6.2
4	33°55'7.10"S	24°12'10.39"E	6.31	153	1.8	1.7	2.7	20.9	36	0.33	0.003	0.084	2.7	4	19.2	<0,02	0.53	-
5	33°55'7.30"S	24°12'10.72"E	6.35	176	1.8	8.5	2.7	20.9	43	0.33	0.007	0.084	2.8	<4	17.7	<0,02	0.73	5.7
6	33°55'7.08"S	24°12'11.10"E	7.18	193	1.8	13.1	2.7	20.9	48	0.31	0.003	0.08	2.7	<4	21.0	<0,02	0.35	6.3
7	33°55'7.60"S	24°12'11.12"E	6.57	165	1.8	2.8	2.7	20.9	37	0.33	0.009	0.085	2.8	4	21.4	<0,02	0.36	5.8
8	33°55'7.58"S	24°12'11.74"E	6.28	252	1.8	28.1	2.7	21.0	61	0.31	0.002	0.078	2.8	4	24.3	<0,02	0.37	6.3
9	33°55'7.66"S	24°12'12.72"E	6.38	154	1.7	2.5	2.6	20.7	38	0.30	0.004	0.089	2.8	4	21.2	<0,02	2.05	5.4
10	33°55'8.39"S	24°12'18.96"E	6.96	168	1.9	7.3	2.7	21.6	43	0.21	0.002	0.067	2.8	<4	24.0	0.02	0.63	7.0
11	33°55'8.39"S	24°12'20.20"E	6.98	153	1.8	2.5	2.7	21.0	38	0.34	0.004	0.073	2.8	<4	21.4	0.02	0.48	6.6
12	33°55'8.38"S	24°12'21.46"E	6.81	156	1.9	1.3	2.8	21.2	38	0.39	0.002	0.067	2.8	<4	19.5	<0,02	0.40	6.6
13	33°55'8.37"S	24°12'22.51"E	6.51	170	2.0	2.5	2.9	21.9	39	0.69	0.004	0.062	2.8	5	27.6	0.04	0.63	7.2
14	33°55'8.32"S	24°12'23.76"E	6.33	171	2.1	1.9	2.9	21.9	39	0.32	0.002	0.052	2.8	5	27.4	0.04	0.66	6.9
15	33°55'8.40"S	24°12'24.66"E	6.08	182	2.5	2.0	3.4	23.9	43	3.07	0.012	0.072	3.3	5	24.0	0.02	0.46	6.7
16	33°55'8.52"S	24°12'25.51"E	6.1	167	2.2	1.5	3.1	23.0	40	0.33	0.002	0.046	3.0	<4	20.6	0.03	0.54	5.9
17	33°55'8.63"S	24°12'26.79"E	6.12	173	2.2	1.8	3.1	23.0	40	0.41	0.005	0.043	3.0	<4	21.9	0.04	0.53	5.8
18	33°55'8.53"S	24°12'28.15"E	6.12	174	2.2	1.3	3.0	22.9	40	0.28	0.002	0.043	3.1	<4	20.7	0.02	0.45	5.7
19	33°55'8.37"S	24°12'28.96"E	6.56	157	2.2	1.9	3.1	22.8	41	0.33	0.004	0.051	3.0	<4	16.2	0.03	0.39	6.0
20	33°55'8.64"S	24°12'29.00"E	6.2	159	2.3	1.5	3.1	23.0	40	0.48	0.012	0.057	3.0	12	14.5	0.03	0.64	5.9
21	33°55'8.83"S	24°12'28.96"E	6.18	161	2.3	1.3	3.1	23.2	39	0.39	0.003	0.046	3.1	<4	16.7	0.03	0.60	6.1
22	33°55'9.03"S	24°12'29.00"E	6.17	163	2.3	1.3	3.2	23.6	41	0.27	0.010	0.042	3.0	<4	16.4	0.03	0.48	5.5
23	33°55'8.21"S	24°12'29.73"E	6.21	150	2.0	1.2	2.9	21.7	37	0.25	0.003	0.046	2.9	<4	16.8	0.02	0.32	5.3
24	33°55'8.59"S	24°12'29.76"E	6.15	149	2.1	1.1	2.9	21.9	39	0.39	0.008	0.056	2.9	<4	17.0	0.02	0.30	5.4
25	33°55'8.34"S	24°12'30.66"E	6.14	151	2.1	1.1	2.9	21.9	38	0.47	0.004	0.093	2.8	<4	19.4	<0,02	0.33	6.7
26	33°55'8.67"S	24°12'30.70"E	6.18	149	2.1	1.3	2.9	21.7	39	0.33	0.011	0.059	2.9	<4	20.0	0.02	0.43	5.9

9

Ecosystem services provided by South African palmiet wetlands: can we justify the true cost of development?

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Palmiet wetlands provide many ecosystem services to society. The palmiet wetland pictured to the right is found in the upper Kromme River in the Eastern Cape of South Africa. Many of these wetlands are threatened by agriculture, and water-related ecosystem services are traded for food production.

Abstract

Palmiet wetlands are valuable valley-bottom systems that are highly threatened by agriculture, and damage associated with it, such as invasion of alien species and infrastructure. Currently most agriculture in these South African palmiet wetlands is marginal due to the challenges of farming a system that experiences severe floods and droughts. The current situation seems to be a lose-lose situation for nature and society. We aimed to assess this conflict between water-related services and agriculture objectively by comparing ecosystem service provision by degraded and pristine wetlands using a rapid ecosystem service assessment tool (WET-Ecoservices) to evaluate fifteen ecosystem services in degraded and pristine wetlands. To test the efficacy of this technique, we compared results to those obtained from examining three key ecosystem service complexes in slightly more detail. We found that pristine palmiet wetlands provide valuable ecosystem services to society, which are currently being compromised for private gain. These pristine wetlands sequester between 23.4-61.6 m^3 of organic carbon per year, nitrogen and phosphorus uptake efficiencies of 62.0-84.9% and 16.2-88.7% respectively, and provide about 16 times more flood attenuation relative to degraded ones. The full impact of degradation on wetland ecosystem services was not entirely captured by the rapid ecosystem service assessment tool: WET-Ecoservices. We suggest some adaptations for the hydrogeomorphic unit: valley-bottom wetlands. Overall these wetlands have high potential for incorporation into a Payments for Ecosystem Services scheme, due to their position above important municipal dams. We recommend collaboration between private landowners struggling with marginal agriculture, and decision makers in cities dealing with water shortages and debt to ensure the most efficient and judicious use of these palmiet wetland ecosystem services.

9.1 Introduction

Wetlands are fragile ecosystems, essential for humans, and yet threatened throughout the world (MEA, 2005). Wetlands are also valuable ecosystems as they are responsible for various complex ecosystem functions and services (Kotze et al., 2007; Moor et al., 2017). Important ecosystem services typically provided by wetlands include water provision, water purification, water regulation, and many others, including cultural services. However, three ecosystem service complexes stand out where wetlands are concerned: water flow regulation (water storage and flood attenuation), climate regulation (energy exchange, carbon sequestration and greenhouse gas emissions) and water quality regulation (biogeochemical transformations, retention or removal of excess nutrients/pollutants from runoff) (Moor et al., 2017). Moor et al. (2017) call these 'complexes' as this illustrates the multiple aspects/components of each ecosystem service (also see **Chapter 2**) that may result in trade-offs or be mutually exclusive. Main threats to wetlands globally are invasive species, which result in loss of suitable habitats and biodiversity (Zedler and Kercher, 2004), as well as eutrophication as a result of increased fertilizer use. In South Africa, wetlands are in a critical state, with more than 65% threatened (Nel and Driver, 2012) and over 50% destroyed (Cowan, 1995). This is mainly due to anthropogenic activities (Nel and Driver, 2012).

Peatlands are rare in South Africa and are classified as wetlands with organic soils constituting an average organic carbon content of 10% occurring at a vertical distance of at least 20cm (Job and Ellery, 2013). Peatlands comprise different plant communities according to which peatland region they occur in, characterized by various dominant species which determine the characteristics of the peat (Job and Ellery, 2013). To date, eleven peatland regions have been defined in South Africa (Marneweck et al., 2001). One type of South African peatland is dominated by a unique plant species called palmiet, *Prionium serratum*, which is endemic to southern Africa. Palmiet is noted to be a remarkable species and is hypothesized to be an ecosystem engineer (Sieben, 2012). Due to its deep, extensive rooting structure and clonal nature, it is thought to have stabilized river valleys within the Cape Floristic Region, turning them into unchannelled valley-bottom wetlands and allowing the formation of peat beds. Due to this structure and their position in the landscape, palmiet wetlands are thought to provide valuable ecosystem services (Rebelo et al., 2015). Their restricted size and distribution, their peat beds and the threats they face in terms of habitat destruction have contributed to their importance (Gründling and Grobler, 2005; Rebelo et al., 2015).

Most palmiet wetlands occur on land that is privately owned. Landowners – usually farmers – are incentivized to optimize ecosystem services, such as food production (providing instant economic benefit to few), over the protection of natural resources that would ensure long-term provision of multiple ecosystem services to society at large. Palmiet peat-beds have rich soils, favourable for agriculture. However, using the wetland for agriculture is not compatible with other ecosystem service supply, most notably clean water. The associated catchments are also not suitable for agriculture, often being narrow and at high risk of floods (Rebelo et al., 2015). Wetlands that are developed for agriculture eventually become eroded, the water table lowered, resulting in marginal agriculture. Additionally, there is the perception that wetlands are ‘wastelands’ that show potential for more productive use (Job and Ellery, 2013). This has often led to the mechanical removal of palmiet wetland vegetation (channelization), as this is perceived to ‘improve riverflow’ (Rebelo, 2012). Therefore a key issue is the trade-off in ecosystem service provision between these two different land-use scenarios: wetlands or the agriculture that would replace them. Ultimately the resulting wetland degradation is neither beneficial to farmers nor to downstream beneficiaries or stakeholders.

Facing challenges such as the presented case of South African palmiet wetlands, ecosystem services can be a valuable tool to aid policy and decision making, by taking into account the entire suite of ecosystem services that an ecosystem provides (de Groot et al., 2010). The ecosystem services concept is particularly useful when trade-offs between various ecosystem services need to be considered (Seppelt et al., 2011). We aim to compare ecosystem service provision between degraded and pristine palmiet wetlands to understand which ecosystem services are affected by degradation, and to have an overview of the true cost (in terms of effects on ecosystem services) of wetland development, and ultimately degradation. To this end we used a rapid ecosystem service assessment tool (WET-Ecoservices) to evaluate fifteen ecosystem services in degraded and pristine wetlands. To test the efficacy of this technique, we examine the three key ecosystem service complexes in slightly more detail, with the aim to compare these findings with the rapid ecosystem service assessment results.

9.2 Methods

Study sites

Three palmiet wetlands within the Cape Floristic Region of South Africa were selected as study sites (**Fig. 1**). Despite being situated as much as 470 km apart, these peatlands are remarkably similar in biochemistry and vegetation composition. The Kromme peat layer has been estimated to be approximately between 0.5-2.8 m deep, and dated to 5620±70 years old, with an accumulation rate of about 0.72 mm per year (Nsor, 2007). The Goukou peat layer has been estimated to be between 3-10 m deep, declining in thickness in a downstream direction (Job, 2014; Sieben, 2012). Some preliminary research on the Theewaterskloof wetland has recorded peat depths of at least 0.5-1 m, in some cases 2 m (Kotze, 2015). From each of these wetlands, degraded and pristine parts of the wetland were compared using the WET-Ecoservices rapid assessment tool. Three ecosystem services, identified as having particular importance for wetland ecosystems, were quantified using data from literature and compared to the results of the rapid assessment. Pristine wetland sections are composed of unchannelled valley-bottom wetlands. Once degraded, for example by invasion of alien vegetation or agriculture, the wetland erodes, becoming channelized (**Table A1**). All wetlands are an important source of water for agriculture, and in addition the Theewaterskloof and Kromme are essential water sources for nearby cities (**Table A1**) (Rebelo, 2012).

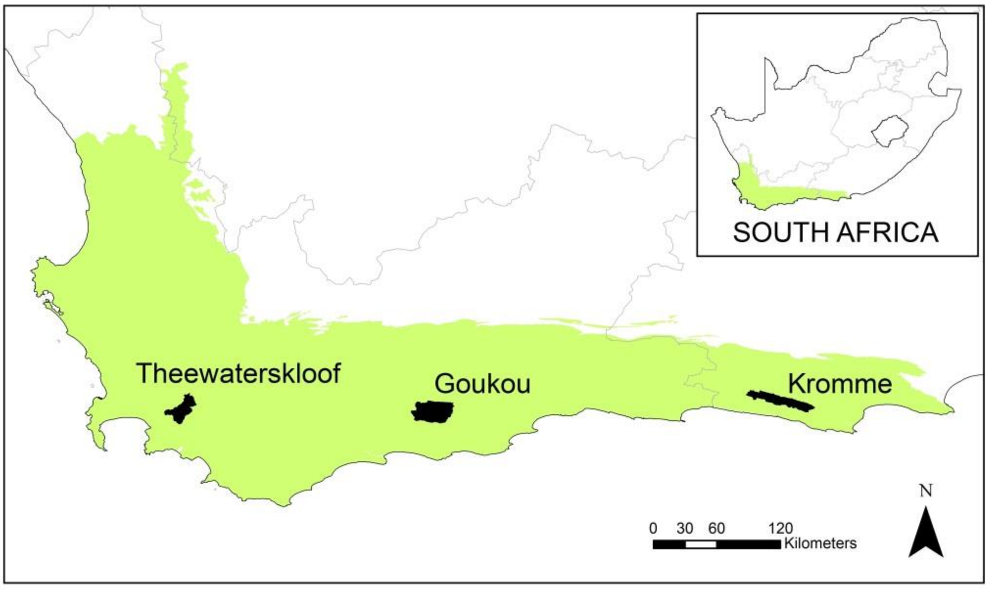

Figure 1. The location of the three catchments in the Cape Floristic Region (green) of South Africa containing the seven palmiet wetlands used in this study.

Rapid assessment: WET-Ecoservices tool

Fifteen ecosystem services were assessed using the rapid WET-Ecoservices tool (Kotze et al., 2007) (**Table A2**). The purpose of this tool is to provide quick ecosystem service assessments of South African wetlands for decision makers, government, planners, consultants and educators. The authors acknowledge that this rapid assessment is not a substitute for a more thorough multi-disciplinary assessment. It is also not a quantitative method. The basis of this tool is the hydro-geomorphic type that each wetland belongs to (e.g. seep, valley-bottom, floodplain, depression) (Kotze et al., 2007). Thus a first step is to identify this hydro-geomorphic type(s) for the wetland in question. Palmiet wetlands tend to be unchannelled in their pristine state, and become channelized through gully erosion with degradation, changing hydro-geomorphic unit (**Table A1**). Users then score characteristics of the 15 ecosystem services from 0-4 based on questionnaires that have been developed for each ecosystem service for these South African wetlands (**Table A2**). Scores are based on field observations or measurements, calculations and information from literature, databases and expert knowledge. A score of 4 would be the highest possible ecosystem service provision, whereas 0 suggests that the wetland is entirely incapable of providing the ecosystem service in question. The tool avoids complicated weighting systems, and instead uses averages to obtain overall comparable ratings.

Provisioning and cultural ecosystem services (direct benefits) are assessed by 'noteworthiness', while regulating ecosystem services are scored both for 'effectiveness' as well as 'opportunities for improvement', and these two categories are averaged. 'Opportunities for improvement' of ecosystem service provision is rated by the realized importance/value of the benefit, (i.e. for the ecosystem service flood attenuation: extent of floodable property downstream), as well as fixed capacity of the catchment (i.e. rainfall intensity, average slope) as well as variable factors (i.e. land-use, runoff potential of soils) which could potentially be restored or improved. Confidence for each characteristic is also assessed on a scale of 1-4 (1 being low confidence and 4, very high confidence). Wetland size is cited to impact certain ecosystem services (positively related), such as flood attenuation, sediment trapping, nutrient and toxicant assimilation, erosion control, carbon storage and food provision. However, in our case, the degraded parts (hydro-geomorphic units) of the study wetlands tended to be larger than pristine parts (**Table A1**), and therefore it would only have the potential to over-estimate ecosystem service provision of degraded wetlands, not that of pristine wetlands, yielding more conservative comparisons. Overall threats (potential detrimental impact on ecosystem service provision) and future opportunities (enhancing the effectiveness of the hydro-geomorphic unit, or increasing the direct use of a wetland) are also scored for each wetland site.

Quantified wetland ecosystem services

We also estimated components of the three wetland ecosystem service complexes cited as important by Moor et al. (2017) in this study:

1. *Carbon sequestration*

Carbon sequestration was estimated based on the long-term peat accumulation rates (mm/a) measured in other studies. In a study on palmiet wetlands in the Goukou, peat at 4 m deep was estimated to be 5050±30 years old based on results of carbon dating (Job, 2014). In a study done on the Kromme palmiet wetlands, peat, at 4.05 m depth, was estimated to be 5620±70 years old (Nsor, 2007). This yields long-term peat accumulation rates of between 0.79 and 0.72 mm/a respectively. These long-term rates of peat accumulation are slow relative to other peatlands globally, e.g. 2.5 to 11 mm/a in the subtropical Everglades of Florida (Reddy et al., 1993), and 1.4 to 2.1 mm/a in the high-altitude Andean peatlands of Bolivia (Hribljan et al., 2015), but comparable to other South African studies (Nsor, 2007). No carbon dating has been done on the Theewaterskloof wetland peat, and therefore an average of these two values was used for long-term peat accumulation rates in these wetlands (0.76 mm/a). Uncertainty was estimated by using the uncertainty in the dating of the peatlands, yielding uncertainties of 0.72-0.79 mm/a for the Theewaterskloof wetland, 0.79-0.80 mm/a for the Goukou and 0.71-0.73 mm/a for the Kromme (**Table 1**). For degraded wetlands, peat accumulation and its uncertainty was estimated for remaining wetland fragments, whereas peat loss and its uncertainty for parts of the wetland that have been entirely eroded or drained were also calculated (**Table 2**).

Table 1. Estimates of uncertainty for carbon sequestration (mm peat formation per annum based on an accumulation rate of 0.76 mm/a). Extent indicates the area of remaining peat.

Wetland	State	Extent (km^2)	Carbon sequestration (m^3/a) lower	mean	upper
Theewaterskloof	degraded	0.09	65.9	69.2	72.4
	pristine	0.60	429.8	450.7	471.6
Goukou	degraded	0.26	205.4	206.7	208.0
	pristine	0.31	245.7	247.3	248.8
	pristine	0.52	406.9	409.4	412.0
Kromme	degraded	0.06	43.1	43.7	44.3
	pristine	0.60	424.6	430.6	436.5

Table 2. Estimates of uncertainty for peat loss from degraded sections of wetland where the alluvium has been lost or soil dried out (Job, 2014; Kotze, 2015; Nsor, 2007)

Wetland	State	Wetland depth (m)	Extent lost (km^2)	Peat loss (m^3) lower	mean	upper
Theewaterskloof	degraded	0.5-1.0	0.29	145 000	217 500	290 000
Goukou	degraded	3.0-10.0	0.33	990 000	2 145 000	3 300 000
Kromme	degraded	0.5-2.8	0.62	310 000	1 023 000	1 736 000

2. *Water quality regulation*

Water quality regulation is a complex ecosystem service; and whether certain water quality parameters are taken up by wetlands depends on the parameter itself, the wetland, the season, and other conditions (**Chapter 8**). One simple way to estimate wetland water quality regulation, is to estimate the nitrogen and phosphorus uptake rates across a stretch of wetland using opportunistic sampling locations (preferential flow paths through the wetlands, or gullies). I estimated mean nitrogen and phosphorus uptake, as well as efficiency (%) in degraded and pristine sections of these three palmiet wetlands (**Chapter 8, Table 3**). Nutrient uptake efficiency was calculated by taking the percentage of the amount of nutrients leaving the wetland from the amount entering the wetland. These estimates have high uncertainty, as (1) they are limited by the level of pollution the system was experiencing at the time of sampling (thus true capacity could be underestimated), (2) uptake rates may change over time, eventually showing saturation and decreased uptake capacity with prolonged eutrophication (Verhoeven et al., 2006), and (3) it is only one measurement in time (Fisher and Acreman, 2004). Estimates of mean total phosphorus and nitrogen uptake by degraded and pristine sections of palmiet wetlands were calculated by multiplying the mean uptake per area by the area of each of the seven study wetlands (**Table 4**). Uncertainty was calculated using the standard deviation (**Table 3**) to obtain an upper estimate of nutrient uptake for pristine sites (**Table 4**). The lower estimate was set as 0, as no pristine wetlands were shown to act as sources of nutrients. For degraded wetlands both the upper and lower estimates were taken from the standard deviation (**Table 4**).

Table 3. Mean and standard deviation of estimates of total phosphorus and nitrogen uptake by degraded and pristine sections of palmiet wetlands (n=9), as well as uptake efficiency as a percentage. Negative values indicate nutrient release from the system.

	Total P uptake per area ($mg.km^{-2}.s^{-1}$)			**Kjeldahl N uptake per area** ($mg.km^{-2}.s^{-1}$)		
	mean	standard deviation	Uptake efficiency (%)	mean	standard deviation	Uptake efficiency (%)
Pristine	215.53	432.58	55.1±32.97	712.15	1409.00	58.9±26.36
Degraded	-159.36	553.73	-1120.4 ±1547.77	-814.65	2052.33	-1284.4 ±1432.58

Table 4. Estimates of total phosphorus and nitrogen uptake by palmiet wetlands including uncertainty (upper and lower limits). Extent indicates the area of wetland, regardless of condition or amount of peat remaining.

		Extent	**N uptake** (mg/s)			**P uptake** (mg/s)		
Wetland	**State**	(km^2)	**lower**	**mean**	**upper**	**lower**	**mean**	**upper**
Theewaterskloof	degraded	0.38	-1089.45	-309.57	470.32	-270.97	-60.56	149.86
	pristine	0.60	0.00	427.29	1272.69	0.00	129.32	388.87
Goukou	degraded	0.59	-1691.52	-480.64	730.23	-420.72	-94.02	232.68
	pristine	0.31	0.00	220.77	657.56	0.00	66.81	200.91
	pristine	0.52	0.00	370.32	1103.00	0.00	112.08	337.02
Kromme	degraded	0.68	-1949.55	-553.96	841.62	-484.90	-108.36	268.17
	pristine	0.60	0.00	427.29	1272.69	0.00	129.318	388.87

3. *Flood attenuation*

I estimated the flood attenuation ability of palmiet wetlands by considering the relationship between rainfall and riverflow in the Kromme catchment (Rebelo et al., 2015). The flashier the system is (poor flood attenuation), the steeper the gradient of the relationship between riverflow and rainfall. This relationship has been related to percentage cover of the wetland relative to the valley-floor using historical data from the Kromme River (Rebelo et al., 2015, **Table 5**). I used a sigmoidal curve (nonlinear regression) using the nls() function in the Stats Package in r to model the relationship, which produced a very good fit. The model ($y = 0.97/(1+\exp((0.25-x)/0.04))$) was then applied to the area of other wetlands relative to the valley bottom of their catchment to estimate respective flood reduction (**Table 6**). Uncertainty was quantified overall from the R-squared values for the relationship between riverflow and rainfall (Rebelo et al., 2015, **Table 5**). The values for the three years were averaged, giving a relative uncertainty of 45.97%. This was applied to each estimate to give an upper and lower bound of uncertainty for each flood retention value. This method is over-simplified, as there are more factors contributing to the attenuation of floods than simply the area of wetland in a catchment. Examples of these are geomorphological considerations such as the gradient of the catchment, the width of the valley-floor, the connectivity with groundwater, the depth of the peat and the quality of the wetland itself, as well as ecological considerations: the vegetation cover on the watersheds and biomass of the wetland vegetation.

Table 5. Relating area of wetland relative to the valley floor (1330.8 ha) to the observed reduction in flooding (runoff during stormflow) from previous research on the Kromme palmiet wetland (Rebelo et al., 2015)

	Estimated area of palmiet wetland (ha)	**Wetland : valley-bottom** (%)	**Reduction in flood** (%)
1950's	668.58	50.24	94.7
1960's	381.34	28.66	67.0
1980's	241.43	18.14	14.0
2000's	209.03	15.71	34.0

Table 6. Estimates of uncertainty for flood attenuation: mean values as well as upper and lower estimates are given based on uncertainty in the fit of the relationship between rainfall and runoff.

Wetland	**State**	**Extent** (km^2)	**% of valley bottom**	**% flood reduction** lower	mean	upper
Theewaterskloof	degraded	0.09	16.99	6.2	11.6	16.9
	pristine	0.60	100.00	52.4	97.0	100.0
Goukou	degraded	0.26	13.86	3.1	5.7	8.3
	pristine	0.31	100.00	52.4	97.0	100.0
	pristine	0.52	100.00	52.4	97.0	100.0
Kromme	degraded	0.06	3.77	0.3	0.5	0.7
	pristine	0.60	100.00	52.4	97.0	100.0

9.3 Results

According to the rapid ecosystem service assessment, pristine palmiet wetlands provided a greater suite of ecosystem services compared to degraded ones (**Fig. 2**). Specifically, pristine wetlands scored higher for water-related ecosystem service provision as well as carbon storage, compared to degraded ones. Degraded wetlands consistently scored highly for maintenance of biodiversity. Cultural significance scored low for all palmiet wetlands, whether degraded or pristine. Both Kromme wetlands (degraded and pristine) provided the greatest suite of ecosystem services compared to the other wetlands, Theewaterskloof wetlands scoring the lowest overall. Theewaterskloof differed from the other two catchments in that it currently has no agriculture, therefore provides no cultivated food. The pristine Theewaterskloof wetland provided more regulating ecosystem services, including carbon storage and erosion control, whereas the degraded wetland scored higher for 'water supply for human use'.

The pristine Goukou wetlands provided a similar suite of ecosystem services (high regulating ecosystem services provision, moderate provisioning ecosystem services) despite being composed of different vegetation communities. The degraded Goukou wetland scored lowest for carbon storage as well as tourism and recreation. The pristine Kromme wetland provided higher levels of regulating ecosystem services (particularly streamflow regulation, erosion control and carbon storage) and some provisioning ecosystem services (water supply for human use) compared to the degraded wetland. In terms of risk of potential threats (**Table A3**), the degraded Theewaterskloof and both Kromme wetlands scored the highest. Degraded wetlands had the highest scores for opportunities for improvement of ecosystem service provision, which tended to increase their overall ecosystem services scores (**Table A3**).

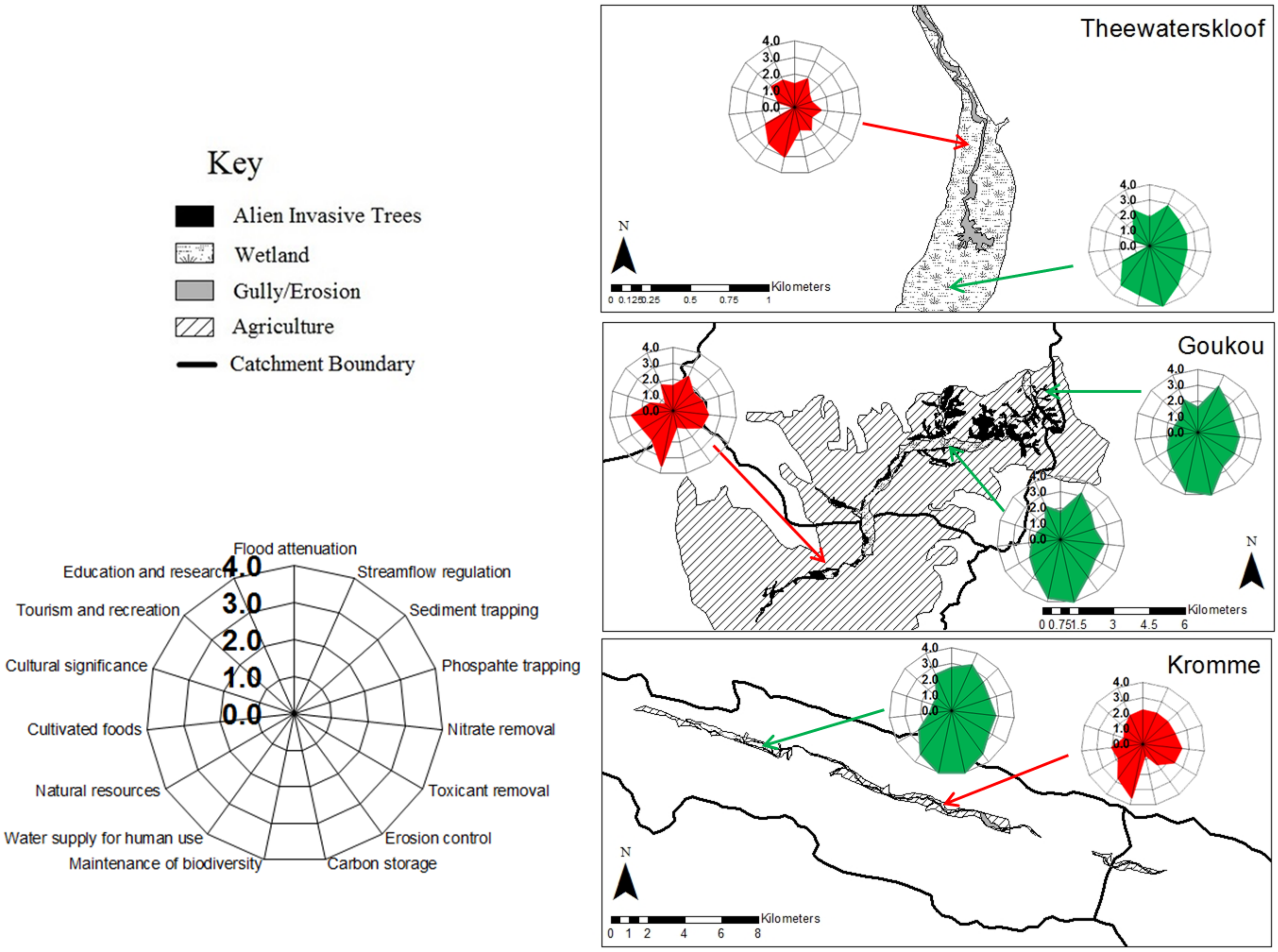

Figure 2. Results of ecosystem service provision for three South African palmiet wetlands displayed on radar charts. The 15 ecosystem services are scored from 0-4; red charts indicate degraded wetlands and green pristine. For location of catchments in South Africa see **Fig. 1**. See **Fig. A1** for scores for each ecosystem service.

Pristine palmiet wetlands build up peat over time, storing carbon and acting as a CO_2 sink, whereas degraded wetlands erode, releasing sediment downstream and CO_2 into the atmosphere. Long-term rates of peat accumulation of pristine wetlands are estimated at between 0.72 and 0.79 mm/a (**Table 7**). For pristine wetlands from 6-60 ha in size (**Table 7**), peat accumulation could be between 247.3 m^3 and 450.7 m^3 per annum, though this will probably be lower as it is based on the long-term average. With on average 24.75% of the peat composed of organic matter and 13.05% of carbon, this would equate to between 32.15 m^3 and 58.82 m^3 of carbon being sequestered per annum by these wetlands (**Chapter 4**). Degraded wetlands tend to be net exporters of sediment (and therefore peat and carbon) due to extensive erosion damage which outweighs any carbon capture by vegetation at these sites. To use the example of the gully formed in the degraded Theewaterskloof wetland (**Chapter 3**), which is 15618.4 m^3 in size, formed over 10 years, could imply a loss of 1561.8 m^3 alluvium per annum (an estimated 203.8 m^3 of carbon, but possibly less since it has been shown that not all the alluvium is peat (Kotze, 2015)). From the degraded wetlands, around 3 385 500m^3 of alluvium has been lost, translating to 441 807.75 m^3 carbon (**Table 2**). Not considering the emissions from gully erosion, pristine wetlands considered in this study provide 4.8 times more carbon sequestration than degraded wetlands. However, the rapid assessment tends to score degraded palmiet wetlands as a 1 and pristine ones as a 4 for carbon storage.

Pristine wetlands had nitrogen and phosphorus uptake rates of 220.8 to 427.3 mg/s and 66.8 to 129.3 mg/s respectively (**Table 7**). Degraded wetlands appeared to act as a source of nutrients. Conversely, the rapid assessment yielded very similar scores for water quality regulation for pristine and degraded wetlands. Estimates of the ecosystem service flood attenuation suggest that pristine wetlands provide about 16 times higher flood attenuation compared to degraded ones (**Table 7**). Again, the rapid assessment tended to score flood attenuation very similarly for degraded and pristine wetlands.

Table 7. A comparison of estimated ecosystem service values as a function of wetland area (km^2) and scores from the WET-Ecoservices rapid assessment for three key wetland ecosystem service complexes. Carbon sequestration is given as mm peat formation per annum based on an accumulation rate of 0.76 mm/a. Water purification is based on nutrient uptake rates of N and P respectively. Water regulation is given as the reduction of floods (%), based on the percentage of the valley bottom occupied by the wetland. Details and uncertainty estimates are given in the Methods. Theew: Theewaterskloof, D: degraded, P: pristine.

			Carbon sequestration		**Water quality regulation**			**Flood attenuation**	
Wetland	State	Extent (km^2)	Measured (m^3/a)	Score	N Uptake (mg/s)	P Uptake (mg/s)	Score	Measured (%)	Score
Theew.	D	0.09	69.2	1.3	-309.57	-60.56	1.3	11.6	1.7
	P	0.60	450.7	4.0	427.29	129.32	2.4	97.0	1.8
Goukou	D	0.26	206.7	1.0	-480.64	-94.02	2.2	5.7	1.6
	P	0.31	247.3	4.0	220.77	66.81	2.4	97.0	1.6
	P	0.52	409.4	4.0	370.32	112.08	2.5	97.0	1.4
Kromme	D	0.06	43.7	0.7	-553.96	-108.36	2.5	0.5	2.3
	P	0.60	430.6	4.0	427.29	129.318	2.6	97.0	2.7
Mean Degraded		*0.10*	*79.90*	*0.75*	*-336.04*	*-65.74*	*1.50*	*5.9*	*1.40*
Mean Pristine		*0.51*	*384.50*	*4.00*	*361.42*	*109.38*	*2.48*	*97.0*	*1.88*

If the 16.79 km^2 of palmiet wetland identified in **Chapter 3** are lost to channel erosion or other degradation, it would represent a total estimated loss of 12 758.1 $m^3.a^{-1}$ of peat formation on average (from 12 086.6 – 13 261.7 $m^3.a^{-1}$), as well as the release of thousands of years' worth of stored carbon into the atmosphere (estimated 5000-6000 years (Job, 2014; Nsor, 2007, **Table 8**)). An estimated water purification capacity of roughly 10 g of nitrogen (66.6 $kg.ha^{-1}.a^{-1}$) and 3 g phosphorus per second (222.1 $kg.ha^{-1}.a^{-1}$) would be lost with damage to this ecological infrastructure. Additionally, nutrient uptake efficiencies are estimated to be 55±33.0% for phosphorus, and 59±26.4% for nitrogen (**Table 3**). Finally, a loss of these palmiet wetlands would represent a loss of an estimated 60.97% flood reduction capacity overall (0.6-96.9%). This flood attenuation capacity represents significant protection for downstream agriculture, infrastructure and safety to people (Rebelo, 2012).

Table 8. Palmiet wetland ecosystem service provision as a function of wetland area (km^2) in eight different wetland remnants. Carbon sequestration is given as mm peat formation per annum based on an accumulation rate of 0.76 mm/a. Water purification is based on nutrient uptake rates of N and P of 0.71 g.km^{-2}.s^{-1} and 0.22 g.km^{-2}.s^{-1} respectively. Water regulation is given as the reduction of floods (%), based on the percentage of the valley bottom occupied by the wetland.

Location	Catchment	Extent (km^2)	Carbon sequestration (m^3/a)	Water purification N uptake (mg/s)	Water purification P uptake (mg/s)	Water regulation % of valley bottom	Water regulation % flood reduction
Citrusdal	Berg Catchment (G)	0.27	205.2	192.3	58.2	4.6	0.59
		1.26	957.6	897.3	271.6	18.5	15.96
Theewaterskloof	Breede Catchment (H)	2.43	1846.8	1730.5	523.7	53.8	96.93
		2.92	2222.6	2082.7	630.3	41.2	95.34
Duivenhoks		1.20	908.9	851.7	257.8	38.6	93.87
Goukou		5.80	4408.0	4130.5	1250.1	42.3	95.73
George	Tsitsikamma Catchment (K)	0.82	620.6	581.5	176.0	31.4	80.71
Kromme		2.09	1588.4	1488.4	450.5	15.7	8.64
Total *(Mean)*		16.79	12758.1	*11954.9*	*3618.1*	30.76	*60.97*

9.4 Discussion

An important trade-off appears to exist between the potential food provision of these wetlands and water-related ecosystem services, such as water provision, purification, flood attenuation, as well as with carbon storage. This is evidenced by the fact that pristine wetlands score higher for water-related ecosystem services and carbon storage, and wetlands degraded by agriculture tend to score lower. Interestingly, degraded wetlands only score slightly higher for food provision (cultivated foods) than pristine wetlands. This may be because this ecosystem service is scored not only on the total number of crops cultivated in the hydro-geomorphic unit, but also takes into account the opportunity for supply, with an emphasis on supplying impoverished communities (location of hydro-geomorphic unit in rural communal area, level of poverty, number of households depending on crops, and substitutability of the crops). However commercial cultivation and grazing takes place in the wetlands of the Goukou and Kromme, with little subsistence farming or none at all. Commercial agriculture takes place in these wetlands despite them being listed as South African Resources Agency sites.

Agriculture on the valley floor is at risk of high energy floods characteristic of this wetland type (Rebelo et al., 2015). This leads to marginal agriculture, except where extreme, and illegal, river engineering is undertaken on the valley bottom. As an example: canalization, dredging and the building of berms has been done in the Kromme wetland to protect fruit orchards within the last 10 years (Rebelo, 2012). From the results, it seems that this type of wetland degradation, benefitting one landowner, can be expected to affect water-related ecosystem services for landowners downstream, as well as society at large. To continue with this specific example from the Kromme, the degradation is likely to affect landowners downstream (increased risk of flooding, increased sedimentation, a decrease in water quality), the population of the city Port Elizabeth (decreased water supply in the dry season, increased expense for purifying water, siltation of the Churchill Dam), as well as South Africa at large (increased CO_2 release and loss of ecological infrastructure capable of sequestering carbon). Other studies have noted this loss of ecosystem service provision with loss of wetland integrity (McLaughlin and Cohen, 2013; Zedler and Kercher, 2004).

The reason that degraded wetlands scored highly for maintenance of biodiversity on the rapid assessment was that degraded wetlands – those with cultivation – provide habitats for International Union for Conservation of Nature listed species, such as the Blue Crane (*Anthropoides paradiseus*). However, the Kromme wetland in particular is also known to be home to endangered species of Redfin, endemic to that catchment, whereas Blue Cranes occur on many farmlands. This is not taken into account in the rapid assessment. Additionally, scores for maintenance of biodiversity are assessed based on 'opportunity' (i.e. alteration of ecological regimes, loss of indigenous vegetation, invasion by alien species), which reduces the difference between the score of degraded and pristine wetlands. Degraded wetlands also have a high number of alien plant species, the most damaging of which are invasive, such as Black Wattle (*Acacia mearnsii*), Poplar (*Populus sp.*) and Bramble (*Rubus fructicosus*) (Rebelo et al., 2015). Unlike many other wetland ecosystems, palmiet wetlands have low cultural significance. In fact, it is likely that degraded palmiet wetlands would hold more cultural significance as people tend to prefer open bodies of water for activities such as swimming. There are historical records of indigenous Khoe-San people using pristine palmiet wetlands, however knowledge on these wetlands beyond their source of food (edible apical meristems of Palmiet) has been lost (De Vynck et al., 2016; Skead, 2009).

Three ecosystem service complexes

It must be emphasized that these results are only estimates and they are based on values which have high uncertainty (see methods for details). However, it is certain that the direction of these estimations is correct: that with a loss of wetlands, there would be a loss of ecosystem services. Therefore, these estimations are still useful as they help to highlight the importance of these wetlands. It is clear that losing the remaining palmiet wetland fragments would represent a significant loss of ecological/green infrastructure (or naturally functioning ecosystems that deliver ecosystem services to society (Benedict and McMahon, 2006)).

Water purification estimates compare well with those of other studies, for example uptake rates of 0.13-10 kg $P.ha^{-1}.a^{-1}$ and 52-337 kg $N.ha^{-1}.a^{-1}$ were found in Danish riparian wetlands (Hoffmann et al., 2011), and 2.7 kg $P.ha^{-1}.a^{-1}$ and 339 kg $N.ha^{-1}.a^{-1}$ in constructed wetlands in Illinois, USA (Hoagland et al., 2001). Restored wetlands in Illinois and Iowa, USA, had uptake efficiencies of 68% nitrogen and 43% phosphorus (Woltermade, 2000), and 47% nitrogen and 29% phosphorus in constructed wetlands in Illinois (Hoagland et al., 2001). The loss of the water purification ecosystem service in palmiet wetlands could occur in two ways: either through pollution or through the loss of the wetlands through erosion or removal for agriculture (**Chapter 4**). Pollution of palmiet wetlands through agricultural runoff will make use of the water purification ability of these wetlands, however this too will have a cost, in terms of declining capacity with use, and impacts on biodiversity (Verhoeven et al., 2006). Reduction of palmiet wetland area combined with degradation in other parts of the catchment (e.g. increased fire return interval on the mountains) has been shown to increase flood response (Rebelo et al., 2015). Historically this has resulted in increased damage, in terms of loss of agriculture (orchards washing away), damage to infrastructure such as roads and bridges and even death (Rebelo, 2012).

An assessment of the rapid ecosystem services tool

The WET-Ecoservices tool was useful for rapid assessments of palmiet wetlands, to give an idea of the overall ecosystem service trade-offs and synergies for degraded compared to pristine wetlands. However, when these relative differences between degraded and pristine wetlands were compared with the results of three ecosystem services which had been estimated in more detail, it seemed that the rapid assessment scored degraded wetlands higher than they should. This is particularly evident for the ecosystem service flood attenuation and water purification. The reason for these unrealistically high scores seems to be the fact that ‘opportunities for improvement’ are included in the final score along with ‘effectiveness’. Opportunities for improvements within the pristine wetlands are lower than the degraded wetlands, as they already supply the highest level of ecosystem services they are intrinsically able to provide. The authors do recognize this limitation, and suggest that where appropriate, both scores should be reported (Kotze et al., 2007). However, upon scrutiny, we decided to leave these scores as an average because we considered the ‘opportunities for improvement’ to be less about future improvements and more about whether there were beneficiaries for the ecosystem services, and whether there was in fact a need for the ecosystem services at all. For example, the ecosystem service flood attenuation lists the following as ‘opportunities for improvement’: average slope of the wetland's catchment, inherent runoff potential of soils in catchment, contribution of catchment land-uses to changing runoff intensity from the natural condition, rainfall intensity and extent of floodable property downstream.

It seems highly appropriate that these factors are considered in the scoring of the ecosystem service. Rather, it seems that the problem of the scoring lies in its inappropriateness for this particular hydro-geomorphic type: valley-bottom wetlands. It seems better suited to floodplain wetlands. For example, the ecosystem service is scored on: the size of the wetland, the slope, the surface roughness, presence of depressions, frequency of stormflows, sinuosity of the channel and representation of different hydrological zones. These pristine valley-bottom palmiet wetlands do not have channels nor depressions, and most of the other parameters are constant for the catchment. Therefore degraded wetlands are incorrectly scored similarly to pristine ones. It is recommended that for the valley-bottom hydro-geomorphic unit, different parameters are used for scoring regulating ecosystem services, such as presence of a channel or other erosion, loss of native vegetation due to alien invasion, height/density of the vegetation, width of the valley, amongst others.

Implications for decision making

The WET-Ecoservices tool is particularly useful for rapid appraisals of wetland ecosystem services of most South African hydro-geomorphic units. However, for unchannelled valley-bottom wetlands, there appear to be some challenges, especially for water-related ecosystem services, whereby pristine wetlands are underscored. This could present challenges for decision-makers using this tool, who might decide that agriculture is beneficial holistically, because degradation would not appear to affect ecosystem service supply significantly. However, if analyzed in a little more depth, as done in this study, it is possible to understand where the issues lie, and to adapt the tool for this hydro-geomorphic unit accordingly. It is still a valuable way to understand the relevant trade-offs and synergies between ecosystem services. From the results, it is clear that pristine palmiet wetlands provide valuable ecosystem services to society, both to downstream users and society as a whole. Nowadays most planning, management and development decisions regarding the conservation of wetlands are implemented based on economic grounds and the forces at play within the free-market system (Bullock et al., 2011). Therefore, agriculture and wetland conservation will always be in conflict, as farming is a business and farmers need to make a living (van der Valk and Jolly, 1992).

With a decline in governmental support for conservation within and outside protected areas, a greater pressure to create innovative and maintainable solutions for endorsing and financing conservation is needed. Payments for Ecosystem Services is a tool that has the potential for playing a vital role in reaching conservation goals and supporting ecosystem health in a more general sense (Blignaut et al., 2010; Turpie et al., 2008). The aim of Payments for Ecosystem Services is to remunerate those who are providing ecosystem services as an incentive to protect the system from development, or to restore the system. This involves quantifying ecosystem service provision, and valuing these ecosystem services, and introducing them into the economy (Bullock et al., 2011). Governments may be willing to invest in the protection of ecosystem services that have a tangible (economic) benefit, such as water provision (Tallis et al., 2008). In the case of palmiet wetlands, at least two occur upstream of important dams for large cities (the Kromme for Port Elizabeth and the Theewaterskloof for Stellenbosch and Cape Town). Therefore, there is certainly scope to create an argument for the protection of these palmiet wetlands through a Payments for Ecosystem Services system. Organizations such as ‘Living Lands’ in the Kromme have the potential to act as landscape mobilizers, by improving collaboration between the different stakeholders and beneficiaries of these ecosystem services in the landscape (Cowling et al., 2008). One successful example of this strategy is that of the Catskill Catchment in New York (Postel and Thompson, 2005), where holistic farm planning was developed as an attempt to decrease pollution of the watershed. In this system, farmers were incentivized to pollute less, by having their operational and capital costs of investment into pollution control covered by the city of New York. Through collaboration, cost efficiency was achieved and private as well as social benefits realized.

9.5 Conclusion

Pristine palmiet wetlands provide valuable ecosystem services to society, which are currently being compromised for private gain. These pristine wetlands sequester between 23.4-61.6 m^3 of organic carbon per year, have nitrogen and phosphorus uptake efficiencies of 62.0-84.9% and 16.2-88.7% respectively and provide about 16 times more flood attenuation relative to degraded wetlands. The full impact of degradation on wetland ecosystem services was not entirely captured by the rapid ecosystem service assessment tool: WET-Ecoservices. We suggest some adaptations for the hydro-geomorphic unit: valley-bottom wetlands. Overall these wetlands have high potential for incorporation into a Payments for Ecosystem Services scheme, due to their position above important municipal dams. We recommend collaboration between private landowners struggling with marginal agriculture, and decision makers in cities dealing with water shortages and debt to ensure the most efficient and judicious use of these palmiet wetland ecosystem services.

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9.8 Appendix

Table A1. Characteristics of each of the three South African palmiet wetlands investigated in this study (VB: 'valley-bottom' wetland)

	Theewaterskloof		Goukou			Kromme	
Condition	Degraded	Pristine	Degraded	Pristine 1	Pristine 2	Degraded	Pristine
Hydro-geomorphic Unit	Channelled VB	Unchannelled VB	Channelled VB	Unchannelled VB	Unchannelled VB	Channelled VB	Unchannelled VB
Size of catchment (ha)	52.98	61.80	187.55	24.27	59.35	159.32	55.37
Ave slope of catchment (%)	19.7	18.0	2.7	24.6	9.3	21.0	25.13
Size of original wetland (ha)	38.2	59.7	59.2	31.1	51.5	68.3	59.8
Ave slope of wetland (%)	2.00	3.70	1.29	2.91	4.91	3.43	2.39
Cover of indigenous vegetation (%)	1-5	>50	1-5	>50	>50	<1	>50
Cover of alien vegetation (%)	>50	<1	<50	<1	<1	<50	1-5
Average rainfall (mm/a)	530	530	589	589	589	614	614
Rainfall intensity zone	High	High	High	High	High	High	High
Hydrological zones	Seasonal, but lacking permanent	Seasonal & permanent, collectively >60%	Seasonal, but lacking permanent	Seasonal & permanent, collectively >60%	Seasonal & permanent, collectively >60%	Seasonal, but lacking permanent	Seasonal & permanent, collectively >60%
Underlying geology	Sandstone	Sandstone	Sandstone	Sandstone	Sandstone	Sandstone	Sandstone
Location city/town	Villiersdorp	Villiersdorp	Riversdale	Riversdale	Riversdale	Kareedouw	Kareedouw
Associated river	Riviersonderend	Riviersonderend	Goukou	Goukou	Goukou	Kromme	Kromme
Cities dependent on water supply	Stellenbosch	Stellenbosch				Port Elizabeth	Port Elizabeth

Table A2. A detailed overview of the measures used to score each wetland ecosystem service (adapted from Kotze et al., 2007). All wetlands were scored according to their 'effectiveness' in providing regulating ecosystem services, as well as the 'opportunities' for the enhancement. For provisioning and cultural ecosystem services, 'noteworthiness' was considered. HGM: Hydrogeomorphic.

Ecosystem service		**Definition**	**Parameters used to assess the ecosystem service provided (scored from 0-4)**
Regulating and supporting ecosystem services	Flood attenuation	The spreading and slowing down of flood waters, resulting in the reduction of severity of floods downstream and the potential damage that flooding may cause.	*Effectiveness:* Size of wetland relative to catchment, Slope of wetland, Surface roughness of wetland, presence of depressions, Frequency with which stormflows spread across the wetland, Sinuosity of the stream channel, Representation of different hydrological zones. *Opportunities:* Average slope of the wetland's catchment, Inherent runoff potential of soils in catchment, Contribution of catchment land-uses to changing runoff intensity from the natural condition, Rainfall intensity, Extent of floodable property downstream
	Stream flow regulation	The sustaining effect of a wetland on downstream flow during low flow periods.	*Effectiveness:* Link to stream network, Representation of different hydrological zones, Presences of fibrous peat or unconsolidated sediments below floating marsh, Reduction in evapotranspiration through frosting back of the wetland vegetation, HGM unit occurs on geology with strong surface-groundwater linkages, Presence of any important wetlands or aquatic systems downstream. *Opportunities:* None.
	Sediment trapping	The trapping and retention of sediment carried by runoff waters.	*Effectiveness:* Effectiveness of HGM unit in attenuating floods, Direct evidence of sediment deposition in the HGM unit. *Opportunities:* Extent to which dams are reducing the input of sediment to the HGM unit, Extent of sediment sources delivering sediment to the HGM unit from its catchment, Presence of any important wetland or aquatic system downstream.

Phosphate removal	The removal of phosphates carried by run off waters, enhancing water quality in the downstream catchment.	*Effectiveness:* Effectiveness in trapping sediment, Pattern of low flows within the HGM unit, Extent of vegetation cover, Extent to which fertilisers/biocides are added directly to the HGM unit *Opportunities:* Level of sediment input, Extent of potential sources of phosphate in the HGM unit's catchment, Presence of any important wetland or aquatic system downstream.
Nitrate removal	The removal of nitrates carried by run off waters, enhancing water quality in the catchment.	*Effectiveness:* Representation of different hydrological zones, Pattern of low flows within the HGM unit, Extent of vegetation cover, Contribution to sub-surface water inputs relative to surface water inputs, Extent to which fertilizers/biocides are added directly to the HGM unit. *Opportunities:* Extent of nitrate sources in the HGM unit's catchment, Presence of any important wetland or aquatic system downstream.
Toxicant removal	The removal of toxicants carried by run off waters, enhancing water quality in downstream catchment.	*Effectiveness:* Representation of different hydrological zones, Pattern of low flows within the HGM unit, Extent of vegetation cover, Effectiveness in trapping sediment, Extent to which fertilizers/biocides are added directly to the HGM unit. *Opportunities:* Level of sediment input, extent of toxicant sources in the HGM unit's catchment, Presence of any important wetland or aquatic system downstream.
Erosion control	The control of erosion at the site through on-site factors that prevent the loss of soil from the HGM unit.	*Effectiveness:* Direct evidence of active erosion in the HGM unit, Vegetation cover, Surface roughness of the HGM unit, Current level of physical disturbance of the soil in the HGM unit. *Opportunities:* Slope of wetland, Erodability of the soil, Runoff intensity from the wetland catchment.

	Carbon storage	The trapping of carbon.	Hydrological zones, Abundance of peat, Level of soil disturbance in wetland.
	Maintenance of biodiversity	The provision of habitat and maintenance of natural processes, contributing to the maintenance of biodiversity.	*Noteworthiness:* The wetland type is rare or has become rare due to habitat transformation. Level of cumulative loss of wetlands in the overall catchment, Red data species or suitable habitat for Red data species, Level of significance of other special features. *Opportunities:* Extent of buffer around wetland, Alteration of hydrological regime, Alteration of sediment regime, Alteration of nutrient/toxicant regime, Complete removal of indigenous vegetation, Invasive and pioneers species encroachment, Presence of hazardous restrictive barriers.
Provisioning ecosystem services	Provision of water supply for direct human use	The provision of water for direct human use (water extraction directly from a wetland area for domestic, agricultural and other purposes).	Hydrological zones, Importance for stream flow augmentation, Current use for agricultural purposes, Current use for domestic purposes, Number of households, Substitutability of wetland water sources.
	Provision of harvestable natural resources	The wide variety of harvestable resources availability in wetlands, which are often important from a livelihoods perspective.	Total number of harvestable resources, Location in rural communal area, Level of surrounding poverty, Number of households depending on the wetland, Substitutability of the wetland resources.
	Provision of cultivated foods	The contribution towards food security of subsistence farmers.	Total number of different crops cultivated in the HGM unit, Location in rural communal area, Level of poverty, Number of households who depend on the crops cultivated in the HGM unit, Substitutability of the crops cultivated in the land.
Cultural ES	Cultural significance	Significance for a diversity of different culturally significant plants that provide in terms of being places of special cultural significance.	Registered South African Heritage Resources Agency site, Location in a rural communal area, Known cultural practices, Known taboos/beliefs.

Tourism, recreation and natural scenic beauty	The value of sites for tourism and recreation in terms of abundant wildlife, their scenic beauty and the open water that some wetlands provide for recreation.	Scenic beauty of the HGM unit, Presence of "charismatic" species, Currently used, Suitable locations for facilities, Location within a tourism route, Recreational hunting and fishing opportunities, Extent of open water.
Education and research	The value for education and research, particularly when they are readily accessible.	Currently used, Reference site suitability, Existing long term research and data collected, Accessibility.

Table A3. A summary of the scores for each ecosystem service for each wetland. ES: ecosystem services.

	Theewaterskloof		Goukou			Kromme	
	Degraded	Pristine	Degraded	Pristine	Pristine	Degraded	Pristine
Flood attenuation	1.4	1.8	1.6	1.7	1.6	2.2	2.7
Streamflow regulation	1.8	2.8	2.3	3.2	3.2	2.2	3.2
Sediment trapping	1.1	2.5	1.7	2.5	2.6	2.1	2.7
Phosphate assimilation	1.0	2.4	1.9	2.2	2.4	2.2	2.5
Nitrate assimilation	1.6	2.4	2.2	2.7	2.6	2.5	2.8
Toxicant assimilation	1.1	2.5	2.0	2.5	2.6	2.3	2.7
Erosion control	1.6	3.1	1.3	2.9	2.6	1.6	3.3
Carbon storage	1.3	4.0	1.0	4.0	4.0	0.7	4.0
Biodiversity maintenance	3.0	3.3	3.5	3.8	3.8	3.5	4.0
Regulating ES (mean)	1.54	2.75	1.94	2.83	2.82	2.13	3.1
Water supply (human use)	2.6	3.1	2.2	2.7	2.7	2.7	3.4
Harvestable resources	2.0	2.0	2.2	2.2	2.2	1.8	2.4
Cultivated foods	0.0	0.0	2.6	1.8	1.8	2.0	1.4
Provisioning ES (mean)	1.53	1.70	2.33	2.23	2.23	2.17	2.4
Cultural significance	1.0	1.0	1.5	1.5	1.5	1.3	1.3
Tourism and recreation	1.9	1.4	0.6	1.3	1.4	1.6	1.3
Education and research	1.8	2.5	1.8	2.3	2.3	2.0	2.5
Cultural ES (mean)	1.57	1.63	1.30	1.70	1.73	1.63	5.1
Sum of scores	23.2	34.8	28.4	37.3	37.3	30.7	40.2
Average score	1.5	2.3	1.9	2.5	2.5	2.0	2.7
Threats	4.0	4.0	3.0	1.0	2.0	4.0	4.0
Opportunities	3.0	2.0	4.0	1.0	2.0	3.0	2.0

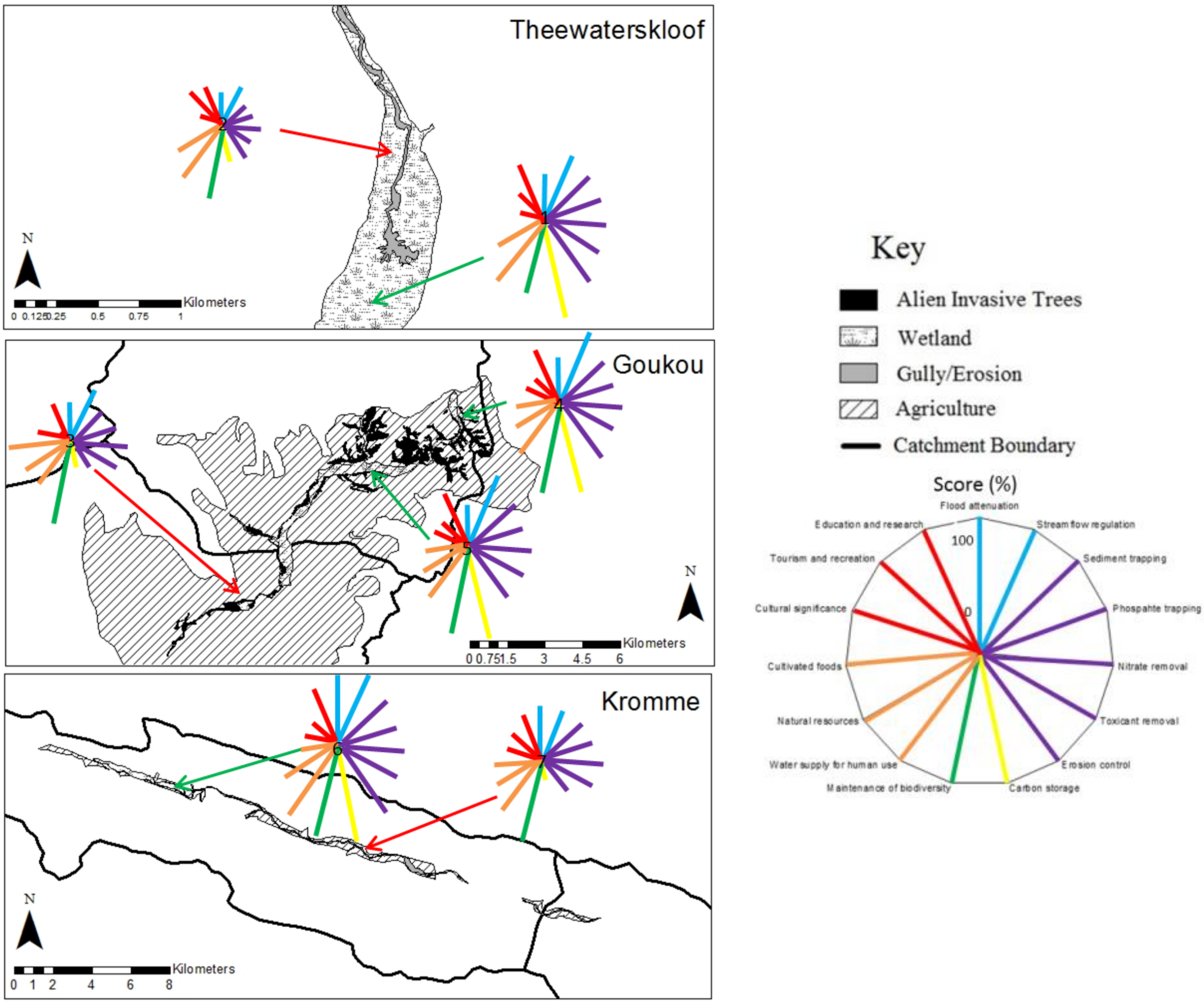

Figure A1. A spatial illustration of the trade-offs & synergies of ecosystem services among three South African palmiet wetlands. Green arrows show the location of pristine wetlands and red arrows degraded wetlands. ■ Blue indicates water-related ecosystem services, ■ purple indicates those related to water quality, ■ yellow indicates carbon storage, ■ green is the maintenance of biodiversity, ■ orange is provisioning ecosystem services including food and water, and lastly ■ red indicates cultural ecosystem services.

10

Synthesis

Fieldwork in a pristine palmiet wetland with three fantastic assistants, from left to right: Timothy De Kleyn, Byron-Mahieu van der Linde and Courtney Morris. Palmiet (*Prionium serratum*) at the centre.

10.1 Introduction

The aim of this dissertation was to develop an understanding of the composition and functioning of South African palmiet wetland systems and how these relate to ecosystem services (ES) provided by these wetlands. In doing so, the aim was to further the theoretical understanding of the links between functional diversity and ecosystem function. It was beyond the scope of this study to measure ecosystem processes in the field, and therefore proxies for ecosystem function were used, such as microbial biomass (nutrient cycling, decomposition), biomass (productivity) and foliar cellulose and lignin (decomposition). Palmiet wetlands were selected as a study system because (1) they are a unique wetland system, (2) they are known to provide multiple ecosystem services to society, (3) there has been very little research on them to date and (4) they are highly threatened ecosystems. The main motivation behind this research was to contribute to knowledge that can inform conservation and restoration efforts of palmiet wetlands, and possibly to even inform policy and land-use planning.

The value that palmiet wetlands provide to society in terms of the provision of ecosystem services is not fully appreciated, largely because their value has not been adequately quantified nor properly understood. The overall nature of this work was therefore exploratory. A series of eight chapters involving a systematic literature review and a combination of fieldwork, mapping and remote-sensing techniques addressed this aim. In this synthesis chapter I draw together the main findings and conclusions of this research, as well as discuss its implications, outline the numerous opportunities for future research and suggest possible management recommendations.

10.2 Ecosystem services: what have we learnt?

When trying to develop a list of scientifically sound measures for ecosystem services in palmiet wetlands, I found that there was a lack of consensus on which measures to use, and that some measures were simply wrong or inadequate at quantifying the ecosystem service in question. Therefore, I recognised a need for an overview of the ecosystem services used in assessments to date. To this end, I collaboratively performed a systematic review of 408 peer-reviewed ecosystem service research papers to address the question: is the biophysical reality of ecosystem services adequately quantified? (**Chapter 2**). We realized that very few measures fulfilled the definition of 'ecosystem service' by failing to capture information from both the ecosystem and the benefit to society, thereby not bridging the gap between nature and society. In this review we assessed each ecosystem service measure both in terms of its scientific veracity (e.g. uncertainty quantified or validation done), as well as to establish which part of the ecosystem service cascade was being quantified (Haines-Young and Potschin, 2010).

Overall we found the field of ecosystem services to be wanting. Measures of uncertainty are often not included in ecosystem service studies and validation and stakeholder engagement are mostly missing. Most ecosystem services were poorly quantified and the gap between nature and society was often not successfully bridged. For example, we found that most ecosystem service measures for food production were linked to the quantification of the benefits to society (e.g. crop yield in kg/ha) without linking this to what the ecosystem was able to provide, nor what was sustainable from an ecological point of view. This is problematic for a concept that is purported to 'bridge the gap' between nature and society, and could mislead stakeholders and policy-makers. Six recommendations were proposed to improve this situation in the future (described below). We also produced a resource that lists measures used or proposed for the quantification of all ecosystem services we analysed. This was useful in future chapters of this dissertation, where adequate measures for three key wetland ecosystem service complexes had to be selected (Moor et al., 2017).

The six recommendations were: (1) Researchers should make an effort to consider bridging the gap, i.e. considering both sides (ecological and socio-economic aspects) of the ecosystem service cascade. This may not be possible in every situation; however, researchers should be aware of and be explicit about which aspect of the cascade they are considering, and recognize the limitations of quantifying only one side of the ecosystem service cascade. (2) We highlight the need for more research on the relationships between ecosystem services, and consensus on what constitutes an ES. We suggest that some ecosystem services may not be 'final', in the sense that measures are often only approximating ecosystem functions, and may well underpin other ecosystem services (e.g. soil quality regulation which may underpin the delivery of *inter alia* food production, which is the tangible benefit to society). (3) We recommend stricter definitions for what is an acceptable measure to use for an ecosystem service, in order to prevent poor science. However, this is contested and many researchers argue that the vagueness in the definitions of ecosystem services and the ecosystem service concept as a whole encourages creativity and transdisciplinary collaboration (Schröter et al., 2014). (4) We recommend some consensus on which components need to be measured for an ecosystem service to be considered 'quantified'. By components we mean the many different, sometimes conflicting, elements making up a particular ecosystem service (e.g. see Moor et al. 2017). The classic example is that of climate regulation, which is made up of many components such as climate moderation and the sequestration of CO_2, CH_4 and NO_2. (5) We suggested that the rigor of accepted indicators should be adequately assessed, as some indicators are very weak (some constituting only stocks e.g. g or ha or $g.ha^{-1}$). (6) Lastly, we call for methods to be reported transparently, for validation to be done where appropriate, and that some effort is made to estimate uncertainty.

This research was published at the end of 2015, and to date the debate around these issues continues; with many researchers favouring the flexibility the current ambiguity affords (Schröter et al., 2014). Despite the debate around its definitions, classifications and naming conventions, the ecosystem service concept is an essential tool – sometimes the only tool – to motivate for the protection, conservation or restoration of ecosystems (Daily et al., 2009; Ingram et al., 2012), and in this case: palmiet wetlands.

10.3 Palmiet wetlands: what have we learnt?

Palmiet wetland distribution

The logical first step in this doctoral research on palmiet wetlands was to determine (a) their distribution: where these wetlands persist, (b) their extent: what remains of them, (c) their historical extent: how their spatial distribution has changed over time and (d) what the main drivers of this change are (**Chapter 3**). I used a combination of aerial photograph analysis, multispectral remote-sensing techniques and modelling to map current and historical wetland distribution and extent. For locating current palmiet wetland distribution, multispectral remote-sensing was deemed the best technique; however, for accurate determination of the extent of these small, narrow wetlands, aerial photograph mapping techniques were found to be superior. For historical extent of known palmiet wetlands, aerial photograph mapping techniques were also the best approach. However in terms of understanding the historical distribution of palmiet wetlands before colonial land-use change, no ideal technique was identified. Therefore, there is still some uncertainty as to the pre-colonial extent of these wetlands throughout valley-bottoms in the Cape Floristic Region of South Africa. The eight palmiet wetland fragments that were mapped in this chapter declined in extent by an average of 31% since 1940. Considering the uncertainty about the pre-colonial extent of these wetlands, the actual loss is probably higher. Nevertheless this percentage is lower than the global average for wetland loss (64-71%) (Gardner et al., 2015).

The habitat quality of remaining valley-bottom palmiet wetlands has also declined over the past 60-70 years, with the wetlands becoming increasingly fragmented and channelized. Most of these significant changes took place between the 1940/50s and the 1980s, though it is clear from the earliest photographs that major changes to these systems had already taken place before the first aerial photographs were available (1940s). The major driver causing this wetland fragmentation, and ultimately destruction, was the construction of roads across these valley-bottom wetlands. These roads, or their construction, formed knick-points which caused destabilization of the alluvium, headcut or gully erosion (de Haan, 2016) and eventually channelization of these typically unchannelled systems. Additionally, gully erosion was found to not take place gradually, but abruptly after large flood events, such as one-in-ten-year floods. This gradual gully development has also been observed in the Ethiopian Highlands (Carnicelli et al., 2009). The resulting wetland drainage, or drop in water table, has facilitated invasion by alien species, often trees, which further perpetuates the cycle of degradation. Agriculture either alongside the wetland, or on the alluvium itself, poses another great threat to wetland integrity as described in **Chapter 4**. These conclusions are in agreement with those of a geomorphological study of the rehabilitation structures for gully erosion in Kromme palmiet wetland (de Haan, 2016). It is concluded that although gully erosion is a natural phenomenon, anthropogenic impacts have accelerated it (de Haan, 2016).

The impacts of degradation on palmiet wetlands

The second logical step towards achieving the dissertation aim was to develop an understanding of baseline abiotic conditions, community composition and how these interact. By measuring abiotic parameters and vegetation composition in degraded and pristine sections of selected palmiet wetlands, I answered the research question: 'what is the impact of degradation on South African palmiet wetlands?' (**Chapter 4**). The main form of degradation in these wetlands was considered: channel/gully erosion. To address this question, I measured vegetation community structure, and soil, groundwater and vegetation parameters in 39 plots in three palmiet wetlands located within the Cape Floristic Region. A loss of alluvium, through channel erosion, resulted in lower soil organic matter and water content and was highly leached, unable to retain nutrients and cations. This resulted in more eutrophic groundwater in terms of nitrogen, and certain cations (Ca^{2+}, Mg^{2+}, Na^{+}) with higher conductivity and pH. The loss of alluvium typically resulted in a completely new plant community, composed mostly of pioneer species with several alien species. The increase in base saturation and soil pH was thought to be the result of runoff from liming practices. Since the research was purely of an exploratory nature, it is not possible to draw conclusions about the mechanisms behind the impacts of degradation from agricultural pollution. However, it is clear that there are some biochemical consequences of agricultural runoff on these palmiet wetlands, which may be an interesting avenue for future research.

Palmiet wetland ecology

The second major observation was the patchy nature of palmiet wetland vegetation communities. Some patches were dominated by palmiet and others by various fynbos species. Therefore, I asked the research question: 'what drives patchiness in plant community composition in South African palmiet wetlands?' (**Chapter 5**). In this chapter I was interested in palmiet wetland vegetation ecology, and sought to determine whether plant functional traits could help unravel the mechanisms behind the patterns observed. I found that soil pH and relative groundwater depth were the main environmental parameters related to plant community assembly in palmiet wetlands. Soil pH was higher for palmiet communities, whereas relative groundwater depth tended to be closer to the surface but more variable for fynbos communities, and deeper below the ground for palmiet communities in the two seasons that I took measurements (September 2014, March 2015). However, I suggest that long-term research is needed to understand the relationship between relative groundwater depth and vegetation community assembly in palmiet wetlands. Community weighted means for stem diameter, leaf length-width ratio, leaf area, as well as cellulose and lignin concentration, were higher in palmiet communities compared to the fynbos ones. These differences in plant functional traits may suggest that palmiet communities, though fire adapted (Boucher and Withers, 2004), are fire retardants (thicker stems) and are adapted to floods (long, thin leaves and flexible shoots). This differs from fynbos communities, which are fire promoters, and recover either by resprouting or by germinating from fire-activated seedbanks (Keeley and Fotheringham, 2000), and are not adapted to floods.

From my findings, I hypothesize that palmiet communities are the climax community of palmiet wetlands, and that the fynbos communities are pioneers. I hypothesize that severe disturbances in palmiet wetlands that kill patches of palmiet-dominated communities (e.g. mainly fires that burn into the wetland), result in fynbos vegetation establishment, as it grows faster than palmiet. Over time, however, palmiet communities slowly invade, typically clonally, favoured by flood events, or long periods of inundation. These hypotheses will need to be opportunistically tested, after severe fire events.

In an exercise (**Chapter 6**), I attempt to untangle relationships between key wetland ecosystem services, plant functional traits and ecosystem properties. This short chapter was more fundamental in nature, and in line with the aim of this dissertation: to 'further the theoretical understanding of the links between functional diversity and ecosystem function'. To this end I used the framework of Díaz et al. (2007) to investigate the following research question: 'can ecosystem properties (which can in turn be related to ecosystem function or to the provision of specific ecosystem services) in palmiet wetlands be explained by abiotic factors, community weighted mean trait values, functional diversity indices (trait value distribution) or a combination of these?'. Three key wetland ecosystem services complexes were considered: water regulation, water purification and carbon sequestration (Moor et al., 2017). I found that both abiotic variables and community weighted means of plant functional trait values were important in explaining ecosystem properties of palmiet wetlands; abiotic variables slightly more so. Functional diversity indices seemed to have little influence. Results were not consistent between the two seasons studied (September 2014 and March 2015) and I propose two possible reasons for this. The first is that perhaps the relationships between ecosystem processes and functional diversity in wetlands are more complicated than those of other ecosystems, for example the sub-alpine grasslands used in the first application of this framework, in Díaz et al. (2007). The second is that I used a large number of input variables in these models (n_{2014}=89, n_{2015}=87), as I had collected large amounts of data for other chapters. It is possible that this method is not robust enough to model ecosystem processes when many input variables are entered, some of which may be more important than others. It may be necessary to be more selective with input variables, which would mean that this approach is less useful as an exploratory method in cases where the main drivers of ecosystem processes or services are not fully known.

Application

The main motivation behind this research was to 'contribute to knowledge that can inform conservation and restoration efforts of palmiet wetlands'. Given this goal, it is necessary that research of a more applied nature is undertaken in addition to the fundamental research. To this end, I saw two opportunities. First, to see whether spectral signatures of dominant wetland species could be used to discriminate between plant functional groups in palmiet wetlands (**Chapter 7**). By establishing that plant functional traits respond to changes in ecosystem properties and functions (**Chapter 6**), it became clear that vegetation composition could be used as an indicator for ecosystem service delivery, or to identify ecosystem service hotspots. Therefore, I attempted to determine if hyperspectral remote-sensing techniques could be used to map plant functional groups in wetlands in order to have a better understanding of the spatial distribution of ecosystem services within these wetlands. Second, I attempted to quantify the ecosystem services provided by palmiet wetlands (**Chapters 8, 9**). Ecosystem service provision of palmiet wetlands was compared between pristine and degraded sections so as to understand what the trade-off or loss of these ecosystem services, with degradation, would entail for society.

There were two main findings from the research on spectral discrimination of plant functional groups (**Chapter 7**). Firstly, several plant functional traits were related to, and were predictable from, leaf and stem reflectance spectra. These seven traits were: leaf area (positively correlated with reflectance spectra across the entire spectrum), structural components lignin and cellulose, expressed per leaf mass (corresponding especially with the NIR portion of the spectrum), leaf mass, leaf length/width ratio, lignin content (%) and tissue C/N ratio. Redundancy analysis suggested that half of the spectrum was not explained by the plant functional traits measured in this study. This means that for dominant palmiet wetland species, other traits may be important in influencing their reflectance. Literature suggests that these may be biochemical traits (Klančnik et al. 2014, Klančnik et al. 2012, Klančnik & Gaberšcik 2016). This has implications for future ecological studies with remote-sensing application: important plant functional traits to measure may include photosynthetic pigments, or correlates, such as leaf thickness. The second major finding was that functional groups, and even species, appeared to be spectrally distinguishable, mostly in the ultraviolet part of the spectrum. Therefore, it appears feasible to discriminate dominant South African wetland species and functional groups using spectral signatures of wet leaf and stem material. This has interesting applications for mapping plant functional traits using remote sensing techniques, and therefore for mapping related ecosystem processes and services. The next step for future research would be to try to link this to hyperspectral remote sensing imagery to test whether the scaling up from leaf to canopy is successful (Bulcock and Jewitt, 2010; Somers and Asner, 2013; Tits et al., 2012).

Currently many palmiet wetlands are threatened by agriculture, and yet agriculture in these wetlands is marginal due to the challenges of farming a system that experiences severe floods and droughts (Rebelo et al., 2015). The present situation is a lose-lose one, for both nature and society. In the second collaborative chapter of this dissertation, ecosystem service provision between degraded and pristine palmiet wetland fragments was compared using the South African WET-Ecoservices rapid assessment for 15 ecosystem services (Kotze et al., 2007) (**Chapter 9,** *also see* **Chapter 8**). I also assessed the rapid ecosystem service assessment tool against more detailed measurements for three key wetland ES: water regulation, water purification and carbon sequestration (Moor et al., 2017). Unsurprisingly, we found that pristine wetlands provide a greater suite of ecosystem services than degraded ones, specifically water-related ES. These pristine wetlands sequester between 23.4-61.6 m^3 of carbon per year, have nitrogen and phosphorus uptake efficiencies of 62.0-84.9% and 16.2-88.7% respectively, and provide about 16 times more flood attenuation relative to degraded wetlands. Many of these water-related ecosystem services had positive synergies, such that optimizing or protecting one ecosystem service, would optimize or protect others. There were, however, important trade-offs to consider, most importantly between food crop provision (replacing the wetland with agriculture) and water-related ES. Additionally, I found that the full impact of degradation on wetland ecosystem services was not entirely captured by the rapid ecosystem services assessment tool: WET-Ecoservices. The WET-Ecoservices Tool tended to overestimate the scores for ecosystem services provided by degraded wetlands. Overall, from the ecosystem service assessment, these wetlands have high potential for incorporation into a 'payments for ecosystem services' scheme, due to their position above important municipal dams. I recommend collaboration between private landowners struggling with marginal agriculture in these ecosystems, and decision makers in cities dealing with water shortages to ensure the most efficient and judicious use of these palmiet wetland ecosystem services.

10.4 Implications of research

This dissertation has made a contribution to knowledge by advancing the theoretical understanding of the linkages between biodiversity, ecosystem function and ecosystem services in South African palmiet wetland systems. From a theoretical perspective, these results are important, as it has shown which plant functional traits and abiotic variables are key in influencing ecosystem properties, and therefore ecosystem services (**Chapter 6**), which abiotic and functional diversity parameters structure plant community composition (**Chapter 5**) and what impact degradation has had on these wetlands (**Chapter 4**). However this dissertation also had an applied aspect. In **Chapter 7** I demonstrated that several plant functional traits were able to be predicted from their spectra, and also that these wetland functional groups, and even species, were spectrally distinct. This presents opportunities to map ecosystem properties throughout these wetlands using hyperspectral remote sensing data, and therefore to estimate ecosystem service provision. I also tried and tested an approach for measuring water purification as an ecosystem service, by measuring water quality parameters entering and leaving a section of wetland (**Chapter 8**). This measures the water purification ability of an ecosystem, rather than just the state of the ecosystem, which is commonly measured in other studies (**Chapter 2**). Finally, I quantified some of the key wetland ecosystem services provided by palmiet wetlands (**Chapter 9**).

To draw these findings together, I made some calculations of ecosystem service provision of the three wetland ecosystem service complexes of Moor et al. (2017) (**Chapter 9**) based on eight remaining palmiet wetlands (**Chapter 3**). These calculations, though we know they are likely to be highly uncertain, are still useful in developing an understanding of the value of these palmiet wetlands, and therefore the potential loss if these wetlands were not protected (in some cases restored) and conserved.

Research into ecosystem service provision is important because decision makers need accurate, scientific measurements of ecosystem services (Schulp et al. 2014; Van der Biest et al. 2015; **Chapter 2**), as well as good spatial understanding of stocks and flows of ecosystem services, and information on synergies and trade-offs between different ecosystem services to be able to make wise decisions about land-use. It is hoped that these results will feed into conservation and restoration planning, and possibly policy, with real implications for the protection of ecosystems and biodiversity. Two of the three palmiet wetlands considered in this research are situated upstream of large municipal reservoirs that provide water for two of South Africa's larger cities: Cape Town and Port Elizabeth. Therefore, protecting and conserving these wetlands will have direct, tangible benefits to society.

10.5 Opportunities for future research

Given the exploratory, foundational nature of this research there are many more questions than answers upon the completion of this dissertation. Here I outline some of the opportunities for future research suggested throughout this dissertation.

The work on community ecology within these palmiet wetlands has raised some important, more theoretical, questions for future research (**Chapter 5**). It is clear that palmiet wetland plant communities are patchy in nature. Different abiotic variables account for these patterns, and plant functional traits can to some extent explain why we see these patterns. However, what has not been researched at all are other possible abiotic reasons for these patterns, such as disturbance (fires, floods), as well as other biotic explanations (competition). It is important to investigate whether the patchiness we see in vegetation communities is a result of disturbances, such as fires and floods, which cause natural, localised erosion, resulting in a system reset for the vegetation within a patch (e.g. see argument of Grenfell et al. 2009). One hypothesis could be that fynbos-dominated communities within these wetlands are younger communities resulting from localised disturbances, and that palmiet-dominated communities are more of a climax stable state. Long-term water table monitoring is also important to understand plant community dynamics.

The findings on the impacts of degradation on palmiet wetlands also raise some important questions for future research (**Chapter 4**). It is clear, for example, that there are some interesting consequences of agricultural runoff on these palmiet wetlands. An increase in pH is evident in degraded wetlands, which could possibly be linked to liming practices. Direct measurement of this agricultural runoff in a few catchments at various times in a year is needed to quantify what pollutants are actually entering the wetlands, and what impact this is having on internal wetland biochemistry (Jordan et al., 2003). Another interesting avenue for future research is to do some experimental work: taking some peat extracts and treating them with commonly used lime and fertilizer, to understand and untangle the mechanisms involved in the overall increase in pH that we see with agricultural influence.

The failure to find a good method to determine the pre-colonial extent of palmiet wetlands deserves some more attention (**Chapter 3**). Possibilities for the future include Bayesian Belief Networks or developing better products for input into habitat suitability models (such as MaxEnt), or further exploration of historical diary extracts and archives (Skead, 2009). The reason this information is so important, is that it can tell us more about whether the high rates of erosion currently observed would be occurring without colonial interference, or whether they are entirely natural (*e.g. see* Grenfell et al. 2009). This would answer questions related to the usefulness and appropriateness of rehabilitation measures in these palmiet wetlands (de Haan, 2016).

In terms of more applied research, the development of an application for ecosystem hotspot mapping in wetlands based on spectrally discriminating dominant species holds much promise (**Chapter 6**). This could be an interesting opportunity for future research, but would involve the acquisition of a hyperspectral sensor and either a drone or an aircraft to launch it. Scaling spectra up from leaf/stem reflectance to canopy level is also not without its challenges (Klančnik et al., 2015), and requires additional research. In terms of ecosystem services of palmiet wetlands, in this dissertation I have only attempted to quantify three in detail (**Chapter 9**). However a full ecosystem assessment, including socio-economic aspects and monetary valuation, would be beneficial. This would need to be undertaken with relevant stakeholders to ensure that the findings are applicable and that the findings would be taken up by managers, landowners or policy-makers (**Chapter 2**)

10.6 Management recommendations

Palmiet wetlands are threatened by channel erosion and invasion by alien species at an alarming pace. Therefore, if the ecosystem services that these wetlands provide are worth protecting, it is essential that managers and policy-makers act quickly. Where palmiet wetlands occur within nature reserves, and there is little or no threat of agriculture, the situation is simpler. However, where landowners are involved, conservation organizations or policy-makers may need to intervene, or work together with these stakeholders to protect and restore these wetlands. Some effective strategies are needed to ensure that all parties including farmers, private landowners, scientists, managers, and decision makers work cohesively to decide on management strategies that prioritize maximal ecosystem service provision to society (Cowling et al., 2008).

Prevention is always better than cure, and in the case of damage to palmiet wetlands, the cure – ecological restoration – is extremely expensive (Grenfell et al., 2009; Hosking and Preez, 2004). The greatest driver of wetland degradation was found to be the construction of roads through or over palmiet wetlands (**Chapter 3**). It is unlikely that any more roads should be constructed through or over these wetlands. However, should road construction take place, one major recommendation would be to take all necessary precautions to ensure that the wetland itself is not damaged in the process. Bridges should be constructed over the wetlands, with high clearance and no culverts or obstructions beneath. The greatest current concern is, however, the management of agriculture encroaching on or into the wetland, and of drainage canals being dug for agriculture. These practises are still continuing, and should be monitored and prevented, in accordance with the National Environmental Management Act 107 of 1998 (NEMA), the National Water Act 36 of 1998 (NWA) and the Conservation of Agricultural Resources Act 43 of 1983 (CARA). As well as law enforcement, this would involve working with landowners and providing evidence as to why it would be beneficial for landowners not to drain these wetlands through drainage canals, and why buffers – areas which would protect wetlands from agricultural runoff – are important (as opposed to agricultural practises that extend into the wetland itself).

Active restoration initiatives are already at work in these wetlands, including activities by the national Working for Water and Working for Wetlands programmes (Hobbs, 2004). Working for Water targets the removal of alien invasive species and Working for Wetlands use engineering interventions to halt gully erosion in wetlands. Recent research into the effects of these erosion-control structures on groundwater dynamics in the Kromme wetland found that these structures did indeed restore the water table in wetlands upstream and prevented further migration of the main headcut, but may have increased gully erosion downstream (de Haan, 2016). One finding from this dissertation: that gully/headcut erosion does not take place gradually, but abruptly after flood events, has important management and rehabilitation implications (**Chapter 3**). Once damage has occurred, causing a knick-point, it should be rehabilitated before the next large floods occur, otherwise substantial wetland loss is risked. Therefore, timing is critical in these rehabilitation projects; early intervention on a small scale could save substantial sums of money needed for large structures in the future.

Lastly, it is apparent that palmiet wetlands are not adequately represented in the South African National Freshwater Ecosystem Priority Areas (NFEPA) Atlas (Nel et al., 2011) (**Chapter 3**). Many of these palmiet wetlands are misclassified, and there is no information available on the condition of these wetlands. Many are degraded or no longer exist, and yet are indicated as wetlands in the atlas. The data from small scale studies such as this one can be used to supplement coarser national-scale wetland inventories, improving the knowledge of wetland distribution, type and condition. This is essential for prioritizing wetland rehabilitation and conservation in the future.

10.7 Conclusion

Palmiet wetlands are valuable ecological infrastructure in that they provide many ecosystem services to society. They are also complex ecosystems and present an interesting study system to investigate fundamental ecological questions. With over 30% of palmiet wetlands already lost, and the remaining fragments highly degraded and threatened by channel erosion and agricultural pursuits, the protection and restoration of these unique peatlands should be a national priority. If steps are not taken immediately to restore palmiet wetlands threatened with erosion, it is possible that these wetlands will be drained or lost in the next 50 years (by 2065).

10.8 References

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S.M.

Supplementary Material
Ecosystem Service Measures Tables

Boerema A.*, Rebelo, A.J.*, Bodi M.B., Esler K.J, and Meire P. (2017). Is the reality of ecosystem services adequately quantified? *Journal of Applied Ecology*. **54**: 358–370.

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Contents

Key:

Measure:
B = Biophysical Measure
M = Monetary Measure
B+M = Both Biophysical & Monetary Measures

Cascade:
EP: Ecosystem Properties
EF: Ecosystem Functions
ES: Ecosystem Services
B: Benefits
V: Values
S: Score
O: Other

Entries in italics = theoretical studies
C.P: Chemical Properties
P.P: Physical Properties

PROVISIONING ECOSYSTEM SERVICES

Food Production

Type	Measure	References	#	Cascade
Score	Community	Raymond et al. 2009; Calvet-Mir et al. 2012; Klain & Chan 2012; Allendorf & Yang 2013; Liu et al. 2013; Pataki et al. 2013; Abram et al. 2014; Zorrilla-Miras et al. 2014	9	S
	Expert judgement	Harrington & McInnes 2009; Burkhard et al. 2012; Scholz & Uzomah 2013; Abram et al. 2014; Zorrilla-Miras et al. 2014	10	S
	Biophysical data (probability index, suitability index, GIS model)	Metzger et al. 2006; Ritz et al. 2009; Barral & Oscar 2012; Hinojosa & Hennermann 2012; Rutgers et al. 2012; Jackson et al. 2013; Namaalwa et al. 2013; Willemen et al. 2013; Van der Biest et al. 2014;	9	S
Land use	**B: Land use area** (ha) for food/crop/fodder (Landsat images, CORINE land use map, remote sensing, EMLC data set using remote sensing, ATEAM land use change scenarios)	Maes et al. 2012; Turner et al. 2014	2	EP
	B: Land use area with additional information: soil specifications (soil type, soil fertility map), cropping pattern from IMAGE, Animal distribution map (map created from governmental data on livestock)	Lautenbach et al. 2011; Gulickx et al. 2013	3	EP
Economic value	**M: Economic value based on land use area** (€/ha) (market price, net (habitat) value (market price corrected for production cost), habitat value, total sector value)	Zhao et al. 2004; Asafu-Adjaye et al. 2005; Martínez et al. 2009; Crossman et al. 2010; Bastian et al. 2013; Butler et al. 2013; Boerema et al. 2014	11	V
	M: Market price (€/kg) crops, fish, livestock (governmental data, interviews local government, industry)	Gren et al. 1995; Banerjee et al. 2013	2	V
	M: Net value (€/ton;€/ha) crops, fish, livestock (producer cost function (market price and other factors)	Gren et al. 1995	3	V
	M: Total sector value: agriculture, fishery (government data)	Hein et al. 2006	1	V
	M: Model: profitability of a farm, function of soil type, farm type, fertilizer use, crop price, hydrology; correction value greenhouse gas emissions	Lant et al. 2005	1	V
	M: Farm size in standardized livestock units (economic units)	Willemen et al. 2010	1	V
Food Harvest: crop, fodder	**B: Crop yield** (kg/ha, GJ/ha gross energy, g/kg protein yield): theory, literature data, government data (per ha, per county), data from farmers and local people, field measurements, production function, model (e.g. crop yield model, Agricultural Production Systems sIMulator ASIM); grain equivalent unit GEU/ha/y; unit of forage UF/ha/y (UF = 1 kg barley)	DuPont et al. 2009; Kahiluoto et al. 2009; Swallow et al. 2009; Quijas et al. 2010; Smukler et al. 2010; Snapp et al. 2010; van Eekeren et al. 2010; Evans et al. 2011; Gang et al. 2011; Lal 2011; Briner et al. 2012; Burkhard et al. 2012; Carreño et al. 2012; Holzschuh et al. 2012; Keesstra et al. 2012; Larondelle & Haase 2012; Su et al. 2012; Logsdon & Chaubey 2013; Lorencova et al. 2013; Pan et al. 2013; Ruijs et al. 2013; Sabatier et al. 2013; Schlüter et al. 2013; Williams & Hedlund 2013; Derak et al. 2014; Lauf et al. 2014; Meyer & Priess 2014; Syswerda & Robertson 2014; Williams & Hedlund 2014	34	B
	B: Crop yield (data from literature; government/databases/local experts; model; field measurements; also in gross energy per unit) + food demand and consumption, energy content or potential of food, caloric value of food + **resources** used (water productivity for food provisioning, energy use per food type (GJ/kg))	Nangia et al. 2008; Molden et al. 2010; Kroll et al. 2012; Firbank et al. 2013; Lal 2013; Porter et al. 2014	7	B, O
	B+M: Crop yield (theoretic; data from government/datasets/local experts; production function; field measurements; data from farmers and local people; dry sheep	Xiao et al. 2005; Rodríguez et al. 2006; Ashworth et al. 2009; Pinto et al. 2010; Posthumus et al.	28	B, V

	equivalent DSE/ha; Grain equivalent unit GEU/ha/y) + **economic value** (habitat value, market price, net value (market price corrected for production costs e.g. man hours), replacement cost, total value of the sector; model farm profitability)	2010; Sandhu et al. 2010; Chang et al. 2011; Klemick 2011; Yu et al. 2011; Burkhard et al. 2012; Liu et al. 2012; Ausseil et al. 2013; Bryan & Crossman 2013; Kandziora et al. 2013; Koschke et al. 2013; *Peh et al. 2013*; Silvestri et al. 2013; Baral et al. 2014; Birch et al. 2014; Dominati et al. 2014; Garratt et al. 2014 (b); Ghaley et al. 2014; Martín-López et al. 2014; Renwick et al. 2014		
Livestock	**B: Livestock density**: number of animals, livestock units (number), tropical livestock unit (TLU), large stock unit (LSU), standard sheep units, sheep grazing days, dry sheep equivalent (DSE/ha); Methods: theory, database (FAOstat), conservative estimate, measured (counted deer kills), respondents questionnaire, model	Ford et al. 2012; Maes et al. 2012; Brandt et al. 2014; Schröter et al. 2014; Schulte et al. 2014; Turner et al. 2014	6	B
	B: Livestock productivity (ton/ha), meat equivalent based on average dry matter (kg/ha); Methods: theory, literature, governmental data, databases World Bank and FAO; model; field measurements	Descheemaeker et al. 2010; Hoffmann 2011; Pan et al. 2013; Pan et al. 2014	4	B
	B+M: Livestock: Number of animals and productivity (ton, ton/ha) (standard sheep units, sheep grazing days, livestock units, large stock units; data from datasets, measures, questionnaires with locals) + **economic value** (habitat value, market price, net value (market price corrected for production costs), replacement cost, total sector value)	Posthumus et al. 2010; O'Farrell et al. 2011; Burkhard et al. 2012; Dong et al. 2012; Kandziora et al. 2013; Silvestri et al. 2013; Jones et al. 2014; Kragt & Robertson 2014; Martín-López et al. 2014	11	B, V
Fish catch	**B:** Fish stock (number, ton): literature, observations, model	Simonit & Perrings 2011; Hannesson 2013; Brandt et al. 2014; Reithe et al. 2014	4	EP
	B+M: Fish stock (in number; data from literature, datasets, observations, model, production function) + economic value (value fish catch per unit effort, market price, net value (market price corrected for production costs), habitat value, total sector value)	Cordier et al. 2011	1	EP, V
	B: Fish catch (number, ton): literature, governmental data, production function, model	Natuhara 2013	1	B
	B+M: Fish catch (in ton; data from literature, datasets, observations, model, production function) , actual harvest when multiplied with wetland or mangrove area (remote sensing, land use data, survey community) + economic value (value fish catch per unit effort, market price, net value (market price corrected for production costs), habitat value, total sector value)	Pinto et al. 2010; Cui et al. 2012; Forsius et al. 2013; Kandziora et al. 2013; Kuenzer & Tuan 2013; Uddin et al. 2013; Johns et al. 2014; La Peyre et al. 2014; Martín-López et al. 2014; Micheli et al. 2014	11	B, V
Food products: other	**B:** Milk production m^3/ha/y (data from literature **B:** Salt production in ton (data from literature	van Oudenhoven et al. 2012 Pinto et al. 2014	1 1	B B
Emergy	**B+M:** Biomass consumption in solar emergy joules (seJ) + value for solar emergy joules (seJ); Emergy/money ratio (seJ/€) + land use map + food demand and consumption	Dong et al. 2012; Lin et al. 2013	2	B , V

Water Provision

Type	Measure	Reference	#	Cascade
Score	Community	Raymond et al. 2009, Delgado et al. 2013, Liu et al. 2013, Abram et al. 2014	4	S
	Expert judgment: water provision	Harrington & McInnes 2009, Bai et al. 2011, Burkhard et al. 2012, Hinojosa & Hennermann 2012, Namaalwa et al. 2013	5	S
	Expert judgment: groundwater recharge	Larondelle & Haase 2012	1	S
	Expert judgment: access to water (distance)	Hinojosa & Hennermann 2012	1	S
	Expert judgment: state of drinking water	Zorrilla-Miras et al. 2014	1	S
	Both expert judgment & community	Pataki et al. 2013, Zorrilla-Miras et al. 2014	2	S
	Biophysical: model	Barral & Oscar 2012, Chiang et al. 2014	2	S
Economic	M: Market Price/Avoided Cost methods (€/y)	Bernard et al. 2009, Banerjee et al. 2013	2	V
Water provision per area/habitat type	B: Area/habitat type (ha/%)	Maes et al. 2012, Ferraz et al. 2013, Turner et al. 2014	3	EP
	B+M: Area/habitat type (ha/%); economics: Benefit Transfer (unit value per habitat type, (€/ha/y), unit values from Costanza et al. 1997)	Asafu-Adjaye et al. 2005, Martínez et al. 2009, Liu et al. 2012, Brander et al. 2013, Di Sabatino et al. 2013	5	EP/V
Water yield (m^3):	B+M: Water yield (€/m^3): effect of LULC change (model), economics: benefit transfer (unit value per habitat type, market price water, prevailing water cost in € ML−1)	Zhao et al. 2004, Núñez et al. 2006, Chisholm 2010, Bryan & Crossman 2013, Baral et al. 2014, Boerema et al. 2014	6	EF/V
	B+M: Water yield (€/m^3): value of water for improving ecosystem health (NPV)	Crossman et al. 2010	1	B/V
	B+M: Water yield (€/m^3): value of irrigation	Dymond et al. 2012	1	B/V
	B+M: Water yield (€/m^3): total yield (either /infrastructure lifetime or /area)	O'Farrell et al. 2011, Cui et al. 2012	2	EP/V
	B: Runoff (MAR) (m^3)	Egoh et al. 2008, Biao et al. 2010, Leh et al. 2013a, Leh et al. 2013b	4	EF
	B: Groundwater storage/aquifer recharge/abstraction (m3/y)	Kroll et al. 2012, Baral et al. 2013, Schlüter et al. 2013, Vidal-Legaz et al. 2013, Meyer & Priess 2014	5	EF
	B: Freshwater yield algorithm, InVEST (m^3)	Su & Fu 2013, Gao et al. 2014, Shoyama & Yamagata 2014	3	EF
	B: Actual use (e.g. water pumped for use, hydro-electric plant, agriculture, food production)	Pinto et al. 2010, Kandziora et al. 2013, Lal 2013, Nguyen et al. 2013, Pinto et al. 2013	5	B
	B: Stream discharge	Garmendia et al. 2012	1	EF
	B: Simple soil-water balance model	Descheemaeker et al. 2010	1	EF
	B: Modeled environmental flows	Schlüter et al. 2013	1	EF
Water Availability	InVEST/TESSA/Water Balance Model (mm/yr)/precipitation	Liquete et al. 2011, Dymond et al. 2012, Bangash et al. 2013, Bhagabati et al. 2014, Birch et al. 2014, Meyer & Priess 2014, Terrado et al. 2014	6	EF
Water Provision - Rate	Rate (m^3/s) (model output (SWAT), regression co-efficients)	Lara et al. 2009, Notter et al. 2013	3	EF
Water Provision - Percent	Water supply/water use -demand (%)	Pandeya et al. 2013, Morri et al. 2014	2	B
Groundwater Availability	Groundwater Availability (%)	Bjorklund et al. 1999, Derak et al. 2014	2	EF
Evapotranspiratio n	Evapotranspiration (mm/yr)	Pandeya et al. 2013	1	EF
Water Productivity	Water Productivity (crop/animal yield (kg/m^3)	Nangia et al. 2008, Molden et al. 2010	2	O

Materials & Fibre

Type	Measure	Reference	#	Cascade
Score	Expert	Harrington & McInnes 2009; Scholz & Uzomah 2013; Volchko et al. 2013	3	S
	Community	Schaberg et al. 1999; Raymond et al. 2009; Calvet-Mir et al. 2012; Liu et al. 2013; Pataki et al. 2013; Abram et al. 2014	8	S
	Biophysical	Metzger et al. 2006; Barral & Oscar 2012; Burkhard et al. 2012; Namaalwa et al. 2013; Van der Biest et al. 2014	5	S
Land use	B: Land use map (ha), e.g. forest area as proxy for wood productivity	Hinojosa & Hennermann 2012; Geneletti 2013	2	EP
Economic	M: Land use map (ha), habitat values Costanza et al 1997 (€/ha) or market price method (€/ha costs of harvesting)	Gret-Regamey et al. 2008; Zhao et al. 2004	2	V
	M: Area per production system (ha) + gross margin per ha per soil type (€/ha; from product prices and costs management practices)	Butler et al. 2013	1	V
	M: total extraction rights for timber extraction forest administration (royalties) minus development costs	Lele & Srinivasan 2013	1	V
	M: forestry rent; rent mining sector	Asafu-Adjaye et al. 2005	2	V
Biomass or volume	B: ton or m^3, per year, per ha (theoretic; government data (standing) forest biomass; model plant productivity; production function, data from locals)	Hein et al. 2006; Ritz et al. 2009; Sasaki et al. 2009; Quijas et al. 2010; Larondelle & Haase 2012; Maes et al. 2012; Ooba et al. 2012; Su et al. 2012; Ausseil et al. 2013; Baral et al. 2013; Delphin et al. 2013; Kandziora et al. 2013; Koschke et al. 2013; Willemen et al. 2013; Brandt et al. 2014; Derak et al. 2014; Meyer & Priess 2014; Shoyama & Yamagata 2014	20	B
	B: Model: Area of forest land harvested, function of growing rates and fixed harvest rate as function of tree type and tree age of the standing stock)	Sohngen & Brown 2006	1	EF, B
	B+M: Biomass and/or volume (government data, field measurement, questionnaires, models) + economic value (€/ton or €/m^3; theoretic, market price, net price with correction for harvesting costs, replacement cost, statistics, local co-operatives, interviews with locals); gives a value €/ha/y	Rose & Chapman 2003; Venn 2005; Hein & van Ierland 2006; Rodríguez et al. 2006; Chisholm 2010; Olschewski et al. 2010; Yu et al. 2011; Briner et al. 2012; Liu et al. 2012; Ojea et al. 2012; Delgado et al. 2013; Ghaley et al. 2014; Lele & Srinivasan 2013; Miettinen et al. 2014; Baral et al. 2014; Birch et al. 2014; Kragt & Robertson 2014; Nghiem 2014; Qin et al. 2014; Schmidt et al. 2014; Schröter et al. 2014; Yi et al. 2014	22	B, V
	B+M: Biomass and/or volume (theoretic, models), €/ha/y (theoretic, statistics)	Forsius et al. 2013; Kandziora et al. 2013; Peh et al. 2013; Jones et al. 2014	5	B, V
	B+M: timber harvest m^3/y + sector revenue earnings for timber €/y (data government); from that timber revenue €/m^3	Guo et al. 2001; Uddin et al. 2013	3	B, V
	B+M: households, ton/households (existing datasets for the region based on questionnaires) + market price €/ton (existing datasets for the region based on questionnaires)	Schaafsma et al. 2014	1	B, V
Use	B+M: forest area (remote sensing and household survey), number of households + replacement cost €/household (cost for households to purchase the same amount of timber that they take from the forest on the local market)	Kuenzer & Tuan 2013	1	B, V

Energy & Fuel

Type	Measure	Rereference	#	Cascade
Score	Expert	Harrington & McInnes 2009	1	S
	Community	Raymond et al. 2009; Abram et al. 2014	2	S
	Biophysical	Metzger et al. 2006; Burkhard et al. 2012	2	S
Firewood and energy crops	B: forest area (proxy for availability firewood)	Hinojosa & Hennermann 2012	1	EP
	B: biomass firewood and energy crops (theoretic, model, field measurements bioenergy from seeds); area energy crops and biomass (GJ/ha)	Quijas et al. 2010; Burkhard et al. 2012; Kroll et al. 2012; Wani et al. 2012; Logsdon & Chaubey 2013; Willemen et al. 2013; Kantar et al. 2014; Lauf et al. 2014; Meyer & Priess 2014	9	B
	B: Model: Area of forest land harvested, function of growing rates and fixed harvest rate as function of tree type and tree age of the standing stock)	Sohngen & Brown 2006	1	EF, B
	B+M: biomass firewood and energy crops (theoretic, data government, field measurements) and economic value (theoretic, data government, market price)	Kandziora et al. 2013; Uddin et al. 2013; Ghaley et al. 2014	4	B, V
	M: land use forest (land use map and household survey), number of households depending on the forest (for firewood), replacement cost to purchase the firewood on the market (for the amount of firewood that one family uses per year) (market price); benefit per capita consumption of firewood and its variation by location (fringe versus interior) (data from literature)	Kuenzer & Tuan 2013; Lele & Srinivasan 2013; Schaafsma et al. 2014	3	V
Hydropower	B: water available (m^3)	Notter et al. 2013	1	EP
	B: Water available (m^3) and power generated (data power stations, model); surface river area (hectare) and installed power of water Energy & Fuel plants (MW)	Kroll et al. 2012; Bangash et al. 2013; Nguyen et al. 2013	3	B
	B+M: proportion of water retention to the flow used by the station (INVEST model), volume water from the system used for hydroelectricity, total amount of energy produced by the three plants (GWh/y), number of families that could benefit from this service (if it was only dedicated to domestic use) + economic value hydropower (literature review, maintenance cost hydropower station)	Bernard et al. 2009; Fu et al. 2014	2	B, V
Energy production	B: theoretic produced electricity kWh/ha; Energy resources in the region (solar, wind, lignite, brown coal) (GJ/y, MW)	Burkhard et al. 2012; Kroll et al. 2012; Kandziora et al. 2013; Lauf et al. 2014	9	B
	B+M: energy savings with shading effects trees (computer simulations that incorporated building, climate, and shading effects; literature) + retail prices electricity (€/kWh) and gas (€/GJ)	McPherson et al. 2011	1	B, V

Genetic Resources

Type	Measure	Reference	#	Cascade
Score	Community	Raymond et al. 2009, Calvet-Mir et al. 2012, Liu et al. 2013	3	S
	Expert Judgement	Harrington & McInnes 2009, Scholz & Uzomah 2013	2	S
Economic	**M:** Benefit Transfer (unit values from Costanza et al. 1997 (€/ha/y))	Zhao et al. 2004, Asafu-Adjaye et al. 2005	2	V
	M: Willingness to Pay (€/household/yr)	Boerema et al. 2014	1	V
Diversity	**B:** Species Richness	Ford et al. 2012	1	EP
	B: Intraspecific Diversity (Genome characteristics)	Riggs 1990, Schaberg et al. 2008, Kantar et al. 2014	5	EF
Extinction/Endangered Species	**B:** Endangered Species (% of total endangered)	Bjorklund et al. 1999	1	O
	B: % Extinct Species (% since 1950)	Bjorklund et al. 1999	1	O

Medicinal Resources

Type	Measure	Reference	#	Cascade
Score	Community	Abram et al. 2014, Raymond et al. 2009, Zorrilla-Miras et al. 2014	3	S
	Expert judgement	Scholz & Uzomah 2013, Zorrilla-Miras et al. 2014	2	S
Medicinal species	**B:** Number of medicinal plants	Calvet-Mir et al. 2012, De Boer et al. 2012, Derak et al. 2014	3	EP
	B: Production of biochemicals and medicine (Amount or number of products used (kg/ha)	Burkhard et al. 2012	1	B
	B+M: Production of biochemicals and medicine (natural products used as biochemical, medicine, cosmetics) (Amount or number of products used (kg/ha/y, number/ha/y); Net Primary Production (ton C/ha/y, KJ/ha/y); yield (€/ha/y))	*Kandziora et al. 2013*	1	B, V

Ornamental Resources

Type	Measure	Reference	#	Cascade
Score	Community: Local perception of the ornamental service	Raymond et al. 2009	1	S
Harvest of an important natural resource for ornamental use	**B:** Plants of ornamental interest (Number, %)	Calvet-Mir et al. 2012; Derak et al. 2014	2	B
	B+M: Collection of natural ornaments for ornamental or religious purposes, e.g. sea shells, leafs, twigs (Harvested plant biomass or yield; ton carbon/ha/y, €/ha/y)	*Kandziora et al. 2013*	1	B, V
	B+M: Craft making (Area used for collection of raw material for craft making (ha), Average income from handicraft sale (Nuevos Soles))	Rodriguez et al. 2006	1	EP, V
	B+M: Number of animals landed, marine life harvest (economic indicator)	Johns et al. 2014	1	B, V

REGULATING ECOSYSTEM SERVICES

Water Purification

Type	Indicator	Reference	#	Cascade
		Measured on Land (catchment/region/multiple different LULC types)		
Water quality	B: P.P: (TSS, TDS, EC)	*Kandziora et al. 2013*	3	EP
	B: C.P: (nutrients, DOC, Chl-a)	Bjorklund et al. 1999, Aherne & Posch 2013, Ausseil et al. 2013, *Kandziora et al. 2013, Meyer & Priess 2014*	6	EP
	M: Economic: production function for fertilizer and pesticide	Klemick 2011	1	V
Water purification	Score: community/expert judgment	Raymond et al. 2009, Burkhard et al. 2012	3	S
	B: P.P: modeled purification at catchment scale/per LULC	Bangash et al. 2013, Erol et al. 2013, Logsdon & Chaubey 2013, Bhagabati et al. 2014, Meyer & Priess 2014	5	EF
	B: C.P: index: N&P retention InVEST model	Bai et al. 2011, Rutgers et al. 2012, Chiang et al. 2014	3	EF
	B: C.P: theory (N&P leakage/reduction/turnover rates/denitrification, pesticide immobilization rates)	*Spencer & Harvey 2012, Kandziora et al. 2013, Meyer & Priess 2014, Schulte et al. 2014*	7	EF
	B: C.P: model: N&P retention/losses/export/loadings/turnover rates/in vegetation	Fu et al. 2012, Erol et al. 2013, Firbank et al. 2013, Geneletti 2013, Jantz & Manuel 2013, Leh et al. 2013a, Leh et al. 2013b, Logsdon & Chaubey 2013, Bhagabati et al. 2014, Campbell & Tilley 2014, Terrado et al. 2014	12	EF
	B: C.P: measured in the soil (N&P, other elements)	Smukler et al. 2010, Snapp et al. 2010, Keesstra et al. 2012, Syswerda & Robertson 2014	4	EP
	B: C.P: NO3 emissions	Jenkins et al. 2010, Burgin et al. 2013	2	EF
	B: Landover: NPP, slope, infiltration capacity, bare ground, vegetation, biomass, erosion potential, sediment retention, N removal per LC	Lautenbach et al. 2011, Barral & Oscar 2012, Carreño et al. 2012, Leh et al. 2013b, Birch et al. 2014, Villamagna et al. 2014	6	EP
	B+M: P.P: modeled purification (salinity) at catchment scale/per LULC; economic: sale of potable water	George et al. 2012	1	EF/V
	B+M: C.P: N retention under different LULC scenarios; economic: avoided costs/willingness to pay	Maes et al. 2013	1	EF/V
	B+M: Filtering capacity of the soil (N); economic: mitigation costs of leaching and an artificial wetland	Dominati et al. 2014	1	EF/V
	B+M: C.P: model: N&P retention in vegetation; economic: production function	Hill et al. 2014	1	EF/V
	B+M: C.P: theory (N reduction in the leachate); economic: benefit transfer	*Wüstemann et al. 2014*	1	EF/V
	M: Economic: Avoided costs: estimated dollar benefit per unit of salinity avoided (€/EC)	Crossman et al. 2010	1	V
Waste purification	Score: community (pollution prevention/bioremediation)	Calvet-Mir et al. 2012, Abram et al. 2014	2	S
	B: Decomposers (n/ha), Decomposition rate (kg/ha*a)	*Kandziora et al. 2013*	1	EP/EF
	B: Xenic nutrients and compounds	*Boumans et al. 2002*	1	EP
	B: Physical properties: NPP & size of water body	Barral & Oscar 2012	1	EP
	B+M: Decomposition rate (soil); economic: provision cost (to maintain artificial wetland)	Dominati et al. 2014	1	EF/V
	M: Economic: benefit transfer (area), provision cost (to maintain artificial wetland)	Asafu-Adjaye et al. 2005	1	V
		Measured in a Wetland/River (natural or artificial)		
Water quality	Score: biophysical/community/expert judgment	Mavsar et al. 2013, Martín-López et al. 2014, Tooth et al. 2014, Zorrilla-Miras et al. 2014	4	S
	P.P: (TSS, TDS, EC, DO, pH, temp, color, wetland area)	Clutterbuck & Yallop 2010, Schäfer et al. 2012, *Kandziora et al. 2013*, Lau 2013, La Peyre et al. 2014, Turner et al. 2014	6	EP
	C.P: (nutrients, DOC, Chl-a)	Pinto et al. 2010, Brito et al. 2012, *Kandziora et al. 2013*, Lau 2013, Pinto et al. 2013, Cabezas et al. 2014, La Peyre et al. 2014, *Meyer & Priess 2014*, Pinto et al. 2014	9	EP
	B+M: P.P: Sediment (deposition & increase in wetland area); economic: cost of disease due to sedimentation, cost of damage to infrastructure, and loss of land (Yuan/hm2)	Cui et al. 2012	1	EP/V

Water purification	Score: biophysical (chemical trapping/removal: N,P, toxicants)	Namaalwa et al. 2013	3	S
	Score: community/expert judgment	Harrington & McInnes 2009, Pataki et al. 2013	2	S
	B: P.P: input&output/spatial pattern measurements/water column-sediments	Martínez et al. 2009, Johnston et al. 2011, Díaz et al. 2012, Glendell et al. 2014, Palmer et al. 2014	6	EF
	B: P.P: modeled purification	Marques et al. 2013, Randhir et al. 2013, Schlüter et al. 2013	3	EF
	B: P.P: theory (i.e. no details given)	*Meyer & Priess 2014*	1	EF
	B: C.P: input&output/spatial pattern measurements	Fisher et al. 2009, Harrington & McInnes 2009, Johnston et al. 2011, Díaz et al. 2012, Hefting et al. 2013, Glendell et al. 2014, Palmer et al. 2014	9	EF
	B: C.P: modeled purification	Taguchi et al. 2009, Liquete et al. 2011, Jouquet et al. 2012, Butler et al. 2013, Natho et al. 2013	5	EF
	B: C.P: wetland soil holding capacity	Dunne et al. 2011	1	EP
	B: C.P: pesticide purification (inlet/outlet)	Tournebize et al. 2013, *Meyer & Priess 2014*	2	EF
	B: C.P: theory (i.e. no details given)	*Kandziora et al. 2013, Peh et al. 2013*	2	EF
	B: Biota: algae/bacteria/phytoplankton/aquatic plants (models/indicators/filtration rate)	Taguchi et al. 2009, Johnston et al. 2011, Díaz et al. 2012, La Peyre et al. 2014	4	EP/EF
	B: Land cover (of wetland/river): riparian buffer width, wetland area, biomass, plant nutrient/heavy metal uptake (e.g. Hg)	Carreño et al. 2012, Plieninger et al. 2012, Anastácio et al. 2013, Kuenzer & Tuan 2013	4	EP
	B+M: Change in nutrient concentrations with vegetation removal from river; economic: avoided cost method (€/kg)	Boerema et al. 2014	1	EP/V
	B+M: C.P: input&output; economic: net revenues fishery sector and agricultural household as function of nutrient buffering (wetland) (€/y)	Simonit & Perrings 2011	1	EF/V
	M: Benefit transfer/replacement cost for N&P or Hg removal	Gren et al. 1995, Trepel 2010, Cui et al. 2012, Grossmann 2012, Miettinen et al. 2014, Natuhara 2013, Schmidt et al. 2014, *Wüstemann et al. 2014*	10	V
Waste purification	Score: community/expert judgment	Harrington & McInnes 2009, Klain & Chan 2012, Cook et al. 2013, Scholz & Uzomah 2013, Gilvear et al. 2013	5	S
	B: Measuring agricultural inputs (NO_3)	Posthumus et al. 2010	1	O
	B: Xenic nutrients and compounds	*Boumans et al. 2002*	1	EP
	B: Decomposers (#) or decomposition rate (wetland soil)	*Kandziora et al. 2013*	2	EF
	B: Emissions from a constructed wetland (CH4/N2O)	Mander et al. 2014	2	O
	M: cost of sewage treatment/benefit transfer from meta analysis/pollution treatment costs	Yu et al. 2011, Cui et al. 2012, Brander et al. 2013, Johns et al. 2014	4	V
Groundwater	B: Acetate mineralization rates, groundwater turnover times	Lerner et al. 2009, Van Beelen et al. 2011	2	EF

Water Regulation

Type	Indicator	Reference	#	Cascade
Score	Biophysical	Tooth et al. 2014	1	S
	Community	Schaberg et al. 1999, Raymond et al. 2009, Liu et al. 2013, Scholz & Uzomah 2013	4	S
	Expert judgment	Yapp et al. 2010, Gilvear et al. 2013	2	S
	Expert judgment & community	Zorrilla-Miras et al. 2014	1	S
Economic	M: Unit value per habitat type (€/ha/y): data from literature (benefit transfer)	Asafu-Adjaye et al. 2005	1	V
Regulation of Water Flows				
Landuse/ landcover (LULC)	B: biophysical: area, interception, literature, InVEST model	Brandt et al. 2014, Wang et al. 2012, Baral et al. 2013, Ninan & Inoue 2013	4	EP, EF
	B: evapotranspiration/yield	Guo et al. 2001, Bai et al. 2012	2	EF
	B+M: area; economic: unit value per habitat type (€/ha/y)	Zhao et al. 2004, Martínez et al. 2009, Schmidt et al. 2014	3	EP, V
Infiltrability / storage of soil	B: score: biophysical	Maes et al. 2012, Radford & James 2013	2	S
	B: LULC	Harrington & McInnes 2009, Carreño et al. 2012, Fu et al. 2013	3	EP, EF
	B: water storage	Biao et al. 2010, Lavelle et al. 2014, Syswerda & Robertson 2014	3	EF
	B: model (water content, permeability)	Aitkenhead et al. 2011, Jackson et al. 2013, Onaindia et al. 2013	3	EF
	B: infiltration rate (measured in field, simulator, literature)	O'Farrell et al. 2009, Smukler et al. 2010, van Eekeren et al. 2010, Liquete et al. 2011, Ford et al. 2012, Nedkov & Burkhard 2012, Benegas et al. 2014, Palm et al. 2014	8	EF
	B+M: score: community; economic: avoided cost and replacement cost methods	Banerjee et al. 2013	1	S, V
	B+M: LULC; WTP	Niu et al. 2012	1	EP, EF, V
	B+M: infiltration rate (measured in field, simulator, literature); provision cost (construction costs of farm dam)	Dominati et al. 2014	1	EF, V
Groundwater	Level change: B	*van Oudenhoven et al. 2012, Meyer & Priess 2014*	2	EF
	Recharge Rates: B: theory	*Kandziora et al. 2013*	1	EF
	Recharge Rates: B: LULC (change in LULC, score)	Burkhard et al. 2012, Campbell & Tilley 2014	2	EP, EF
	Recharge Rates: B: percolation rates	Mills et al. 2011	1	EF
	Recharge Rates: B+M: LULC (change in LULC); economics (Ex-ante simulation)	Lele 2009	1	EP, EF, V
	Recharge Rates: B+M: theory; (construction costs of dam)	*Natuhara 2013*	1	EF, V
Riverflow	M: WTP & Contingent valuation method (CVM)	Ojeda et al. 2008	1	V
	B: score: biophysical (riverflow regulation)	Namaalwa et al. 2013	1	S
	B: hydrological methods (water balance, inlet/outlet, model)	Schlüter et al. 2013, Tournebize et al. 2013	2	EF
	B+M: estimates/secondary data/observed streamflow & model/water balance model; economic: price changes, secondary data, choice experiments, contingent valuation	Lele 2009	4	EF, V
Runoff	B: model	Tratalos et al. 2007, Jim & Chen 2009, Ooba et al. 2010, Johnston et al. 2011, Erol et al. 2013, Jantz & Manuel 2013, Lin et al. 2013, Dobbs et al. 2014, Kragt & Robertson 2014, *Meyer & Priess 2014*	10	EP, EF
	B: (exp & control, depth at points, simulator, ratio (runoff/MAP), paired catchment experiment)	Otero et al. 2011, Notter et al. 2013, Hill et al. 2014, Palmer et al. 2014	4	EF
	B+M: paired catchment experiment/ threshold model; economic: net income from irrigated and unirrigated agriculture through sample plot monitoring and survey/ex-ante simulation	Lele 2009	2	EF, V
Yield	B: index	Ausseil et al. 2013	1	EP
	B: water balance model	Pan et al. 2013, Jia et al. 2014, Pan et al. 2014	3	EF
	B Storage capacity: aquifer/wetland	Feng et al. 2011, Yu et al. 2011, Fu et al. 2014	3	EP

	B+M: water balance model/expert judgment; economic (direct estimation, cost data from water purification plant and hydropower plant)	Lele 2009	1	EF, V
	B+M: decrease due to sedimentation (paired catchment study); economic: gross revenues from tourism	Lele 2009	1	EP, V
Water balance	B: Runoff & Aquifer recharge (hydrological model)	Willaarts et al. 2012, Watanabe & Ortega 2014	2	EF
Regulation of Peak Flows (flood attenuation)				
Flood attenuation	Score: community	Calvet-Mir et al. 2012, Allendorf & Yang 2013, Pataki et al. 2013, Abram et al. 2014	4	S
	Score: biophysical (relative magnitude per unit area/wetland storage capacity/surface roughness/stream sinuosity etc)	Harrington & McInnes 2009, Barral & Oscar 2012, Namaalwa et al. 2013	3	S
	Social: # households, settlements in floodplains	Larondelle & Haase 2012	2	O
	M: economic (benefit transfer/avoided storm damage costs)	Brander et al. 2013, Johns et al. 2014	2	V
	B: land cover impacts (model, differences between two LULC, curve number)	Reistetter & Russel 2011, Koschke et al. 2013, Campbell & Tilley 2014	3	EP, EF
	B: flood specs: duration, magnitude, frequency, #events, # days flooded, #months with risk	Logsdon & Chaubey 2013, Pataki et al. 2013, Peh et al. 2013	3	EF
	B: hydrology: SWAT model/stormflow responsiveness (ratio of stormflow to rainfall)/peak stormflow	Norman et al. 2012, Le Maitre et al. 2014	2	EP, EF
	B+M: natural barriers (buffer) & economic replacement of damage avoidance cost	Kuenzer & Tuan 2013	1	EP, V
	B+M: score/flood frequency (time series analysis)/flood moderating value/Peak discharge control, economic: avoided cost & replacement cost methods/profitability of agriculture/shadow price	Lele 2009, Cui et al. 2012, Banerjee et al. 2013	3	EF, V
Flood storage capacity	B: score (for water retention of storms)	Liquete et al. 2013	1	S
	B: wetland	Posthumus et al. 2010, Carreño et al. 2012, Spencer & Harvey 2012, Temmerman et al. 2012, Hoggart et al. 2014	5	EP
	B+M: flood storage capacity of wetland; Construction cost of dam	*Natuhara 2013*	1	EP, V
Flood damage	B: # damaging floods; relationship between individual floods and the damage they caused	Burkhard et al. 2012, Fu et al. 2013, *Meyer & Priess 2014*	3	O
Vegetation	B: interception (relating to flood detention capacity)	Biao et al. 2010, Su et al. 2012	2	EF
	B: buffer from storm surges	Cook et al. 2013	1	EP
	B+M: interception during rainfall events; economic (avoided costs, costs of alternatives)	McPherson et al. 2011, Morri et al. 2014	2	EF, V
Regulation of Low Flows (drought regulation)				
Drought regulation	B: water demand, Et; WUE, transpiration	Koschke et al. 2013	1	EF
Evapotranspiration	B: theoretical	*Molden et al. 2010, Meyer & Priess 2014*	2	EF
	B: index (Et/MAP)	Hill et al. 2014	1	EF
Baseflow	B: gives an indicator of groundwater recharge, models, time exceedance graph	Barkmann et al. 2008, Egoh et al. 2008, Lerner et al. 2009, *Meyer & Priess 2014*	4	EF
	B+M: SWAT/water balance model, economic: opportunity costs to upstream landowners; production function, contingent valuation, consumer surplus approach or averting expenditure	Lele 2009	2	EP, EF, V
Drought prevalence	Score: community	Abram et al. 2014	1	S
	B+M: river flow (time series analysis); economic: direct estimation	Lele 2009	1	EF, V
Other				
Transport	Social: boat traffic congestion, perceptions	Klain & Chan 2012	2	O

Air Quality Regulation

Type	Measure	Reference	#	Cascade
Score	Community	Allendorf & Yang 2013	1	S
	Community & expert judgement	Zorrilla-Miras et al. 2014	1	S
Economic valuation	M: Annual value (km^2, US€/y)	Zhao et al. 2004	1	V
	M: Willingness to pay for cleaning the air (€/ha/y)	Niu et al. 2012	1	V
Air composition	B: Air pollutants, air quality	*Kandziora et al. 2013, van Oudenhoven et al. 2012,* Setälä et al. 2013	3	EP
Emissions	B: Emission of air pollutants (measured, model): e.g. N_2O emission (ton/ha/y), NH3 emission from fertilizers (ratios), particle concentrations (cm^3), modeled loss of ammonia to atmosphere (kg/ha)	Chang et al. 2011, Cooter et al. 2013, Steffens et al. 2012, Firbank et al. 2013	4	O
Vegetation cleaning capacity	Score: Leaf area index, Volume of vegetation	Burkhard et al. 2012, *Kandziona et al. 2013*; Scholz & Uzomah 2013	3	S
	B: Volume of vegetation (phytovolume) (m^3/m^2)	Derak et al. 2014	1	EP
	B: Vegetation cleaning capacity: dry deposition rate, pollution removal rate (model) (g/ha/y, kg/km^2), e.g. CO, aerosol particles	Campbell & Tilley 2014, Jantz & Manuel 2013, Jim & Chen 2008, *Jim & Chen 2009*	4	EF
	B: Vegetation cleaning capacity: dry deposition velocity (model) (cm/s, m/s)	Katul et al. 2011, Maes et al. 2012	2	EF
	B: Emissions and Vegetation cleaning capacity (model)	Baumgardner et al. 2012, McPherson et al. 2011	2	EF

Soil Quality Regulation

Type	Indicator	Reference	#	Cascade
Score	Community: perception of soil quality	Raymond et al. 2009, Abram et al. 2014, Zorrilla-Miras et al. 2014	3	S
	Expert judgment	Yapp et al. 2010, Zorrilla-Miras et al. 2014	2	S
Soil property: once-off measurement	B: C.P: SOC/SOM (%, Kg C/ha))	Posthumus et al. 2010, Maes et al. 2012, Marques et al. 2013, Brandt et al. 2014, Derak et al. 2014, Turner et al. 2014	6	EP
	B: C.P: Phosphorous (ton/y)	Schulte et al. 2014	1	EP
	B: Biological: respiration CO_2(mg/g)	Creamer et al. 2014	1	EF
	B: Biological: earthworm population (#,g, #/m2)	Boyer & Wratten 2010	1	EP
	B: Biological: soil fungal community structure (#)	Curlevski et al. 2014	1	EP
	B+M: C.P: Nitrogen (ton/ha); economic: habitat value (€/ha/y)	Portela & Rademacher 2001	1	EP/V
Soil property: monitoring	B: C.P: SOC long term soil experiments (C mg/g, tonC/ha/y, Mg/ha/y)	Lal 2011, Jandl et al. 2014, Srinivasarao et al. 2014	3	EP
Multiple soil properties: once-off measurement	Score: Biophysical (C.P & P.P & Biological (index))	Velasquez et al. 2007, Rutgers et al. 2012, Rousseau et al. 2013, Volchko et al. 2013	4	S
	B: C.P: SOM, P, N, C, Al, base cations (g/m2/y, g/kg, %, Kg C/m2, C/N ratio)	O'Farrell et al. 2009, Snapp et al. 2010, Veum et al. 2011, Aherne & Posch 2013, Cabezas et al. 2014, Lavelle et al. 2014, Syswerda & Robertson 2014	7	EP
	B: Biological: roots, earthworms, enchytraeids, micro-arthropods, nematodes, microbial parameters (#), ammonia oxidisers/denitrifiers	Ritz et al. 2009, van Eekeren et al. 2010, Thomsen et al. 2012	3	EP
	B: Biological: metabolic capacity of microbial community	Guenet et al. 2011	1	EF
	B: Both C.P & P.P: grain size, total organic carbon (%), Soil moisture, TC, TN, TP, bulk density (%, g/cm2), total ammonium and total nitrate (% or PPM), SOC, soil texture, soil pH, CEC (cmol kg−1), porosity, density, permeability, humidity, conductivity, organic matter, C/N ratio (g/cm^3, %, mg/l), K, Ca ,Mg, Mn, Cu, Zn, Fe, Mg:K	Mattheus et al. 2010, Otero et al. 2011, Tesfahunegn et al. 2011, Jouquet et al. 2012, Rousseau et al. 2012, Glendell et al. 2014, Hale et al. 2014, Oldfield et al. 2014, Parras-Alcántara et al. 2014	9	EP
	B+M: Both C.P & P.P: soil nitrogen content, water capacity of soil, soil organic matter storage, soil nitrogen content, water capacity of soil; economic: emergy synthesis approach, market value.	Dong et al. 2012	1	EP
	B: C.P. & Biological: benthic chlorophyll and pore water nutrient analyses (mmol /m3; mg chl m3)	Brito et al. 2012	1	EP
	B: Both C.P & P.P & Biological: SOC, biological activity, heavy metals (kg/ha), soil respiration (ug CO_2–C/g dry soil/day), C&N, Soil pH; cation concentrations, nutrients (meq/100 g soil dwt), earthworms (g), SOM (g,mg/kg), total soil C, earthworms (%), infiltration, soil moisture, vegetation cover, habitat (%), decomposer abundance, biomass and density	Bjorklund et al. 1999, Cécillon et al. 2009, Miralles et al. 2009, Mandal et al. 2010, Quijas et al. 2010, Briones et al. 2011, Ferris et al. 2012, Rousseau et al. 2012, Souza et al. 2012, Wani et al. 2012, Volchko et al. 2014	1 1	EP
Multiple soil properties: monitoring	B: C.P: Ca, Mg, K, Na, Fe, AL, P, Cl, SO_4, Si), pH, CEC, organic carbon (mg/m2)	Tye et al. 2013	1	EP
	B: C.P & Biological: Total C, Total N, NH_4-N, NO_3-N. & nematodes (# species), mycorrhizal effectiveness (%), decomposition rate, P, Cu, Corg (%, g)	DuPont et al. 2009, Kahiluoto et al. 2009	2	EP/EF
	B: C.P & P.P & Biological: earthworms, SOM, nutrients (%)	Fonte et al. 2010	1	EP
Soil Processes	Score: community: nitrogen fixation perception	Cerdán et al. 2012	1	S
	Score: biophysical: soil formation	Calvet-Mir et al. 2012	1	S
	Score: biophysical: natural attenuation of pollutants	van Wijnen et al. 2012	1	S
	B: Soil formation/accumulation (models) (GigaTon/y, g C/ha/y, m, %)	Boumans et al. 2002, Egoh et al. 2008, Campbell & Tilley 2014	3	EF
	B: Potential denitrification (enzyme activity) (µg/g/h)	Barthès et al. 2010	1	EF
	B: Denitrification (g/hour)	Burgin et al. 2013	1	EF
	B: N-mineralization (lab model/mineralization curves): (total kg N/ha/y, min/kg)	Kragt & Robertson 2014, Van Beelen et al. 2011	2	EF
	B: N Leaching (kg NO_3-N/ha, % decrease)	Nangia et al. 2008, Mason et al. 2012	2	EF

	B: C, N Leaching & microbial biomass	Bloor & Bardgett 2012	1	EP/EF
	B: Soil fertility: Gain nutrients, nutrient turnover: N (kg/m2, mg N/g dry wt/day)	Ford et al. 2012, Damour et al. 2014	2	EF
	B: Decomposition: dung (log g/day), litter (%, g/m2), allochthonous organic matter breakdown rate, (C, N, P, K, lignin and cellulose) of plants (mg/g, %)	Balasubramanian et al. 2012, Beynon et al. 2012, Schäfer et al. 2012, Hastwell et al. 2013, D'Acunto et al. 2014, Domínguez et al. 2014	6	EF
	B: Decomposition: organic matter breakdown, as function of pesticide concentration & salinity	Schäfer et al. 2012	1	EP,EF
	B+M: Soil fertility protection: N, P, K loss/gain nutrients using formula for erosion/fertilizer; economic: price (yuan/ha/y) –not specified	Chang et al. 2011	1	EF/V
	M: Habitat value for soil formation (€/ha/y)	Asafu-Adjaye et al. 2005	1	V
Nutrient cycling	Score: Biophysical (nutrient cycling)	Harrington & McInnes 2009	1	S
	B: Nutrient cycle (model) (GigaTon/y, kgN/ha/y), N use efficiency (kg N/ha)	Boumans et al. 2002, Nangia et al. 2008, Ooba et al. 2012, Dungait et al. 2012	4	EF
	B+M: Nutrient accumulation; economic: value nutrient cycle: market price of fertilizers (€/ton), willingness to pay	Niu et al. 2012	1	EF/V
	B+M: Loss of the nutrient cycling function (t/y); economic value nutrient cycle: market price of fertilizers (€/ton), price for fertilizers (€/ton)	Qin et al. 2014	1	V
	M: Economic value nutrient cycle: habitat value (€/ha/y), habitat value based on many local studies (literature review)	Zhao et al. 2004, Asafu-Adjaye et al. 2005, Ninan & Inoue 2013	3	V
Both soil properties and processes	B: Properties: nutrient concentration; SOC, bulk density. Processes: nutrient fluxes & litter turnover; nutrient turnover and uptake (mg/l), soil formation (cm/y), available water holding capacity (cm/cm), saturated hydraulic conductivity (cm^3/s)	Marrs et al. 2007, Meyer & Priess 2014	2	EP, EF
	B: Properties: Soil characterization, metal concentrations, bulk density(g cm3), moisture content(%), TC (g/kg), TN (g/kg), TP(mg/kg), SOC (g/kg), water holding capacity (%), NO3, NH4, S, available P, K, organic C, Exchangeable Na, K, Al, Ca, Mg, pH; conductivity; Surface dwelling invertebrates: number of species, abundance; Microbial biomass Carbon, Nitrogen(mg/kg), microbial community composition. Processes: Soil fauna: feeding activity (bait lamina test), basal respiration; dehydrogenase activity, acid phosphates activity; nitrification rate, net N mineralization (mg/kg), potential mineralizable nitrogen (mg/kg), potential denitrification (g N2O-N/m3/d), denitrification, nutrient cycling: N-fixation, litter decomposition; Pollution: Widianarko's pollution index (metals); farmer questionnaires (management e.g. fertilizers use)	Kachenchart et al. 2012, Niemeyer et al. 2012, Perring et al. 2012, Theriot et al. 2013, Williams & Hedlund 2013; Williams & Hedlund 2014	6	EP,EF
	B+M: Properties: earthworm population; soil C and N, soil temperature & moisture. Processes: "rate of mineralization": N-mineralisation; feeding activity (bait lamina probe), soil formation (earthworm weight & count). Economic: market price fertilizers (€/ton(N))	Sandhu et al. 2010, Ghaley et al. 2014	2	EP, EF, V

Soil Retention

Type	Indicator	Reference	#	Cascade
Score	Community: perception of erosion control	Rodríguez et al. 2006, Raymond et al. 2009, Cerdán et al. 2012, Allendorf & Yang 2013, Abram et al. 2014	5	S
	Experts judgment: erosion control	Burkhard et al. 2012, Namaalwa et al. 2013, Scholz & Uzomah 2013, Tooth et al. 2014	4	S
Soil properties (soil stability)	B: Aggregate stability (%)	Lavelle et al. 2014	1	EP
	B: Erodibility (factor)	Nahuelhual et al. 2013	1	EP
	B: General properties: soil moisture, bulk density, penetration resistance and soil structure (g/cm3), belowground biomass, root biomass, organic matter contribution by roots, productivity	van Eekeren et al. 2010, Quijas et al. 2010	2	EP
Soil formation	Score: Biophysical	Harrington & McInnes 2009	1	S
	Score: Expert judgment (rapid assessment) (€/ha/y)	Liu et al. 2012	1	EP
	B: Soil loss measured as sedimentation rates (mm/y, ha)	Martín-López et al. 2014	1	EF
	B: Conductivity (mS/cm)	Martín-López et al. 2014	1	EF
Slope stability	B: Slope stability: model slope safety factor using slope, root cohesion & soil depth	Band et al. 2012	1	EF
Shoreline protection	B: Rate of erosion or accretion	Lau 2013	1	EF
	B: Damage sustained in storms	Lau 2013	1	O
Landslide frequency	B: Erosion control: USLE factors for assessment of landslide frequency (n/ha/y)	Kandziora et al. 2013	1	O
Sedimentation prevention in reservoirs	B: Soil retention in reservoirs, bathymetry, InVEST (t/y, kg/y)	Bangash et al. 2013, Leh et al. 2013b, Terrado et al. 2014,	3	EF
	B: Sedimentation prevention by forests: eroded soil (M ton/y)	Nguyen et al. 2013	1	EF
Sediment accretion	B: Sediment accretion, accumulation rates, soil surface evolution: vertical accretion (mm, g/m2/y, mm/y), floodplain sedimentation rates (g/m^2/y, kg/m/y)	Bos et al. 2007, Howe et al. 2009, Mattheus et al. 2010, Spencer & Harvey 2012, Hupp et al. 2013, Cabezas et al. 2014, Rieger et al. 2014	7	O
Soil erosion	B: Erosion rate: soil loss, sediment yield, sediment loads -field measurements/literature review (mm/d, g/ml, g/m2/y, mg/ha/y, ton, ton/ha, %, g/m2)	Lant et al. 2005, O'Farrell et al. 2009, Jouquet et al. 2010, Smukler et al. 2010, Udayakumara et al. 2010, Otero et al. 2011, Jouquet et al. 2012, Kandziora et al. 2013, Derak et al. 2014, La Peyre et al. 2014, Palm et al. 2014	11	O
	B: Erosion, rate, risk, sediment export, sediment yield -model, InVEST, SWAT (m, g/m2/y, mm, ton/km2/y)	Swallow et al. 2009, Mason et al. 2012, Ooba et al. 2012, Jackson et al. 2013, Su & Fu 2013	5	O
	B: Erosion estimated by LULC from remote sensing (km2)	Nascimento et al. 2013	1	O
	B+M: Erosion -model (ton/km2/y), mean annual soil loss (M(mega)g/ha/y), erosion rate per LULC; economic: cost of sedimentation (€/ton/km2), willingness to pay for 1 ton reduction in erosion (€/t), replacement cost – Costanza et al. 1997 (€/h)	Portela & Rademacher 2001, Gascoigne et al. 2011, Dymond et al. 2012	3	O/V
	B+M: Paired catchment experiment comparing sedimentation rates under different LULC (forestry); economic: gross revenues from tourism and fishing before and after logging	Lele 2009	1	EF/V
Soil conservation/ erosion regulation	Score: Biophysical: soil conservation -model	Chiang et al. 2014	1	S
	B: Soil conservation (erosion rates -rUSLE) (ton/ha/y)	Bai et al. 2012, Rao et al. 2014	2	EF
	B+M: Soil protection: habitat & erosion rate (area of forest (ha)), soil density (g/cm3)); economic: cost of replacing the soil (€/ha/y, €/m^3)	Morri et al. 2014	1	EP/EF/V
	B+M: Soil conservation (erosion rates -rUSLE); economic: difference in economic returns from irrigated and rainfed farming, Ex-post analysis: average crop production values	Lele 2009, Lele & Srinivasan 2013	2	EF/V

	M: Soil conservation, habitat value, opportunity cost method, unit price of the service (€/ha/y)	Zhao et al. 2004, Niu et al. 2012	2	V
	M: Soil protection, erosion control (habitat value, willingness to pay to prevent erosion) (€/ha/y, €/household/y)	Martínez et al. 2009, Dong et al. 2012, Liu et al. 2012, Natuhara 2013, Ninan & Inoue 2013	5	V
	M: Soil protection, erosion control - emergy (€/y)	Dong et al. 2012, Lin et al. 2013	2	V
Erosion control/ erosion prevention/ soil retention	Score: Biophysical : soil retention –model; erosion prevention	Harrington & McInnes 2009, Bai et al. 2011, Barral & Oscar 2012	3	S
	B: Erosion control: vegetation cover, slope (Index, %)	Egoh et al. 2008, Hinojosa & Hennermann 2012, Maes et al. 2012, Kandziora et al. 2013, Koschke et al. 2013	5	EP
	B: Erosion control: water stable aggregates	Perring et al. 2012	1	EP
	B: Erosion control: sediment traps/surface microtopography, sediment yield (t/ha)	Norman et al. 2012, Perring et al. 2012	2	EF
	B: Erosion control: LULC (ha, ton/ha/y) & erosion rate (mm/y, kg/ha/min, kg/ha/y), erosion reduction potential –USLE + model (ton/ha/y)	Hein & van Ierland 2006, Fu et al. 2011, Lorenz et al. 2013, Lorencova et al. 2013, Lu et al. 2013, Jia et al. 2014	6	EP/EF
	B: Erosion control: soil retention, soil retention capacity – model, SWAT, InVEST, USLE (ton/y; g/ha/y, ton/ha, m^3/ha/y)	Guo et al. 2001, Carreño et al. 2012, Su et al. 2012, Wang et al. 2012, Ausseil et al. 2013, Bangash et al. 2013, Geneletti 2013, Logsdon & Chaubey 2013, Pan et al. 2013, Campbell & Tilley 2014, Watanabe & Ortega 2014	11	EF
	B+M: Erosion reduction potential –USLE + model (ton); economic: avoided damage, substitute cost approach (€/ton)	Bastian et al. 2013	1	EF/V
	B+M: Soil retention by calculation (ton/ha/y); economic: price (€/ha/y), values for erosion prevention: economic value of soil: price of the soil available for vegetable gardens (€/ton)	Chang et al. 2011	1	EF/V
	B+M: Erosion control by vegetation cover or LULC (ton/ha/y, ha); economic: hedonic price method, willingness to pay (€/ha), damage avoidance cost (€/ha/y), market price of soil (€/ha/y)	Kuenzer & Tuan 2013, Ghaley et al. 2014, Yoo et al. 2014	3	EP/EF/V
	M: Soil retention using habitat value (€/ha/year), avoided cost & replacement cost methods (€)	Asafu-Adjaye et al. 2005, Banerjee et al. 2013	2	V

Climate Regulation

Type	Indicator	Reference	#	Cascade
Score	Community	Raymond et al. 2009, Allendorf & Yang 2013, Liu et al. 2013, Abram et al. 2014, Martín-López et al. 2014,	5	S
	Expert judgement	Yapp et al. 2010, Zorrilla-Miras et al. 2014	2	S
	Biophysical: Aboveground C storage (mgC/ha) and potential evapotranspiration (mm)	Larondelle & Haase 2012	1	S
	Biophysical: Carbon sequestration (aboveground carbon, mgC/ha), potential evapotranspiration (mm), surface emission (index), tree cooling potential (°C change)	Larondelle & Haase 2013	1	S
	Biophysical: Climate change adaptation and mitigation (recycling facilities, transport links, renewable energy technology, double glazing of properties)	Radford & James 2013	1	S
	Biophysical: Index with soil organic carbon (% dry weight), biomass bacteria (number/m^2), pH KCI, diversity bacteria. All weighted by locals and expert judgement. (Ecosystem Performance Index)	Rutgers et al. 2012	1	S
	Biophysical: Index with land use & land cover, drainage class, soil texture	Van der Biest et al. 2014	1	S
Economic	M: Habitat value: €/ha/y	Zhao et al. 2004, Asafu-Adjaye et al. 2005, Liu et al. 2012	3	V
	M: Willingness to pay index (WTP): €/ha/y	Niu et al. 2012	1	V
	M: Marginal damage of carbon dioxide emissions €/tCO2	Miettinen et al. 2014	1	V
	M: Emergy: value of CO2 fixation per year (Yuan/y)	Dong et al. 2012	1	V
Climate moderation/ regulation (general)	B: Climate regulation: habitat natural forest surface area (ha)	Martín-López et al. 2014, Turner et al. 2014	2	EP
	B+M: Global climate regulation: global average temperature (GUMBO model), Marginal product (€/°C/kg(C))	Boumans et al. 2002	1	EF/V
	B+M: Simple equation: plant biomass (g) absorbs a certain amount of CO2 (ton) x weighting (expert opinion of the ability of plant species to control climate); Economic: current carbon tax rate standards (€/t, €/hm^2)	Cui et al. 2012	1	EP/V
Carbon stocks:	Score: biophysical (model)	Chiang et al. 2014, Namaalwa et al. 2013	2	S
Organic carbon storage	B: Soil organic carbon stock in topsoil (kg/m^2), soil profile (mgC/g, g/kg), 2.5m soil profile (kg/ha), two different depths (%, kgC/m^2)	Jouquet et al. 2010, Edmondson et al. 2014, Jandl et al. 2014, Kragt & Robertson 2014, Oldfield et al. 2014, Parras-Alcántara et al. 2014	6	EP
	B: Soil: Organic and Inorganic Carbon	Washbourne et al. 2012	1	EP
	B: Vegetation: aboveground Carbon (ton C/ha, g), mg CO2e/ha	George et al. 2012, Delphin et al. 2013, Peh et al. 2013	3	EP
	B: Vegetation: above and belowground: measured (mg C/ha, t/ha)	Kirby & Potvin 2007, Peh et al. 2013, Willemen et al. 2013, Renwick et al. 2014	4	EP
	B: Vegetation: Above and belowground C storage: model, calculation, literature (mg/ha)	Maes et al. 2012, Baral et al. 2013, Leh et al. 2013a, Leh et al. 2013b, Onaindia et al. 2013, Powers et al. 2013, Brandt et al. 2014, Liu et al. 2014	8	EP
	B: Carbon stocks in the soil & vegetation (vegetation, litter, topsoil carbon stocks) (g/m2)	Peh et al. 2013, D'Acunto et al. 2014, Schmidt et al. 2014	3	EP
	B: Carbon storage potential	Egoh et al. 2008, Henry et al. 2009, Jackson et al. 2013	3	EP
	B+M: Vegetation: aboveground carbon (ton C/ha); economic: benefit transfer (unit values from Costanza et al. 1997) (€/ha), multi-period bioeconomic optimization model.	Portela & Rademacher 2001, Börner et al. 2007	2	EP/V
	B+M: Above & below ground Carbon (t/ha); economic: opportunity cost of meeting mitigation policy goals (€/t CO2)	Tardieu et al. 2013,	1	EP/V
	B+M: Carbon stocks (€/t CO2); economic: price of carbon on international compliance markets (€/ton CO2)	Chisholm 2010	1	EP/V
	B+M: Carbon stocks measured, carbon accumulation calculated using plantation age; economic: price CO2 in voluntary markets (€/tonCO2). Multiplied with ton/ha accumulation gives €/ha.	Somarriba et al. 2013	1	EF/V
Carbon sequestration	Score: biophysical (C sequestration in vegetation; number of trees)	Barral & Oscar 2012, Scholz & Uzomah 2013	2	S
	B: Carbon sequestration per habitat	Lauf et al. 2014, Campbell &	2	EF

		Tilley 2014		
	B: Carbon sequestration in the soil, carbon accumulation rates (kg C/y, t C/ha, kg C/m2/y, mg/ha/y, kgC/m²/y)	Havstad et al. 2007, Howe et al. 2009, Arnalds et al. 2013, Booker et al. 2013, Bouchard et al. 2013, Rieger et al. 2014, Srinivasarao et al. 2014	7	EF
	B: Carbon sequestration in vegetation (aboveground C) (kg CO2/ha) (measurement, InVEST model: maps of LULC + data on above-ground C, photosynthesis & formula (g/m²/y), tree cover converted to sequestration by formula (ton/acre/y), model for timber forest.	Ceotto 2005, Jim & Chen 2009, Bai et al. 2011, Bastian et al. 2012, Ford et al. 2012, Liu & Li 2012, Ooba et al. 2012, Jantz & Manuel 2013, Lorencova et al. 2013, Radford & James 2013, Dobbs et al. 2014, Pan et al. 2014, Schulte et al. 2014, Serna-Chavez et al. 2014	14	EF
	B: Carbon sequestration: tree volume index (cm3/tree & m3/ha), in biomass (equation) (mg, mg/ha), C accumulated in vegetation (from literature)	Thomas et al. 2007, Evans et al. 2013, Toth et al. 2013, Timilsina et al. 2014	4	EF
	B: Carbon sequestration by productivity: carbon stores (NPP) (tons C/km2, t/ha)	Su et al. 2012, Ruijs et al. 2013, Jia et al. 2014, Pan et al. 2014	4	EF
	B: Carbon sequestration in vegetation (above and belowground C) (mg C/ha, mg C/ha/y, gC/m2/yr, MtC)	Venn 2005, Tratalos et al. 2007, Gang et al. 2011, Wang & Lin 2012, Wani et al. 2012, Rodriguez-Loinaz et al. 2013, Beaumont et al. 2014	7	EF
	B: Total Carbon sequestration (aboveground biomass, belowground biomass, soil and dead organic matter) (kg/m2), InVEST model (mgC/ha), carbon sequestration or emissions avoided (tonC/y).	Aitkenhead et al. 2011, Perring et al. 2012, Wang et al. 2012, Geneletti 2013, Lau 2013, Bhagabati et al. 2014, Hill et al. 2014, Schröter et al. 2014, Shoyama & Yamagata 2014	9	EF
	B: Carbon sequestration potential (GgC/y, % C, g C/m², g C/m²/y)	Xiaonan et al. 2008, Moore & Hunt 2012	2	EF
	B+M: Carbon sequestration in vegetation (aboveground C) (mg(CO2)/ha/y); economics: market price. (1) Five carbon price scenarios: €/tonCO2. Net present value of economic returns are calculated, (2) dollar benefit per tonne of CO2e reduction (€/tCO2). Multiplied with area (ha) converted and CO2-eq per ha (carbon captured in tree biomass), (3) current international market value (€/ton CO2), (4) value for avoided damages based on market price carbon credits (€/ton), (5) CO2 tradable emission permit value (€/tCO2), (6) carbon price (€/ton, €/mgCO2), carbon price on the carbon market (€/ton), (7) carbon tax (€/t), (8) cost of afforestation method or marginal social damage cost (€/ha/y), (9) average cost of forest carbon fixation (€/ton), estimated social costs of C, (10) exchange-based value method; price of C emission (€ mg-CO2 e−1), (11) C certificates or credits, (12) value per ton CO2 removed (€/ton CO2) or value for carbon sequestration per ha habitat (€/ha/y) ()	Guo et al. 2001, Yu et al. 2011, Bryan & Crossman 2013, Crossman et al. 2010, Olschewski et al. 2010, Ooba et al. 2010, Dymond et al. 2012, Kuenzer & Tuan 2013, Lele & Srinivasan 2013, Ninan & Inoue 2013, Nowak et al. 2013, Baral et al. 2014, Morri et al. 2014, Nghiem 2014, Yi et al. 2014	15	EF/V
	B+M: Carbon sequestration in vegetation (above and belowground C); economic: carbon market price (European Union Emissions Trading Scheme) (€/ton)	Ghaley et al. 2014	1	EF/V
	B+M: Total Carbon sequestration (aboveground biomass, belowground biomass, soil and dead organic matter); economic: price (yuan/ha/y), social cost of carbon (€/ton CO2), Emergy.	Chang et al. 2011, Gascoigne et al. 2011, Watanabe & Ortega 2014	3	EF/V
	B+M: Carbon sequestration potential, economic: cost CO2 sequestration: marginal abatement cost curves from agricultural systems (€/tonCO2)	Lal 2011	1	EF/V
	B+M: Carbon sequestration by productivity (NPP); economic: price of carbon (CO2 stock exchange) (C seq tC/ha/y, €/tonCO2)	Padilla et al. 2010	1	EF/V
	M: Habitat value for carbon sequestration: Transfer value (€/ha/y)	Martínez et al. 2009	1	V
Emissions	B: Carbon emissions (gCO2/m2/h)	Beauchemin et al. 2010, Posthumus et al. 2010, Bloor & Bardgett 2012, Peh et al. 2013	4	O
	B: Comparison of greenhouse gas emissions for different LULC/crop types (carbon dioxide (CO2), methane (CH4) and nitrous oxide (N2O)) (kg CO2 eq, mgN/m²/d, g N2O-N /ha/y, kg CO2/kg of food)	Smukler et al. 2010, Kachenchart et al. 2012, Firbank et al. 2013, Hefting et al. 2013, Lal 2013, Ripoll-Bosch et al. 2013, Emery & Fulweiler 2014	7	EF
	B: Carbon emissions & storage/burial in the soil: (mg/ha, gC/kg soil)	Lavelle et al. 2014, Palm et al. 2014	2	EF

	B+M: Carbon emissions; economic: price of CO2 reductions (t/area, €)	Cui et al. 2014	1	EF/V
	B+M: Greenhouse gas emissions (carbon dioxide (CO2), methane (CH4) and nitrous oxide (N2O))(t/ha/y), economic: opportunity costs & maintenance costs (€/y); economic value of O2 emission using the average value of the price of industrial O2 and the cost of afforestation (€/ha/y).	Wüstemann et al. 2014, Xiao et al. 2005	2	EF/V
Combined: carbon emissions & carbon sinks/burial	Score: Biophysical: Carbon emissions & carbon storage (soil & vegetation)	Burkhard et al. 2012	1	S
	B: Carbon emissions & carbon storage aboveground (vegetation) MtCO2e/y)	Bjorklund et al. 1999, Sohngen & Brown 2006, Olschewski et al. 2010, Smukler et al. 2010, Ausseil et al. 2013	5	EP
	B: Carbon emissions-& carbon sequestration (aboveground storage -vegetation) (MtCO2e/y)	Ausseil et al. 2013	1	EF
	B: Carbon sequestration & GHG/N emissions: (total, or from vegetation) (t CO2eq ha-1 y-1)	Jenkins et al. 2010, Mason et al. 2012, Syswerda & Robertson 2014	3	EF
	B: N retention and CH4 emissions	Thiere et al. 2011	1	EF
	B: Source-sink of methane, CO2 and water vapour (t C/ha/y)	Kandziora et al. 2013	1	EF
	B: Source-sink of stored trace gases (t C/h)	Kandziora et al. 2013	1	EF
	B+M: Carbon emissions & carbon storage aboveground (vegetation); economic: social cost of carbon (€/ton C), value of CO2 reductions (€/ton CO2)	Birch et al. 2014, McPherson et al. 2011	2	EF/V
	B+M: Carbon sequestration (annual net flow of carbon into soil (SOC)) & N2O emission from fertilizer and animal waste (model); economic: market prices for carbon (€/ton)	Dominati et al. 2014	1	EF/V
	B+M: Carbon fixation & O2 release; economic: carbon-tax, replacement cost	Qin et al. 2014	1	EF
Atmospheric and climate conditions	Score: biophysical (temperature, wind, albedo)	Burkhard et al. 2012	1	S
	B: Temperature, wind, albedo	Bastian et al. 2012, Depietri et al. 2013, Dobbs et al. 2014, Jim & Chen 2009, Kandziora et al. 2013, Lauf et al. 2014, Lehmann et al. 2014, Natuhara 2013, Tratalos et al. 2007	9	EP
	B: Change in atmospheric CO2 concentration (ppm, g/m3)	van Oudenhoven et al. 2012	1	EP

Pollination

Type	Measure	Reference	#	Cascade
Score	Community	Calvet-Mir et al. 2012, Cerdán et al. 2012, Raymond et al. 2009	3	S
	Expert judgement	Burkhard et al. 2012, Scholz & Uzomah 2013	2	S
	Community & Expert judgement	Zorrilla-Miras et al. 2014	1	S
	Biophysical: terrestrial biodiversity index (TBI), three parts (extent/abundance of flowering plants, variety in color, diversity), habitat for pollinators, INVEST model	Butler et al. 2013; Radford & James 2013; *Harrington & McInnes 2009;* Bai et al. 2011	4	S
Economic	M: Transfer value (ha, €/ha/y)	Martínez et al. 2009; Zhao et al. 2004	2	V
	M: Crop dependency (US€/ha), producer price of crop multiplied with dependence ratio per crop (EUR, %, EUR/km^2), Avoided loss (Avoided loss of coffee yields)	Ashworth et al. 2009; Leonhardt et al. 2013; *Ninan & Inoue 2013*; Bjorklund et al. 1999	4	V
	M: Replacement (cost involved in hiring the beehives for pollination) (€/ha/y)	Ghaley et al. 2014	1	V
Habitat	B: Pollination potential of ecosystems (Mapping land cover types)	*Maes et al. 2013*	1	EP
	B: Amount of natural habitat in the landscape, complexity, connectivity, mean distance from agriculture to natural habitat (%, m/ha, m) (mapping)	Plieninger et al. 2012	1	EP
	B: Vegetation cover of natural/semi-natural land (%)	Serna-Chavez et al. 2014	1	EP
	B: Habitat, probability for visitation (distance between nesting habitat and agriculture, distance between nesting habitat and foraging habitat) (m^2, %)	Lautenbach et al. 2011, Schulp et al. 2014	2	EP
Number of bees or species	B: Number of pollinators and species, Nectar feeder biodiversity and abundance (number), Diversity of pollination agents (especially insects)	Bjorklund et al. 1999, *Kandziora et al. 2013,* Samnegård et al. 2011, *Sabatier et al. 2013; Ford et al. 2012;* Fontana et al. 2014	6	EP
Visitation rates	B: Visitation rates, flower preference of pollinators (visits/min, number of pollinators per tree relative to number of flowers per tree)	Campbell et al. 2012, Holzschuh et al. 2012	2	EF
	B: Pollinator preferences/ability (visits/flower/min)	Garratt et al. 2014(a)	1	EF
	B+M: Visitation rates: bee visits per flower per time, pollen deposition per visit (pollination success), replacement method (to bring in bees), attributable net income (annual income €/ha/y minus production value), €/y	Winfree et al. 2011	1	EF, V
Pollination effectiveness	B: Pollinator effectiveness, pollen grain deposition (pollen grains per flower per hour, number per hour)	Rader et al. 2013, Potts et al. 2006	2	EF
	B: Pollination effectiveness: maximum capacity of honey bees to satisfy optimal pollination service demand (ratio of effective hives over total pollination service demand of crops)	Breeze et al. 2011	1	EF
	B: Number of developed fruit per plot, Numbers of fruits produced per inflorescence, number of seeds per fruit	Andersson et al. 2014, Pellissier et al. 2012	2	EF, B
	B+M: Pollination effectiveness for fruit quality (width, weight, sugar content, firmness, mineral content) and quantity (number); Economic: Market value (added value due to added quality and quantity), Net revenues (function of distance to forest), €/kg, kg/ha, €/ha	Garratt et al. 2014 (b); Olschewski et al. 2010	2	EF, B, V
Combined pollination processes and complex models	B: Number and richness of pollinators, Seed set	*Perring et al. 2012*	1	EP, EF
	B: Index: abundance and species richness, and insect pollinator visitation rate (% per species, number of visits)	Otieno et al. 2011	1	EP, EF
	B: Visitation rates & number of seeds set (visits/m^2/min)	Gemmill-Herren & Ochieng 2008	1	EF
	B: Complex Model of pollination process (effects of plant traits and special distribution and effects of pollinator behavior on pollination services)	Qu et al. 2013	1	EF
	B+M: Emergy, area crop land ha, % crops pollinated by wild pollinators, €	Campbell & Tilley 2014	1	O

Life Cycle Maintenence

Type	Indicator	Reference	#	Cascade
Score	Community	Raymond et al. 2009	1	S
Biophysical	B: Number of individuals (#)	Lau 2013	1	EP
	B: Productivity: Number of individuals per year, #/area/animal (#/yr; tonnes/yr) or per area (#/ha)	Hougner et al. 2006, Johnston et al. 2011, Hannesson 2013, Pinto et al. 2014	4	EF
Economic	M: Avoided cost and replacement cost methods by semi-structured interview with government and industry (€/yr)	Banerjee et al. 2013	1	V
	M: Willingness to pay (€/household/y)	Boerema et al. 2014	1	V
Combined approach	B+M: Seed dispersed oak trees (#); economic: replacement cost -human dispersal	Hougner et al. 2006	1	EP/V

Biological Control

Type	Indicator	Reference	#	Cascade
Score	Expert judgement	Scholz & Uzomah 2013	1	S
	Community	Raymond et al. 2009, Calvet-Mir et al. 2012, Abram et al. 2014	3	S
	Community & expert judgement	Zorrilla-Miras et al. 2014	1	S
	Biophysical (diversity of local trees & habitat)	Dobbs et al. 2014	1	S
Monetary Value	M: Avoided cost of chemical control/Avoided damage (€/area/yr)	Colloff et al. 2013, Ghaley et al. 2014, Dominati et al. 2014	3	V
	M: Benefit Transfer (unit values from Costanza et al. 1997 (€/ha/y))/Transfer Value Method (€/area/yr)	Zhao et al. 2004, Asafu-Adjaye et al. 2005, Martínez et al. 2009	3	V
Invertebrate-Indicator	B: # Pest-Controlling Species: # or #/area	Fiedler et al. 2008, Yadav et al. 2012, Kandziora et al. 2013, Meyer & Priess 2014	4	EP
	B: # Pest-Controlling Species: visits/time	Campbell et al. 2012	1	EP
	B: # Pest-Controlling Species: #/host species	Evans et al. 2011	1	EP
	B: # Pest-Controlling Species: Literature	Quijas et al. 2010	1	EP
	B: # Pests (#, # species, %)	Bjorklund et al. 1999, Quijas et al. 2010, Niemeyer et al. 2012, Perring et al. 2012, Sabatier et al. 2013, Martín-López et al. 2014	6	EP
	B: Invertebrate Diversity	Ford et al. 2012, Dobbs et al. 2014	2	EP
	B: Herbivore Productivity & Survival	Quijas et al. 2010	1	EF
	B: Predation Rates	Sandhu et al. 2010, van Oudenhoven et al. 2012	2	EF
Vegetation-Indicator	B: % Cover of Weed Species	Perring et al. 2012	1	EP
	B: Damage to Vegetation	Quijas et al. 2010, Otieno et al. 2011	2	O
	B: Habitat -Area (ha)	Plieninger et al. 2012, Butler et al. 2013	2	EP
	B: Plant Growth Rate (cm2/day)	Damour et al. 2014	1	EF
	B: Infestation Rate	Quijas et al. 2010	1	EF

CULTURAL ECOSYSTEM SERVICES

Recreation & Tourism

Type	Measure	References	#	Cascade
Score	Expert	Harrington & McInnes 2009; Scholz & Uzomah 2013; Zorrilla-Miras et al. 2014	3	S
	Community	Schaberg et al. 1999; Raymond et al. 2009; Posthumus et al. 2010; Burkhard et al. 2012; Calvet-Mir et al. 2012; Klain & Chan 2012; Norton et al. 2012; van Riper et al. 2012; Kandziora et al. 2013; Liu et al. 2013; Nahuelhual et al. 2013; Pataki et al. 2013; Radford & James 2013; Abram et al. 2014; Loomis & Paterson 2014; Zorrilla-Miras et al. 2014;	26	S
	Biophysical	Lacitignola et al. 2007; Maes et al. 2012; Moore & Hunt 2012; Hernandez-Morcillo et al. 2013; Namaalwa et al. 2013; Ruijs et al. 2013; Willemen et al. 2013; Brandt et al. 2014; Weyland & Laterra 2014	9	S
Land use (ha)	B: land use map, model or function (distance function, population density, hiking road map…)	Metzger et al. 2006; Lautenbach et al. 2011; Bastian et al. 2012; Larondelle & Haase 2012; Gulickx et al. 2013; Larondelle & Haase 2013; Dobbs et al. 2014; Lauf et al. 2014; Turner et al. 2014	11	EP
Economic value	M: land use map (e.g. wetland area surrogate indicator for floodplain fisheries production) + habitat value (theoretic, literature, value transfer, value commercial tourism and recreational boat fishing in the region, value commercial fisheries)	Zhao et al. 2004; Asafu-Adjaye et al. 2005; Martínez et al. 2009; Rees et al. 2010; Liu et al. 2012; Butler et al. 2013; Ghermandi et al. 2013	8	V
	M: habitat value (travel cost model, value transfer)	Gren et al. 1995; Baerenklau et al. 2010; Crossman et al. 2010; Cui et al. 2012; Kandziora et al. 2013; Ninan & Inoue 2013	6	V
	M: economic value recreation (theoretic, value transfer, consumption by tourists)	Yu et al. 2011; Forsius et al. 2013; Hernandez-Morcillo et al. 2013	4	V
Area specifications (distance, infrastructure, facilities etc)	B: Accessibility, distance to closest park, distance from road, density hiking paths (score, road density, model, databases)	Lacitignola et al. 2007; Willemen et al. 2010; Sander et al. 2012; Nahuelhual et al. 2013; Schröter et al. 2014	8	EP
	B: fish abundance density individuals/10m² (for fishing recreation); bird species richness (areas with high richness are mapped)	Lara et al. 2009; Villamagna et al. 2014	2	EP
	B+M: game population (model) + economic value	Rose & Chapman 2003	1	EP, V
Visits (# visits, bed nights)	B: # Visits, number of registered boats, number of fishing licenses, participation rate, diving trips hired, number of moose hunted, number of sightings of species submitted by people via the nature observation portal (theoretic, interviews local people, hotels)	Burger 2011; van Oudenhoven et al. 2012; Allendorf & Yang 2013; Hernandez-Morcillo et al. 2013; Kandziora et al. 2013; Plieninger et al. 2013; Satterfield et al. 2013; Johns et al. 2014; Pinto et al. 2014; Schröter et al. 2014; Turner et al. 2014	19	B
	B+M: #visits, #fishing days (theoretic, government data, interviews, model) + economic value €/visit (theoretic, travel cost method, willingness-to-pay, choice experiment, literature, value transfer, expenditures, income nature-based activities and local recreational sector (hotels etc))	Guo et al. 2001; Hein et al. 2006; Lacitignola et al. 2007; Bernard et al. 2009; Butler et al. 2009; Jim & Chen 2009; Pinto et al. 2010; Vejre et al. 2010; O'Farrell et al. 2011; Hernandez-Morcillo et al. 2013; Kuenzer & Tuan 2013; Lele & Srinivasan 2013; Maes et al. 2013; Mavsar et al. 2013; Natuhara 2013; Peh et al. 2013; Ruiz-Frau et al. 2013; Silvestri et al. 2013; Termansen et al. 2013; Uddin et al. 2013; Bayliss et al. 2014; Birch et al. 2014; Jones et al. 2014; Martín-López et al. 2014; van Berkel & Verburg 2014	29	B, V
	M: economic value per visit, annual consumer surplus per person for recreation, revenue hunting licences (value transfer, willingness-to-pay, choice experiment, Integrated hedonic housing price and recreation demand model), also non-monetary values	Klain & Chan 2012; Kovacs 2012; Logar er al. 2012; Banerjee et al. 2013; Carbone & Smith 2013; Chen et al. 2013; Hernandez-Morcillo et al. 2013; Liekens et al. 2013; Czajkowski et al. 2014	12	V
Property	B+M: number of houses with green environment (# houses) + increase property value green environment (% €/house)	Boerema et al. 2014	1	B, V
Health	B: Stress level reduced (theoretic)	Hernandez-Morcillo et al. 2013	1	B
"Other"	B+M: Gigaton/social capital index SCI, €/(kg/SCI)	Boumans et al. 2002	2	V

Scientific & Educational Services

Type	Measure	References	#	Cascade
Score	Expert	Harrington & McInnes 2009; Scholz & Uzomah 2013	2	S
	Community	Raymond et al. 2009; Calvet-Mir et al. 2012; Klain & Chan 2012; Norton et al. 2012; van Riper et al. 2012; Satterfield et al. 2013; Zorrilla-Miras et al. 2014	7	S
	Biophysical	Moore & Hunt 2012; Namaalwa et al. 2013; Loomis & Paterson 2014	3	S
Sites	B: Number of sites (interview)	Plieninger et al. 2013	1	EP
Education	Score: Places where one can learn, educational possibilities	Harrington & McInnes 2009; Calvet-Mir et al. 2012; Norton et al. 2012; van Riper et al. 2012; Klain & Chan 2012; Namaalwa et al. 2013; Scholz & Uzomah 2013	7	S
	Number of excursions	van Oudenhoven et al. 2012	1	B
	Educational programs (number), college courses	Hernandez-Morcillo et al. 2013; Johns et al. 2014	2	B
	Knowledge systems: Number of environmental educational-related facilities and/or events and number of their users (n/ha/y)	Johns et al. 2014	1	B
	Formal and informal educational opportunities created by access and proximately to coastal and marine ecosystems (species richness, opportunities to see megafauna, wildlife interactions, family programs, …)	Loomis & Paterson 2014	1	EP
	Environmental volunteering initiatives (Number)	Martín-López et al. 2014	1	B
Research	Cognitive development, research (score)	Calvet-Mir et al. 2012; Namaalwa et al. 2013	2	S
	Local ecological knowledge	Hernandez-Morcillo et al. 2013	1	B
	Funding for scientific research and education facilities within the ecosystem	Hernandez-Morcillo et al. 2013	1	B
	Scientific publications (number of scientific publications)	Martín-López et al. 2014	1	B
	Number of visiting researchers	van Oudenhoven et al. 2012	1	B
	Scientific study site	Klain & Chan 2012	1	EP
	M: Scientific resources: research activity in coastal marine ecology and management (€ federal and international research grant)	Johns et al. 2014	1	V
Living	B+M: Number of houses + property value (added value green environment)	Boerema et al. 2014	1	B, V

Heritage, Cultural, Bequest, Inspiration & Art

Type	Measure	References	#	Cascade
Score	Expert	Yapp et al. 2010; Butler et al. 2013; Gilvear et al. 2013; Scholz & Uzomah 2013; Nahuelhual et al. 2014	5	S
	Community	Raymond et al. 2009; Calvet-Mir et al. 2012; Klain & Chan 2012; Norton et al. 2012; Tengberg et al. 2012; van Riper et al. 2012; Allendorf & Yang 2013; Pataki et al. 2013; Satterfield et al. 2013; Abram et al. 2014; Derak et al. 2014; Zorrilla-Miras et al. 2014	14	S
	Biophysical	Tengberg et al. 2012; Namaalwa et al. 2013; Loomis & Paterson 2014; Martín-López et al. 2014; Nahuelhual et al. 2014	5	S
Area	B: per land use type	Willemen et al. 2010	1	EP
Economic	M: area per land use type and area value (€/ha) (value transfer, willingness-to-pay)	Zhao et al. 2004; Asafu-Adjaye et al. 2005; Nahuelhual et al. 2014	3	V
	M: Choice experiment: non-use value, or biodiversity value (€/household)	Liekens et al. 2013	1	V
	M: Value expressing social preference according to its cultural relevance	Derak et al. 2014	1	V
Biology	B: Satisfaction for conserving biodiversity: trend in populations of emblematic species	Martín-López et al. 2014	1	EP
	B: Native trees and elm trees: gives sense of place	Dobbs et al. 2014	1	EP
	B: Conservation (#)	Ford et al. 2012	1	EP
	B: Natural heritage and natural diversity: number of endangered, protected and/or rare species or habitats (N° species/ha)	Kandziora et al. 2013	1	EP
Site conditions	B: Amount, quality, intensity, and distribution of cultural/historical/spiritual opportunities (historically designated sites, cultural/historical events, citizen involvement (ngo's), Perceptions of ecosystem health…)	Loomis & Paterson 2014	1	EP
	B: Tangible object in sea contributing to sense of place	Hernandez-Morcillo et al. 2013	1	EP
Authentic, historic sites	B: Number of sites; Places with historical, cultural, traditional value (per pixel: yes, no); % of authentic land use/cover in cultural heritage landscape; Cultural heritage site; percentage of territory governed or claimed by indigenous peoples	Hinojosa & Hennermann 2012; Klain & Chan 2012; van Riper et al. 2012; Hernandez-Morcillo et al. 2013; Plieninger et al. 2013	5	EP
	B+M: number of hotspots and economic value per hotspot	van Berkel & Verburg 2014	1	EP, V
Tradition, folklore	B: Maintenance of traditional ecological knowledge (score)	Calvet-Mir et al. 2012	1	EP
	B: Benefits in production of folklore	Hernandez-Morcillo et al. 2013	1	EP
	B: History, place, inspiration, calm, escape (score)	Norton et al. 2012	1	EP
Inspiration	B: Inspiration for culture, art and design (score)	Calvet-Mir et al. 2012	1	B
	B: Inspirational: benefits	Hernandez-Morcillo et al. 2013	1	B
	B: Inspiration (score)	Scholz & Uzomah 2013	1	B
Visit	B+M: number of tourists and tourist expenses in the area	Yu et al. 2011	1	B, V
Activity	B: Fish, crab, or hunt/Collect herbs, berries, etc. (# times/month)	Burger 2011	1	B
	B: use of marine biodiversity	Hernandez-Morcillo et al. 2013	1	B
Social	B: Creation and maintenance of social relations (score)	Calvet-Mir et al. 2012	1	B
Art	B: Number of lyrics purporting sustainable use of Opuntia scrub	Hernandez-Morcillo et al. 2013	1	B
Psychological	B: impact on human well-being: impacts of sand blowing on people	Hernandez-Morcillo et al. 2013	1	B
Living	B+M: Number of houses + property value (added value green environment)	Boerema et al. 2014	1	B, V

Aesthetic Services

Type	Measure	References	#	Cascade
Score	Expert	Harrington & McInnes 2009; Radford & James 2013; Scholz & Uzomah 2013	3	S
(*general 'aesthetic value', visual quality, beauty, aesthetic appreciation and cultural inspiration*)	Community	Schaberg et al. 1999; Raymond et al. 2009; Lindemann-Matthies et al. 2010; Calvet-Mir et al. 2012; Klain & Chan 2012; van Riper et al. 2012; Allendorf & Yang 2013; Dobbie 2013; Hernandez-Morcillo et al. 2013; Kandziora et al. 2013; Liu et al. 2013; Nahuelhual et al. 2013; Satterfield et al. 2013; Vidal-Legaz et al. 2013; van Berkel & Verburg 2014; Zorrilla-Miras et al. 2014	16	S
	Biophysical	Butler et al. 2013; Frank et al. 2013; Kandziora et al. 2013; Koschke et al. 2013; Nahuelhual et al. 2013; Brandt et al. 2014; Fontana et al. 2014; Loomis & Paterson 2014	8	S
Area	**B:** Area per land use	Sander et al. 2012; Vidal-Legaz et al. 2013	2	EP
Economic value	**M:** area per land use and unit value per land use type arable land, grassland and wooded land (€/ha) (contingent valuation)	Ghaley et al. 2014	1	V
	M: Travel cost	Kandziora et al. 2013	1	V
	M: Willingness to pay	Grala et al. 2012; Kandziora et al. 2013; Kopmann & Rehdanz 2013	3	V
	M: Amenity (€/household)	Liekens et al. 2013	1	V
	M: Value expressing social preference according to its beauty (relative unit)	Derak et al. 2014	1	V
Sites	**B:** Number of sites, places to enjoy sounds, smells; Number Of scenic roads, views used for photos	Van Riper et al. 2012; Hernandez-Morcillo et al. 2013; Plieninger et al. 2013; van Berkel & Verburg 2014	4	EP
	B+M: number of hotspots detected from people and tourist attractions, and economic value per hotspot	van Berkel & Verburg 2014	1	EP, V
Site conditions and presence of unique/intresting ecologic features (tree attributes, presence alien species (neg), biodiversity score)	**B:** Intrinsic tree attributes and related tree-condition, location and outstanding features	Hernandez-Morcillo et al. 2013	1	EP
	B: Large native trees	McPherson et al. 2011; Nahuelhual et al. 2013	2	EP
	B: Impacts of alien species on aesthetic perception of landscape	Hernandez-Morcillo et al. 2013	1	EP
	B: Flower abundance	Ford et al. 2012	1	EP
	B: annual increase in tree leaf area (m^2)	McPherson et al. 2011	1	EF
	B: Site characteristics: Trees in front gardens, Absence of litter and vandalism, Presence of trees…	Radford & James 2013	1	EP
	B: Biodiversity score	Butler et al. 2013	1	EP
	B: Scenic beauty estimation via landscape metrics	Kandziora et al. 2013	1	EP
	B: Artistic, Natural beauty, Unique natural feature (score)	Klain & Chan 2012	1	EP
	B: Aesthetic quality of physical and biological components: visual, olfactory, and auditory (viewscape, watchable wildlife, species richness, degree of unobstructed view, opportunities for ocean viewing…)	Loomis & Paterson 2014	1	EP
Visits	**B:** Number of visit days/years, number of visit hours	Johns et al. 2014;	1	B
	B+M: number of visits, economic value per visit (willingness-to-pay)	Gret-Regamey et al. 2008; McPherson et al. 2011	2	B, V
Living	**B:** Number of houses	van Oudenhoven et al. 2012	1	B
	B: Net migration	Johns et al. 2014	1	B
	B+M: Number of houses + property value (added value green environment, difference with and without trees)	Sander et al. 2012; Hernandez-Morcillo et al. 2013; Boerema et al. 2014; Johns et al. 2014; McPherson et al. 2011	5	B, V
Art	**B:** Number of paintings/illustrations, songs, products portraying the respective landscape/ecosystem (#/landscape type)	Kandziora et al. 2013	1	B

Symbolic, Sacred, Spiritual & Religious Services

Type	Measure	References	#	Cascade
Score	Expert	Harrington & McInnes 2009; Radford & James 2013; Scholz & Uzomah 2013; Schröter et al. 2014	4	S
	Community	Raymond et al. 2009; Calvet-Mir et al. 2012; Klain & Chan 2012; Norton et al. 2012; van Riper et al. 2012; Liu et al. 2013; Satterfield et al. 2013; Abram et al. 2014; Zorrilla-Miras et al. 2014	9	S
Site conditions	B: Natural sounds, opportunities for quiet contemplation	Radford & James 2013	1	EP
Sacred, spiritual sites	Score: Spiritual experience	Harrington & McInnes 2009; Calvet-Mir et al. 2012; Norton et al. 2012; Scholz & Uzomah 2013; Abram et al. 2014	5	S
	B: Riparian forest composition in sacred sites	Hernandez-Morcillo et al. 2013	1	EP
	B: Number of intact ecosystems providing sacred grounds	Hernandez-Morcillo et al. 2013	1	EP
	B: Sacred sites to determine beneficial differences in different riparian forests	Hernandez-Morcillo et al. 2013	1	EP
	B: Places with sacred, religious, spiritual meaning	van Riper et al. 2012	1	EP
	B: Ceremonial site, spiritual/inspiration/awe, peace, sense of place/home, community identity, existence	Klain & Chan 2012	1	EP
	B: Number of sites	Plieninger et al. 2013	1	EP
	B+M: number of hotspots and economic value per hotspot	van Berkel & Verburg 2014	1	EP, V
Spiritual activity	B: Pray or meditate/commune with nature/vision quest or other ceremony (# times/month)	Burger 2011	1	B
	B: Number of people participating in sacred activities	Hernandez-Morcillo et al. 2013	1	B
Facilities and activity	B: Number of spiritual facilities and number of their visitors for performance of rituals and maintain the relationship with ancestors	Kandziora et al. 2013	1	O, B
Property	B+M: Number of houses + property value (added value green environment)	Boerema et al. 2014	1	B, V

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S.M.

Supplementary Material
Species Lists

Table 1: Species lists for identified species on degraded and pristine sites in 2014 and 2015. Species are sorted by abundance.

Pristine 2014	Degraded 2014	Pristine 2015	Degraded 2015
Prionium serratum	*Prionium serratum*	*Prionium serratum*	*Prionium serratum*
Restio paniculatus	*Cliffortia strobilifera*	*Restio paniculatus*	*Cliffortia strobilifera*
Cliffortia strobilifera	*Isolepis prolifera*	*Pteridium aquilinum*	*Rubus fruticosus*
Epischoenus gracilis	*Pennisetum macrourum*	*Cliffortia strobilifera*	*Pteridium aquilinum*
Cliffortia odorata	*Acacia mearnsii*	*Epischoenus gracilis*	*Pennisetum macrourum*
Todea barbara	*Psoralea pinnata*	*Todea barbara*	*Helichrysum odoratissimum*
Isolepis prolifera	*Cyperus thunbergii*	*Cliffortia odorata*	*Isolepis prolifera*
Psoralea aphylla	*Juncus lomatophyllus*	*Isolepis prolifera*	*Acacia mearnsii*
Elegia asperiflora	*Laurembergia repens*	*Psoralea aphylla*	*Juncus lomatophyllus*
Acacia mearnsii	*Rubus fruticosus*	*Wachendorfia thyrsiflora*	*Carpha glomerata*
Pteridium aquilinum	*Helichrysum odoratissimum*	*Acacia mearnsii*	*Searsia angustifolia*
Psoralea axillaris	*Searsia angustifolia*	*Helichrysum odoratissimum*	*Digitaria sp.*
Hippia frutescens	*Pteridium aquilinum*	*Helichrysum cymosum*	*Laurembergia repens*
Helichrysum helianthimifolium	*Wachendorfia thyrsiflora*	*Psoralea axillaris*	*Eleocharis limosa*
Helichrysum odoratissimum	*Zantedeschia aethiopica*	*Sphagnum sp.*	*Wachendorfia thyrsiflora*
Helichrysum cymosum	*Persicaria decipiens*	*Zantedeschia aethiopica*	*Persicaria decipiens*
Cyclopia maculata	*Sphagnum sp.*	*Hippia frutescens*	*Phragmites australis*
Wachendorfia thyrsiflora	*Eleocharis limosa*	*Helichrysum helianthimifolium*	*Restio paniculatus*
Sphagnum sp.	*Phragmites australis*	*Carpacoce spermacocea*	*Wahlenbergia procumbens*
Cliffortia graminea	*Berzelia lanuginosa*	*Platycaulos compressus*	*Zantedeschia aethiopica*
Zantedeschia aethiopica	*Restio paniculatus*	*Juncus lomatophyllus*	*Psoralea pinnata*
Elegia capensis	*Digitaria sp.*	*Elegia capensis*	*Eragrostis sarmentosa*
Juncus lomatophyllus	*Fuirena hirsuta*	*Liverwort (Marchantiales)*	*Juncus acutus*
Liverwort (Marchantiales)	*Helichrysum cymosum*	*Persicaria decipiens*	*Sphagnum sp.*
Senecio coleophyllus	*Juncus capensis*	*Psoralea pinnata*	*Helichrysum cymosum*
Psoralea floccosa	*Hypochaeris radicata*	*Watsonia angusta*	*Pycreus nitidus*
Lobelia sp.	*Athanasia trifurcata*	*Panicum coloratum*	*Thelypteris confluens*
Persicaria decipiens	*Pelargonium grossularioides*	*Searsia rehmanniana*	*Conyza bonariensis*
Laurembergia repens	*Pseudognaphalium sp.*	*Ursinia serrata*	*Hypochaeris radicata*
Carpha capitellata	*Arctotheca calendula*	*Hypolepis sparsisora*	*Fuirena coeulescens*
Carpha glomerata	*Brabejum stellatifolium*	*Juncus capensis*	*Paspalum dilatatum*
Erica bergiana	*Carpha glomerata*	*Cliffortia graminea*	*Pseudognaphalium sp.*
Gnidia oppositifolia	*Conyza bonariensis*	*Lobelia sp.*	*Pycreus polystachyos*
Hypolepis sparsisora	*Eragrostis sarmentosa*	*Cyclopia maculata*	*Eragrostis sp.*
Juncus capensis	*Ficinia trispicata*	*Dilatris viscosa*	*Searsia rehmanniana*
Searsia rehmanniana	*Imperata cylindrica*	*Erica bergiana*	*Nidorella ivifolia*
Senecio rigidus	*Nidorella ivifolia*	*Gnidia oppositifolia*	*Seneceio burchelli*
Watsonia angusta	*Paspalum dilatatum*	*Laurembergia repens*	*Typha capensis*
Panicum coloratum	*Searsia rehmanniana*	*Osteospermum*	*Nidorella undulata*
Ursinia serrata	*Senecio rigidus*	*Osteospermum moniliferum*	*Brezelia lanuginosa*
Blechnum capense	*Thelypteris confluens*	*Senecio halimifolius*	*Cyperus longus*
Centella asiatica	*Typha capensis*	*Thelypteris confluens*	*Eragrostis sp.*
Osteospermum moniliferum	*Ficinia sp*	*Blechnum capense*	*Pelargonium grossularioides*
Cyperus thunbergii	*Monopsis simplex*	*Didymodoxa sp.*	*Acacia saligna*
Drosera capensis	*Oxalis sp.*	*Histiopteris incisa*	*Agrostis sp.*
Elegia sp.	*Acacia saligna*	*Nidorella ulmifolia*	*Lobelia sp.*

**Table 1 continued...*

Pristine 2014	Degraded 2014	Pristine 2015	Degraded 2015
Ficinia nodosa	*Agrostis sp*	*Psoralea monophylla*	*Monopsis simplex*
Ficinia sp.	*Centella asiatica*	*Pycreus polystachyos*	*Athanasia trifurcata*
Histiopteris incisa	*Osteospermum moniliferum*	*Senecio coleophyllus*	*Briza minor*
Otholobium sp.	*Cyperus denudatus*		*Cyperus durus*
Psoralea plauta	*Lobelia sp.*		*Cyperus sp.*
Pycreus polystachyos	*Panicum coloratum*		*Cystopteris fragilis*
			Didymodoxa sp.
			Helichrysum sp.
			Nymphoides thunbergiana
			Ursinia sp.

Curriculum Vitae

Alanna Rebelo started her undergraduate studies in Zoology and Ecology in 2006 at the University of Cape Town, South Africa. The course 'Inland Freshwater Ecosystems' was pivotal in inspiring her to do research on the ecology of rivers and wetlands in South Africa. She completed her Masters Research *cum laude* at Stellenbosch University, where she investigated the hydrological benefits of restoration in the Kromme palmiet wetlands. In 2011 she received a Green Talents Fellowship in Germany, which was followed by a three month research stay at the DLR in 2012 (Deutsches Zentrum für Luft und Raumfahrt) in Munich. This experience inspired her to pursue research using remote sensing techniques. Being an alumnus of the Green Talent programme led to the opportunity to attend the ProSPER.Net Young Researchers' School in Yogyakarta, Indonesia as well as the Stockholm +40 Forum for Sustainability in 2012. In 2013 she received funding to start her doctorate at Stellenbosch University (South Africa). In 2014 she joined a joint degree programme with the University of Antwerp (Belgium) through the European Commission Erasmus Mundus Partnerships (EUROSA). During her doctorate she was able to attend numerous international courses, fieldtrips and present her work at international conferences.

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Sept 2016, Ecosystem Services Partnership Conference, Antwerp, Belgium. Paper Presentation: Is the reality of ecosystem services adequately quantified?

May 2016, Society for Wetland Scientists, European Chapter, Potsdam, Germany. Paper Presentation: Water purification of South African Palmiet Wetlands.

Nov 2015 Ecosystem Services Partnership Conference, South Africa. Paper Presentation: Is the reality of ecosystem services adequately quantified?