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Incorporating microclimate into species distribution models

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Abstract

Species distribution models (SDMs) are widely used to make predictions and assess questions regarding the spatial distribution and redistribution of species under environmental changes. Current SDMs are, however, often based on free-air or synoptic temperature conditions with a coarse resolution, and thus may fail to capture apparent temperature (cf. microclimate) experienced by living organisms within their habitats. Microclimate is nevertheless crucial in habitats characterized by a vertical component (e.g. forests, mountains, or cities) or by horizontal variation in surface cover. The mismatch between how we usually express climate (cf. coarse-grained free-air conditions) and the apparent microclimatic conditions that living organisms experience has only recently been acknowledged in SDMs, yet several studies have already made considerable progress in tackling this problem from different angles. In this review, we summarize the currently available methods to obtain meaningful microclimatic data for use in distribution modelling. We discuss the issue of extent and resolution, and propose an integrated framework using a selection of appropriately-placed sensors in combination with both detailed measurements of the habitat 3D structure, for example derived from digital elevation models or airborne laser scanning, and long-term records of free-air conditions from weather stations. As such, we can obtain microclimatic data with finer spatiotemporal resolution and of sufficient extent to model current and future species distributions.

Keywords: biodiversity, climate change, environmental niche modeling, humidity, microclimate, microrefugia, remote sensing, temperature

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Introduction

Species distribution models (SDMs), also known as environmental niche models, are widely used to make predictions and assess questions regarding the spatial distribution and redistribution of species under environmental changes (Elith and Leathwick 2009). Applications of SDMs range from studies on the effects of anthropogenic climate change to predictions of biological invasions (Guisan and Thuiller 2005). SDMs are usually created by relating known species occurrence (or presence-absence) data with information about the environmental conditions at these locations (Guisan and Thuiller 2005, Elith and Leathwick 2009, Jiménez-Valverde et al. 2011). The most common strategy is to work with a set of bioclimatic variables at 30 arc-second resolution (ca. 1 km at the equator) or coarser (Hijmans et al. 2005, Warren et al. 2008, Sears et al. 2011, Slavich et al. 2014, Gonzalez-Moreno et al. 2015) which usually represent free-air conditions averaged over 30 years or more. While such macroclimatic data might be sufficient in flat terrains with little variation in land use, they may not adequately characterize the microclimatic conditions organisms experience. Differences between macro- and microclimate are expected to be particularly pronounced where habitat includes a vertical dimension with significant variation along it, originating from either biotic, abiotic or human-made features (e.g. in mountains, forests, or cities) (Bramer et al. 2018).

For example, in mountain regions with heterogeneous topography, microclimate can vary noticeably over short distances due to a steep elevational gradient and rugged terrain (Gottfried et al. 1999, Holden et al. 2011, Sears et al. 2011, Opedal et al. 2015, Graae et al. 2018). Annual average temperatures have been found to vary up to 6°C within spatial units of 1 km² in Northern Europe (Lenoir et al. 2013). This large temperature variation also affects snow distribution (both snow depth and cover) in cold environments and consequently the local length of the growing season and many associated processes (Körner 2003, Aalto et al. 2018). The fine-grained thermal variability in mountains is usually attributed to physical processes such as air motion and solar radiation, interacting with topographic complexities such as aspect, slope angle and roughness; i.e. topoclimate (Geiger and Aron 2003), with vegetation cover and anthropogenic disturbance additionally known to affect local temperatures (Lembrechts et al. 2017). Consequently, the necessity to incorporate topoclimatic processes into SDMs for organisms in mountainous regions is now well acknowledged (Randin et al. 2009, Dobrowski 2011).

Similar microclimate heterogeneity has been reported for forest systems, where daily maximum temperatures in the understory, i.e. sub-canopy temperatures, have been found to be more than 5°C lower – and occur significantly later in the day – than in comparable clear-cuts (Chen et al. 1999). It has also been recently suggested that sub-canopy temperatures are not only instantly buffered, but also partially decoupled from free-air temperatures (Ewers and Banks-Leite 2013, Varner and Dearing 2014, Locosselli et al. 2016, Lenoir et al. 2017, Aalto et al. 2018), with important consequences for forest-dwelling species redistribution under anthropogenic climate change (Lenoir et al. 2017). Temperature buffering is defined here as a reduction in climatic extremes, which increases stability over time, while the term decoupling is used for a deviation from the 1:1 reference line of perfect coupling between sub-canopy and free-air temperatures. In cities, the urban heat island (UHI) effect results in higher air and surface temperatures than in rural surroundings, especially at night (Grimm et al. 2008). Differences between urban and adjacent rural temperatures are increasing (from around 0.5°C differences in 1950 to 1.5°C in 2005 for

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Brussels) as urbanisation has increased in the last decade (Hamdi 2010), indicating a similar decoupling between urban microclimate and the background free-air conditions as observed in forests. The UHI effect results from the interaction between the vertical use of space (e.g. buildings) with the different land cover in urbanised areas, with a lower evaporative cooling and reductions in heat convection to the atmosphere thought to be the driving factors (Zhao et al. 2014). In general, temperature variation occurs at multiple scales, from the smallest boundary layer of air to the landscape level (Pincebourde et al. 2016, Bramer et al. 2018).

In order to accurately predict species distributions in natural or anthropogenic environments with such small-scale climatic variability (e.g. arctic-alpine, forest, urban), fine resolution climate data is needed (Illan et al. 2010, Scherrer and Körner 2011, Suggitt et al. 2011, Graae et al. 2012, Opedal et al. 2015). This is important for example in regard to holdouts, which are isolated populations that persist in a favourable microclimate for a limited period of time amidst deteriorating climatic conditions; and microrefugia, where these isolated populations can persist for a longer time until climatic conditions return to baseline or suitable (Ashcroft 2010, Dobrowski 2011, Hannah et al. 2014, Lenoir et al. 2017, Meineri and Hylander 2017). Indeed, the spatial heterogeneity in temperature computed from local measurements has been shown to be almost twice as large as the one computed from global interpolated temperatures (Lenoir et al. 2013), suggesting local persistence opportunities through short-distance escapes for populations experiencing anthropogenic climate change (Graae et al. 2018). Overlooking such microrefugia likely results in overestimations of future species' range shifts (Lenoir et al. 2013). Climatic variability within an area can also buffer climate warming effects considerably (Lenoir et al. 2013, Lenoir et al. 2017), yet this buffering likewise often remains undetected using macroclimatic data at coarse spatial resolution (e.g. CHELSA (Karger et al. 2017), WorldClim (Fick and Hijmans 2017), TerraClimate (Abatzoglou et al. 2018) or ENVIREM (Title and Bemmels 2017)). Overlooking this buffering can lead to overestimation of extinction rates (Willis and Bhagwat 2009). Another use of microclimatic data lies in the assessment of stepping stones, referring to areas with favourable microclimates that facilitate species' range shifts, e.g. upward or poleward movement during climate change (Hannah et al. 2014). Such stepping stones can exist in mountain environments (Lembrechts et al. 2017), yet the urban matrix can also act as such for the poleward expansion of both heat-loving native and non-native species (Menke et al. 2011).

This mismatch between how we traditionally use climate (cf. free-air conditions) and the apparent microclimatic conditions that living organisms experience has only recently been acknowledged in SDMs (Dobrowski 2011, Pradervand et al. 2014, Slavich et al. 2014), yet considerable progress in tackling this problem has been made and has produced improvements in SDM predictions (e.g. Ashcroft et al. 2008, Dobrowski 2011, Pradervand et al. 2014, Slavich et al. 2014, Meineri and Hylander 2017, Bramer et al. 2018). In the following sections, we shortly summarize the current available methods to obtain meaningful microclimatic data for ecology, after which we show their current application in SDMs.

Sources of microclimatic data

In-situ measurements

Miniature data-loggers can provide high-resolution measurements of surface, soil and air temperatures, with the major advantage that conditions can be measured where they are expected to be ecologically

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most relevant to living organisms (Rae et al. 2006, Ashcroft et al. 2008, Bramer et al. 2018). Small sensors can even be attached to the organisms themselves to obtain temperature information at the level of the study object (Potter et al. 2013). Such measurements also allow high temporal detail, and focusing on extreme weather conditions has as such been shown to be often more relevant for species distributions than the average climate over seasons with many different weather patterns (Ashcroft and Gollan 2012). However, a drawback of microclimate data from in-situ loggers lies in the short temporal extent (Table 1). These techniques are currently indeed limited to the measurement of "micro-weather" data instead of microclimate data. To improve the accuracy of SDMs, the high spatial and temporal accuracy of these in-situ measurements will need to be combined with long-term records, either by maintaining loggers in the field over periods of several years or by coupling these loggers with historical data from the long-established networks of national weather stations. The use of such loggers over large geographic extents is also still limited by the cost (Lenoir et al. 2013), despite the increasing availability of small, relatively cheap and robust temperature sensors (Bramer et al. 2018). In-situ measurements with miniature data-loggers additionally provide opportunities to measure air humidity (Ashcroft and Gollan 2012), yet techniques to accurately measure long-term soil moisture and precipitation at numerous locations are currently not readily available (Lenoir et al. 2017), even though global databases of soil moisture have been under development for decades (Robock et al. 2000, Dorigo et al. 2011).

Modelling microclimate

For spatial predictions in SDMs, the above-mentioned in-situ measurements first have to be converted into gridded data across the spatial extent covered by the network of sensors, using interpolation techniques similar to those used to create global climate models based on a global network of weather station data (e.g. WorldClim) (Ashcroft et al. 2008, Meineri and Hylander 2017). As for interpolation techniques, one can use mixed-effects models or geostatistical approaches such as spatial kriging or geographically weighted regressions (Fotheringham et al. 2003, Ashcroft et al. 2008, Fridley 2009, Ashcroft and Gollan 2012, Meineri and Hylander 2017). Although geostatistical approaches may outperform mixed-effects models to spatially interpolate microclimate, the former cannot be used to extrapolate microclimate outside the spatiotemporal extent covered by the data. Mixed-effect models can be used to extrapolate microclimate, yet spatiotemporal extrapolations should always be used with extreme care, and must remain inside the range of conditions covered by the predictor variables used to calibrate the model. This is an important limitation with repercussions for SDMs. These interpolation techniques allow the integration of detailed regional variables (e.g. derived from digital elevation models (DEMs) or similar datasets) in accurate interpolations of microclimate (Bramer et al. 2018). Such methods accounting for well-known topographic climate-forcing have been shown to significantly improve SDMs in regional trials (Ashcroft et al. 2008, Ashcroft and Gollan 2012). Microclimatic interpolation can capture variation at high temporal resolution, yet is limited in its temporal extent by the baseline in-situ temperature data (e.g. Ashcroft et al. 2008) (Table 1). The combination of a high (hourly) temporal resolution and a long temporal extent has however been realized thanks to the application of similar techniques (e.g. mixed-effect models) to interpolate long-term hourly weather station data at 25-m^2 resolution (with the help of fine-scaled DEMs , e.g. Bennie et al. 2013, Meineri and Hylander 2017) or lower (< 10 m, thanks to airborne light detection-and-ranging (LiDAR) images, George et al. 2015; see

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the last paragraph of this section and the next section for the use of remote sensing technologies). However, such interpolations are currently limited to free-air temperature (Table 1).

Similar statistical approaches can be used to downscale macroclimate, i.e. translating macroclimatic variables to a finer spatial resolution by linking global climate models to regional or local variables at that finer resolution. Such downscaling approaches use statistical relationships between local and global climate patterns to estimate local climate (Dobrowski et al. 2009, Ashcroft and Gollan 2013a). They can provide long-term averages of local climate with a long temporal extent, yet have a coarse temporal resolution and are again limited to free-air temperatures (Table 1, Woods et al. 2015, Carroll et al. 2016). Additionally, while regional datasets often include estimates of climate extremes (e.g. the warmest temperature of the warmest month, Hijmans et al. 2005), they do not allow the assessment of variation in frequency and/or intensity of climate extremes over time, as is possible with in-situ measurements.

As opposed to the above-mentioned statistical models, process-based or mechanistic methods seek to model microclimate using mathematical relationships between the processes driving it (e.g. coastal influences, altitudinal effects or cold-air drainage). They originate in meteorology and incorporate the physical processes like energy and mass fluxes or wind speed to predict climate at the local scale, which makes them more likely to provide reliable predictions under future conditions (Bennie et al. 2008, Evans and Westra 2012, Felicísimo Pérez and Martín-Tardío 2017, Kearney and Porter 2017). Mechanistic models still require inputs from weather stations or climate models, but crucially the downscaling process is based on known mechanisms rather than using interpolation or statistical algorithms (Bramer et al. 2018). Finally, one can also use empirically calibrated mechanistic models, which combine a mechanistic understanding of microclimatic processes (e.g. cold-air drainage) with empirical testing using in-situ measurements (Maclean et al. 2017). Such a hybrid model combines the accuracy of empirical models with the transferability of mechanistic models.

The spatial resolution of interpolation and downscaling approaches is unavoidably linked to the resolution of the underlying environmental data: it can only 'fill in the gaps' in a coarser dataset if other fine-grained environmental information is available. Most downscaling approaches make use of DEMs to capture topoclimate. High-resolution DEMs are currently available at horizontal resolutions of 25 m or finer at the global extent (Randin et al. 2009, Hannah et al. 2014, Davis et al. 2016), allowing a significant improvement over the 1-km resolution of global climate data (e.g. WorldClim, CHELSA, ENVIREM). With not only elevation defining microclimate, other topoclimatic variables (e.g. aspect, cold-air drainage, solar insolation) are being derived from high-resolution DEMs to further improve models (Dobrowski 2011, Ashcroft and Gollan 2013b, Lenoir et al. 2017). Recent years have also seen a rapid increase in remote sensing techniques using satellite-based, airborne or terrestrial sensors, and consequently a strong increase in the accuracy and resolution of remotely-sensed gridded data (Table 1, Parmentier et al. 2014, Pradervand et al. 2014, Bramer et al. 2018). At resolutions finer than the 25 x 25 m available in DEMs, both physiographic and biophysical processes affect microclimate (Suggitt et al. 2011, Lenoir et al. 2017, Greiser et al. 2018). Remote sensing techniques such as airborne LiDAR sensors as well as hyperspectral images can provide a 3D analysis of canopy structure and height of the vegetation and ground surface at an unprecedented resolution (Lefsky et al. 2002, Bramer et al. 2018),

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thus providing structural properties of the landscape. To transform this information into microclimatic values, one can use either empirical regressions, or a process-based modelling approach, in which the effects of microtopography and vegetation on temperature are incorporated (Lenoir et al. 2017). Using remote sensing data thus provides climate data with a high spatial resolution and broad extent, and either a high temporal resolution (from interpolation of in-situ data), a broad temporal extent (from downscaling of coarse-grained climatic grids) or both (from interpolation of weather station data). Although the potential of LiDAR tools to assess detailed physiographic and biophysical processes has recently been highlighted (Keppel et al. 2012), their use in SDMs is relatively underexplored (Lenoir et al. 2017). Finally, note that downscaling and interpolation approaches become exponentially more computationally intense with each linear increase in scale-precision (cf. finer resolutions for a given extent), both temporarily and spatially (Potter et al. 2013, Hannah et al. 2014).

Remotely-sensed land surface temperature

The most straightforward option to infer microclimate from remote sensing is by directly measuring it through thermal remote sensing – via satellites (e.g. MODIS, Wan et al. 2015) or portable infra-red (IR) cameras (Scherrer and Körner 2010). These techniques can play a crucial role when spatial variation in temperature needs to be measured with extreme accuracy, or in out-of-reach areas such as forest canopies (Faye et al. 2016). However, the outcomes have so far only been occasionally used as microclimatic data input in SDMs (e.g. Bisrat et al. 2012, Neteler et al. 2013), as IR images are limited to surface temperatures, and suffer from either temporal extent or spatial resolution limitations when using airborne or satellite-borne sensors, respectively (Potter et al. 2013). Moreover, the use of both airborne and satellite-borne sensors is usually biased towards cloudless days, which mathematically leads to biased spatial representations of climatic conditions. The currently available spatial resolution of land surface temperatures (LSTs) (ca. 1 km at the equator) (Wan et al. 2015) does however not provide an absolute increase in spatial resolution compared to the traditionally used free-air temperature gridded datasets like WorldClim or CHELSA (yet see EuroLST at 250-m resolution across Europe: Neteler et al. 2014). LSTs nevertheless give the advantage of a direct measurement for each pixel, instead of an interpolation of weather station data. In addition to the direct measurement of surface temperature, remote sensing can also play an important role in obtaining information on other variables that matter for microclimate, like cloud cover (Wilson and Jetz 2016) and much-needed information on soil moisture (Njoku et al. 2003, Entekhabi et al. 2010).

Inclusion of microclimatic data in SDMs

Current status of microclimate in SDMs

With the recent rapid advances in microclimatic data sources described above, there has been a corresponding steady increase in the application of this data in SDMs (Fig. 1, Table 2), with existing examples often showing significant improvement of model accuracy compared to models using coarse-grained climate data. For example, Ashcroft et al. (2008) showed that local temperature better predicted the distribution of 68% of their 37 studied plant species, and model performance also improved

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significantly using topoclimate for most species living in cold extremes in a study on mountain grasses and ferns (Slavich et al. 2014).

Current applications of microclimate modelling techniques into SDMs include both interpolation of in-situ measurements (e.g. Ashcroft et al. 2008, Ashcroft et al. 2009, Slavich et al. 2014) and statistical downscaling to regional topoclimate (e.g. Randin et al. 2009), with studies across a range of spatiotemporal scales (Fig. 1). However, as microclimate data with a spatial resolution of less than 10 m² have only recently become available through the use of high-resolution LiDAR-techniques (George et al. 2015, Lenoir et al. 2017), fine-scale data has currently not been integrated into SDMs at broad spatial extents (dashed line in Fig. 1a). Up till the recent introduction of LiDAR into SDMs (Lenoir et al. 2017), microclimatic data with the highest spatial resolution for use in SDMs was usually obtained through mechanistic modelling using fine-scaled DEMs at 25 m² (as in Gillingham et al. 2012). Using such techniques in combination with long-term hourly weather station data also allows for the desired combination of a broad temporal scale with a high temporal resolution (Fig. 1b, top left). Such a combination of high temporal accuracy and large temporal extent obtained with downscaling approaches has however not yet been applied in SDMs.

In-situ measurements of temperature and other microhabitat characteristics – without interpolation – have additionally been shown to be valuable for descriptive distribution modelling at the local scale (Opedal et al. 2015, Frey et al. 2016). For example, strong correlations have been observed between changes in the frequency of plant species over time and the in-situ temperature of their preferred microhabitat on mountain summits in Switzerland (Kulonen et al. 2018). Sometimes, topoclimatic variables derived directly from DEMs (like elevation, solar radiation or cold-air pooling) are also used independently in SDMs, thus using an indirect topoclimatic derivative instead of actually downscaled climate to improve the spatial resolution of SDMs (see e.g. Roslin et al. 2009, Maclean et al. 2015, Shinneman et al. 2016, Patsiou et al. 2017).

The use of microclimatic data in SDMs in a changing future climate has been explored less frequently, yet some recent papers have shown that the inclusion of higher temporal and spatial resolution data can improve such predictions, for example by identifying windows of opportunity with both a limited spatial and temporal extent for oak seedlings (Davis et al. 2016). Incorporating microclimatic processes into projections of SDMs under climate change also resulted in lower rates of predicted local extinctions of Swedish alpine species by 2085 (Meineri and Hylander 2017), while it also increased the probability of occurrence of a theoretical species at its warm range edge (Lenoir et al. 2017).

Even though several studies have thus successfully demonstrated the usefulness of accounting for microclimatic processes into SDMs, we identified the need for an integrative approach, maximizing both the spatiotemporal scale and resolution, whilst allowing both descriptive and predictive models at scales relevant to the study species. We propose our framework in the next sections.

Scale: a matter of choosing the right extent and resolution at which key processes operate

First of all, we want to highlight the importance of the scale – both the extent and the resolution – issue when relating climatic data to species distributions. In order to maximally improve the descriptive and predictive power of SDMs, researchers should be aware of the scale at which species experience the

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microclimate (Potter et al. 2013, Hannah et al. 2014, Carroll et al. 2016). Importantly, the scale of microclimate does not necessary imply fine spatiotemporal resolutions; the temporal extents of the data matters as well, as does the spatiotemporal resolution at which the underlying processes operate: the "process resolution". For example, the geographic distribution of tree species will be strongly dependent on long-term patterns of average air temperature, yet also on extremes like minimum winter air temperatures, as the latter affects the vulnerable aboveground tissues (Körner 2003, Williams et al. 2015). Moreover, a tree species could be persisting outside its climatic niche for substantial parts of its life span, e.g. when climate changes throughout its life span (cf. tolerance niche) (Sax et al. 2013) or just due to changing requirements for the growing individual (cf. ontogenetic niche shift) (Werner and Gilliam 1984, Bond and Midgley 2001). Seedlings will react more strongly to seasonal fluctuations in temperatures at the soil surface than later growth stages. Indeed, the environment experienced by germinating seeds, as compared to the one experienced by adult trees, is likely more decoupled from free-air temperatures and more constrained by temperatures near the ground. Yet, the meaningful spatial resolution at which microclimatic processes are operating for a sessile tree seedling is still likely greater than the centimetre scale, as it also depends on the vertical complexity of the vegetation layers from the surrounding individuals that could be located several metres away.

While the necessary spatiotemporal resolution at which microclimatic processes operate is usually finer than the available coarse-grained global and long-term climatic data, this spatiotemporal resolution will thus likely be different for different species, species groups or even different life stages or ontogenetic stages of the same species (e.g. life cycle of a tree or a dragonfly). In general, refining the spatial resolution has been shown to be less important for organisms in spatially homogeneous environments, while fine temporal resolution might matter less in environments where diurnal or seasonal variability is smaller than the environmental tolerance of the studied species (like for plants) (Hannah et al. 2014). For small animals, however, which can buffer their environment by moving, both a fine spatial and temporal resolution could be key. For a temperature-sensitive mammal like the American pika (*Ochotona princeps*), for example, their preferred micro-environment under rocks has been shown to be up to 30°C cooler than ambient temperature maxima (Varner and Dearing 2014), implying that both the availability of habitat at low elevations and the possibility of survival under warming climate conditions is being underestimated in SDMs that do not incorporate these microclimatic effects..

Process resolution also relates to the data quality of the explanatory variables. For example, one could use a limited, or spatially unbalanced, climatic dataset, use too simple extrapolation techniques or ignore important microclimatic process (e.g. cold-air drainage) when applying downscaling procedures (Daly 2006). Even though the resulting spatiotemporal resolution might still be high, the process resolution – and thus true accuracy – of the data would then be lower. It is thus critical to focus not only on the use of high-resolution datasets, yet to also include the relevant spatiotemporal resolution of the underlying climate-forcing factors and ground-truth models with in-situ measurements. In Table 2, we give additional insight in the realized process resolution of the studies depicted in Fig. 1 by listing the used techniques, included drivers, the use of in-situ measurements, and whether climate was extrapolated in space or time.

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Finally, the search for better microclimatic data thus does not necessarily imply a blind run for an increasing refinement in the spatiotemporal resolution of climatic data at the global extent. While thermal physiology is interesting in its own regard, coarse-grained SDMs should maintain their focus on the actual distribution of the species, on a regional, continental or even global scale. Microclimatic precision or resolution is thus only valuable down to the level at which an increased resolution does not affect the actual distribution of a species anymore (Bennie et al. 2014). For example, microclimatic data improved models of moth distribution at the site level, yet not at the regional scale of the full species range in the tropical Andes (Rebaudo et al. 2016). The question of scale thus also relates to the accuracy at which predictions are needed and to situations where mean field approximations are not accurate (Bennie et al. 2014), as is for example the case for microrefugia, holdouts and stepping stones. However, when fine resolution data are available, one can also add the assessment of (both spatial and temporal) heterogeneity within a certain pixel to the commonly used averages and extremes. By doing so, it is possible to capture and assess the impact of local environmental heterogeneity on metapopulation and metacommunity dynamics (Graae et al. 2018). Such a hierarchical approach, including environmental variation obtained at finer resolution into models of a species distribution at a coarser scale promises to bridge the gap between local and global species distribution questions.

A framework to obtain adequate microclimatic data for use in SDMs

How do we best answer to both the need for an increased level of detail and a high flexibility and adaptability to specific case studies? Certainly our goal should not be to fill the entire climatic grid with in-situ temperature sensors, as this is neither desirable nor possible (Potter et al. 2013). On the other hand, however, mechanistically or statistically downscaling macroclimate without relying on microclimate measurements is also limited, as we need a better understanding and validation of the processes underlying microclimate at very fine spatial and temporal resolutions in order to improve the accuracy or process resolution of our models. Combining in-situ microclimate measurements with fine-grained environmental variables derived from remotely sensed images to spatially interpolate microclimate helps solve the spatial issue (Greiser et al. 2018). However, these microclimatic grids are unlikely to reflect the long-term dynamics of climate over time (Lenoir et al. 2017) and instead capture the weather conditions that prevailed during the year the microclimatic data where recorded. To solve this issue, we argue in favour of an improved and unified statistical framework of spatiotemporal interpolations that would combine the use of in-situ microclimate measurements, long-term synoptic measurements from meteorological stations and high-resolution remote sensing images (e.g. airborne LiDAR and hyperspectral images) (Fig. 2). Linking in-situ microclimate measurements at fine temporal resolution with variables derived from remote sensing images at high spatial resolution and with a broad spatial extent will help facilitate spatial interpolation of microclimate (Lenoir et al. 2017, see the left side in Fig. 2). At the same time, linking the high temporal resolution of in-situ microclimate measurements with long-term synoptic measurements from the closest meteorological stations with a broad temporal extent will allow the reconstruction of long-term temporal dynamics of climate change (Wason et al. 2017, see the right side in Fig. 2). The generated grids of microclimate time series at fine spatiotemporal resolution and with a rather broad spatiotemporal extent (e.g. from landscape to regional level) can then be used to generate meaningful predictor variables in SDMs.

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The framework described above highlights the need for accurate in-situ climate measurements, as they provide our best option for assessing microclimate at the level of the studied organism. However, by linking microclimate measurements with remote sensing data at fine spatial resolution, and long-term data from meteorological stations, both the amount of sensors as well as the extent of the measurement period can be limited. This does require a careful sampling design, however, as one should attempt to cover the full range of microclimatic variation available within the study region to avoid the need for extrapolation outside the measured range, and measurements at locations and time intervals relevant to the study organism (Ashcroft and Gollan 2013a). As stated earlier, the selection of candidate predictor variables and the choice of the meaningful spatial resolution for averages, extremes and heterogeneity should also be done carefully and in light of the biology of the studied species. For example, it has been shown that the degree of deviation from perfect coupling between microclimate and the ambient climate depends on the assessed bioclimatic variable, implying that the beneficial effects of microrefugia are limited to species that are restricted by these climatic conditions that are partially decoupled from the regional climate (Hylander et al. 2015, Wason et al. 2017).

To spatially interpolate the microclimate measurements from physiographic, biophysical and anthropogenic variables derived from the above-mentioned remotely-sensed images (e.g. aspect, slope, solar insulation, land cover, disturbance intensity), geostatistical tools (e.g. geographically weighted regressions; Fotheringham et al. 2003) can be used. These tools extend traditional regression techniques by adding variation across space to the estimated regression parameters within the spatiotemporal limits of the available data. The ability to accommodate spatial variation makes geostatistical tools highly relevant for exploring the scale-dependent and spatially variable relationships between measured temperatures and physiographic, biophysical or anthropogenic drivers of temperature (Su et al. 2012). Depending on the scale of the study and the focal organism under study, remote sensing data can be satellite-borne, airborne or even ground-based (e.g. Lenoir et al. 2017). As more and more – mostly satellite-borne – remote sensing data is becoming freely available, the actual costs of our proposed approach can even be limited to those that are related to the maintenance of a carefully designed in-situ sensor network.

To perform temporal extrapolation, an approach as used in George et al. (2015) could be applied. They used temperature logger measurements spread across a forest in Missouri (USA) as the response variable and different combinations of both spatial variables, derived from LiDAR images, and temporal covariates, derived from the closest weather station, as predictors in a mixed-effect model to estimate air temperatures at any time (hourly) of any day between 2012 and 2013, corresponding to the calibration period. Extrapolation before this period is then possible thanks to the long-term records from the weather station. However, extrapolation should be handled with care as one would also need historical information on the likely spatial distribution of the LiDAR-derived variables. In the case of the forest in Missouri, this extrapolation would be possible only if older LiDAR images are available across the study area or by hindcasting tree growth based on a combined use of allometric equations (i.e. a mechanistic approach) and information on past forest management practices. In general, however, hybrid models that combine a mechanistic understanding of the processes underlying microclimate (e.g. dynamic changes in vegetation cover) with a statistical validation based on in-situ measured data provide a promising research

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avenue to accurately predict microclimatic conditions in space and time (Maclean et al. 2017), especially if applied in multi-regional studies.

Once calculated, the microclimate data can be used to calibrate SDMs and predict the distribution of the studied species at the desired scale (spatiotemporal extent and resolution) (Fig. 2). Ideally, one integrates metapopulation and metacommunity dynamics in dynamic SDMs of the focal species to include their potential to actually explore the thermal heterogeneity within the environment (Graae et al. 2018). The broad temporal extent (e.g. several decades) and high temporal resolution (e.g. daily maxima or minima) of the microclimatic data creates unprecedented opportunities here to link available long-term species distribution data to the actual environmental conditions at the moment of the measurement, or to the past environmental conditions occurring several days, weeks, months or years before (cf. legacy or lagging effects). This does, however, require (process-based or empirical) assessments of the relevant temporal window to consider for a certain (group of) focal species. It will also prove valuable to compare the obtained models with “control” or “baseline” models using the traditional coarse-grained climate data to quantify the actual improvement of the SDMs by including microclimate. This can help in the interpretation of the role of microclimate in describing and predicting actual species distributions.

Extrapolating microclimate to the future

The same framework as described in the previous chapter can now be applied to improve our extrapolations of microclimate into the future (Fig. 2, Box). Current practice involves downscaling approaches to obtain future microclimate (Davis et al. 2016). Again, statistical methods can be used, linking current downscaled climate to scenarios of climate change (Lenoir et al. 2017). Yet these approaches starting from a static climate scenario miss many of the dynamics that can be expected from climate change at the smallest scale, like local climatic stability, the process by which local microclimatic conditions are partially decoupled from macroclimatic fluctuations over time (Keppel et al. 2015, Lenoir et al. 2017).

The above-mentioned integration of the high temporal resolution of in-situ microclimate measurements with the long-term measurements from the closest meteorological stations can however be used to reconstruct long-term temporal dynamics by calculating the offset and the thermal coupling between the measurement location (e.g. near-surface soil temperatures) and the atmosphere for use in predictions of the future microclimate (Pepin et al. 2011, Joly and Gillet 2017, Lenoir et al. 2017). Aalto et al. (2018) have recently shown that estimation of the offset and thermal coupling has potential, even for one year of in-situ temperature data, yet they also stress the need for continuous multi-year measurements to improve validity. Nevertheless, with the recent explosive interest in microclimate, dataset quality and spatial and temporal extent of in-situ measurements is growing steadily, indicating that spatiotemporal extrapolation of microclimate will soon become feasible. Integrating these dynamic processes in our predictions of future (micro)climate will greatly increase the accuracy of our predictions of future species distributions under climate change (Wason et al. 2017).

Conclusions

Recent advances in both measuring and modelling techniques have greatly enhanced the resolution of the climatic data available for SDMs. In this review, we suggested that all the necessary techniques and

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resources are now available to obtain a wide range of spatiotemporal microclimatic resolutions, if needed over regional and decadal extents. With the help of statistical models to link in-situ microclimate measurements with remote sensing data at fine spatial resolutions and synoptic measurements from meteorological stations covering several decades, accurate microclimatic data for the past, present and the future can now be obtained to dynamically model species distributions and redistributions at exactly the scale that matters. Developing microclimatic datasets at very fine spatiotemporal resolutions should however not be a goal on its own, yet be embedded in a framework to obtain environmental predictor variables at relevant spatiotemporal resolutions to improve the ecological validity of SDMs, and that similar frameworks can be developed for other relevant predictors, like land use change and habitat availability.

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Figure Legends

Figure 1: Overview of the use of microclimate data in SDMs as a function of their spatial resolution and extent (a, log-scale) and temporal resolution and extent (b, pseudo log-scale). Studies marked in blue used interpolation techniques (with mechanistic modelling approaches in bold), while studies marked in red used topographic downscaling. Infographics in each corner of each graph visualise the theoretical look of the data in question. The dashed line in (a) marks a trade-off, i.e. the lack of studies incorporating microclimate into SDMs with both a high spatial resolution and a broad spatial extent. Literature list obtained through a search of Google Scholar and Web of Science using the search term ‘species distribution modelling microclimate’, and following appropriate citation trails. Studies using in-situ climate measurements without interpolation (i.e. no clear spatial resolution nor extent), as well as studies using topoclimatic proxies (e.g. solar radiation intensity) are excluded.

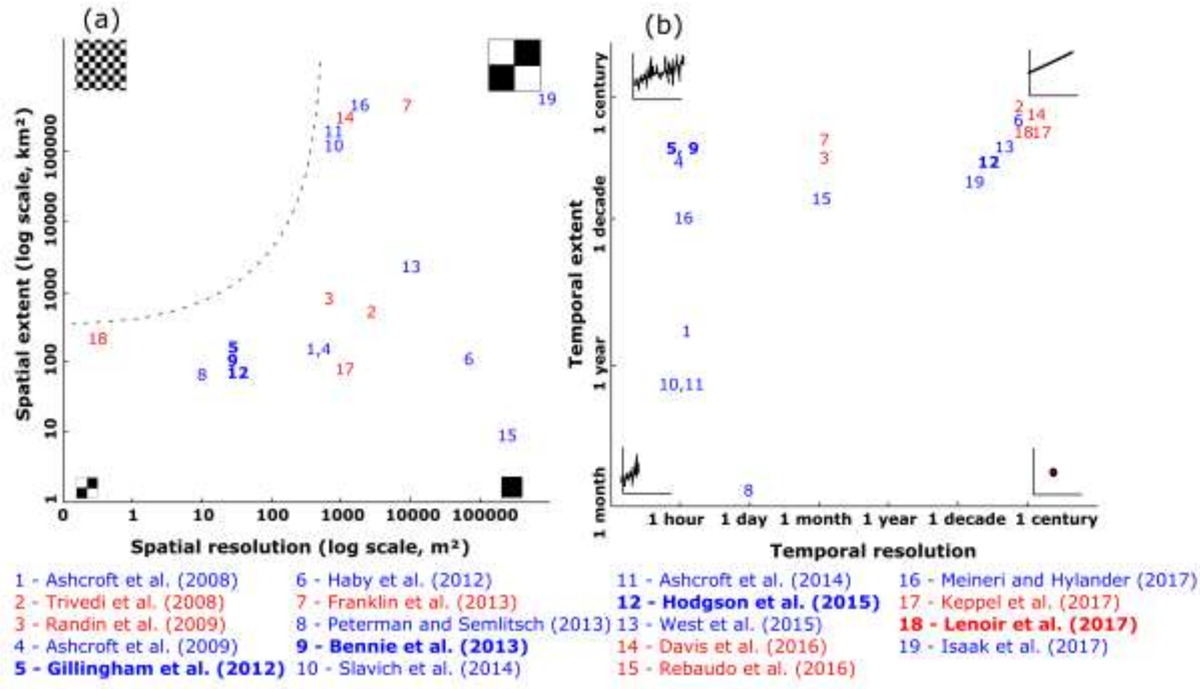

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Figure 2: Schematic overview of the proposed strategy for integrated interpolation, in space and time, of microclimate and its implementation in species distribution modelling. The strength of this unified framework is to combine environmental data at fine spatial resolution thanks to remote sensing approaches with long-term time series from weather stations, and link these data to in-situ microclimatic measurements. For more details, see main text.

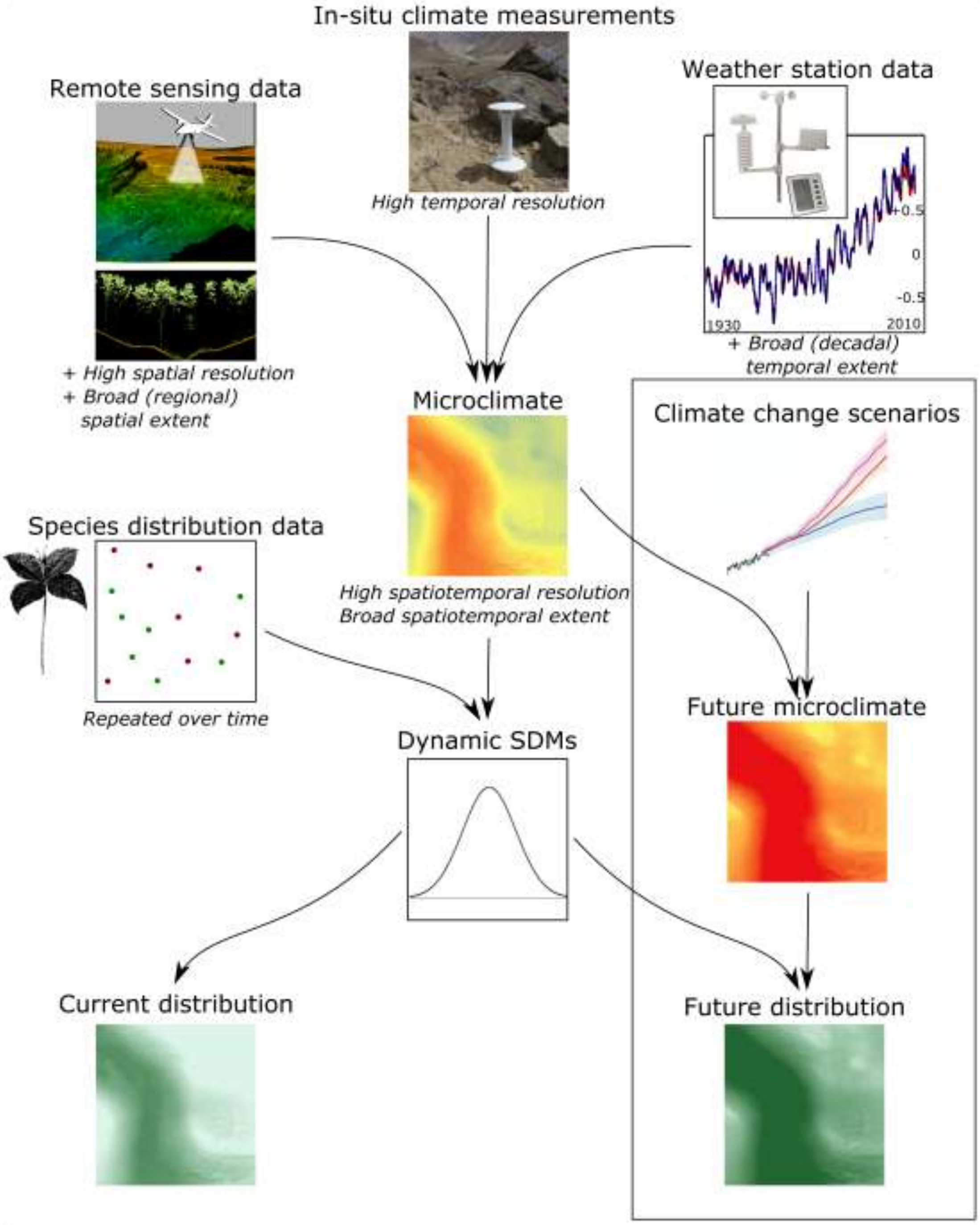

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Table Legends

Table 1: Measurement locations and main advantages (+) and disadvantages (-) of the different sources of microclimatic data for use in SDMs. Spatial and temporal resolution: a more detailed spatiotemporal accuracy provides an advantage. Spatial and temporal extent: data across a larger area and over a longer period provides an advantage.

	Measurement location	Spatial resolution	Temporal resolution	Spatial extent	Temporal extent
In-situ measurements	In-situ	-	+	-	-
Interpolation of in-situ measurements	In-situ	+	+	+	-
Interpolation of weather station data	Free-air	+	+	+	+
Downscaling of macroclimate	Free-air	+	-	+	+
Remote sensed land surface temperature	Surface	+	-	+	-

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Table 2: Specifics of the studies described in Fig. 1, including drivers and techniques, whether microclimate was validated with in-situ data, whether microclimate was extrapolated across space or time, and for which and how many species the data was used in SDMs.

Paper	Used technique (included drivers)	In-situ measurements	Extrapolated relationship in space or time	Modelled species
1 Ashcroft et al. (2008)	Linear regression (elevation, exposure, moisture, radiation)	Yes	Space	37 plant sp.
2 Trivedi et al. (2008)	Linear regression (elevation)	No	Time	20 plant sp.
3 Randin et al. (2009)	Inverse distance weighted interpolations (elevation)	No	Time	78 plant sp.
4 Ashcroft et al. (2009)	Linear regression linking air and soil temperatures	Yes	Time	37 plant sp.
5 Gillingham et al. (2012)	Mechanistic model (wind speed, air temperature, radiation, slope, aspect, topographic shading)	Yes	Space and time	2 insect sp.
6 Haby et al. (2012)	Thin-plate spline models (elevation)	No	Space	4 mammal sp.
7 Franklin et al. (2013)	Gradient-Inverse-Distance-Squared downscaling (elevation)	No	Time	52 plant sp.
8 Peterman and Semlitsch (2013)	Hierarchical mixed-effects model (elevation, exposure, vegetation cover)	Yes	Space	*Plethodon albagula (amphibia)*
9 Bennie et al. (2013)	Mechanistic model (wind speed, air temperature, radiation, slope, aspect, topographic shading)	Yes	Space	*Hesperia comma (insect)*
10 Slavich et al. (2014)	Linear regression (elevation, exposure, relative elevation, canopy cover, distance to coast) Thin-plate spline smoothing (elevation, latitude, longitude)	Yes	Space and time	295 plant sp.
11 Ashcroft et al. (2014)	Topoclimate: linear regression (elevation, exposure, relative elevation, canopy cover, distance to coast) Macroclimate: thin-plate spline smoothing (elevation, latitude, longitude)	Yes	Space	*Petrogale penicillata (mammal)*
12 Hodgson et al. (2015)	Mechanistic model (wind speed, air temperature, radiation, slope, aspect)	Yes	Space and time	*Plebejus argus (insect)*
13 West et al. (2015)	Partial derivative functions of temperature change Elevation	Yes	Time	*Bromus tectorum (plant)*
14 Davis et al. (2016)	Gradient-Inverse-Distance-Squared downscaling (elevation)	No	Time	2 plant sp.
15 Rebaudo et al. (2016)	Linear regression linking air and sub-canopy temperatures	Yes	Time	*Phthorimaea operculella (insect)*
16 Meineri and Hylander (2017)	Linear regression + thin-plate spline geographic interpolation Latitude, elevation, solar radiation, aspect, relative elevation, topographic wetness index, distance to sea/water bodies	Yes	No	78 plant sp.
17 Keppel et al. (2017)	Cubic convolution resampling	No	Space	2 plant sp.
18 Lenoir et al. (2017)	Geographically weighted regression + mechanistic transformation Physiographic: elevation, slope, eastness, northness, distance to the coast, clear-sky insolation time, land cover, relative concavity Biophysical: canopy density	No	Time	1 virtual plant sp.
19 Isaak et al. (2017)	Moving averages	Yes	Space and time	14 fish and amphibian sp.

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