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## Effects of species evenness can be derived from species richness – ecosystem functioning relationships

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## Abstract

Although species richness effects on ecosystem functioning have been studied thoroughly in countless experiments, the effects of the other side of diversity – species evenness – remain less identified, especially at high species richness. Due to the large number of different model ecosystems that need to be created, the explanatory power of the experimental approach for evenness is indeed limited. We show here that experimental studies on the influence of species richness on ecosystem functions contain hidden information on the influence of species evenness. Both the effects of maximum and minimum evenness, and of a key set of intermediate evenness levels, can be derived from species richness – ecosystem function curves, and that for every richness level, by using communities with low species richness as the equivalent of highly uneven communities with higher richness. We show that evenness effects on ecosystem functioning have the same direction as richness effects, however with increasing effect sizes at higher richness levels. We validated our technique for a wide range of ecosystem functions and applied it to the species richness – community biomass data from an existing biodiversity experiment. Our approach could provide a fast and easy alternative to resource-intensive experiments in which evenness is experimentally varied, as we can build on the elaborate existing literature on species richness to assess its effects.

## Introduction

Since Naeem et al. (1994) published the first experiment on the influence of species richness on the productivity of plant communities, dozens of studies have done the same for a variety of ecosystem processes (Balvanera et al. 2005, Cadotte et al. 2008, Hector et al. 1999, Hooper et al. 2005, Tilman et al. 1996, Van Peer et al. 2004, van Ruijven and Berendse 2010). Many of these studies used synthesized communities to create the desired richness levels, often yielding saturating response curves (Chapin et al. 1998, Symstad et al. 1998, Tilman et al. 1996), as theoretically described in Tilman et al. (1997). Much less work has been done however on the effects of species evenness on ecosystem functioning. Species evenness describes how uniform the population sizes of the different species in a community are and, together with species richness, determines a community's species diversity (Smith and Wilson 1996). The first experiments on the influence of species evenness on ecosystem processes are relatively recent (Mattingly et al. 2007, Wilsey and Polley 2002, Wilsey and Potvin 2000) and the debate on the effects of evenness on ecosystem functioning still continues today (Assaf et al. 2011, Rohr et al. 2016, Schmitz et al. 2013), due to differences in methodology and practical limitations of testing species evenness effects at high richness levels in experiments (Naeem 2009). Indeed, because the number of different communities that are required to manipulate species evenness becomes excessive once there are more than just a few species, studies on synthesized communities have only rarely expanded to more than four plant species (Kirwan et al. 2007, Mattingly et al. 2007, Schmitz et al. 2013, Wilsey and Potvin 2000, Wittebolle et al. 2009). As a consequence, the pure effects of evenness on ecosystem functioning, especially at these higher richness levels, remain weakly identified, although theory suggests they can be strong. For example, in more even systems, there is a higher probability that species resistant to a certain stressor are present in large enough numbers to safeguard community resistance (Wittebolle et al. 2009). Species evenness itself can also affect species richness through its interaction with ecosystem processes: in a meta-analysis of fertilization experiments, Hillebrand et al. (2007) showed that increased nutrient availability caused decreases in species richness at low evenness, as it enhanced the success of the dominant competitor. Additionally, natural and anthropogenically induced changes to ecosystems influence species evenness more easily and more rapidly than species richness, with important consequences for these ecosystems well before a species is threatened by extinction (Hillebrand et al. 2008, Wittebolle et al. 2009). These observations justify the persistent interest in experimental manipulations of species evenness in order to identify its role as a driver of ecosystem functioning (Ribas

et al. 2015, Wilsey and Potvin 2000), although the abovementioned methodological difficulties up till now limit conclusive findings (Hillebrand et al. 2008).

### **Theoretical approach**

In this paper we show that experimental studies on the effect of species richness on ecosystem functions contain information on the effect of species evenness on those same functions, providing a fast and easy alternative to the experimental manipulation of evenness levels. As an example, imagine a typical species richness – ecosystem function (SR-EF) curve as described in Tilman et al. (1996) and Tilman et al. (1997) (Fig. 1). The underlying response values at every richness level are in this case the community biomasses of all possible species assemblages at that richness level – or a random subset of those if this requires too many species combinations to construct experimentally (Hector et al. 1999). As a consequence, community biomass can be compared between richness levels without bias from species composition, since all species are equally represented across the richness gradient. The assemblages yielding such curves are typically sown or planted with the same number of individuals per species and are thus fully even (Roscher et al. 2004, Tilman et al. 1996), so that the curve represents the community biomass at maximum evenness for each richness level. In the following we demonstrate that the biomass at the lowest possible evenness can also be found on the graph (see for example Kirwan et al. (2007) and Dooley et al. (2015), who used this principle in experiments).

Assume a community contains 20 species and 1000 individuals; at maximum evenness each species will thus be represented by 50 individuals. Note that evenness in this paper is based on numbers of individuals rather than on biomass or cover, following common practices in diversity experiments (Roscher et al. 2004, Tilman et al. 1996). Minimum evenness at this species richness would arise if one species comprises 981 individuals while the other 19 species would all be represented by only a single individual. A community with such characteristics is virtually a monoculture: the difference would be 19 individuals on 1000, or only 1.9%. Consequently, for the entire species pool of Fig. 1, the resulting community biomass at the lowest possible evenness is well represented by the average of all the monoculture biomasses (since each species should be allowed to be dominant in turn). This average is present in species richness – biomass curves. With the saturating curves that typically emerge for these relationships (cf. example for biomass in Fig. 1), the biomass range between minimum and maximum evenness is greatest for high richness levels, and declines increasingly rapidly towards lower richness levels, as the lower Y-axis value remains the same while the upper Y-axis value is limited by the curve.

Why is the lower Y-axis value, representing minimum evenness, always the same, regardless of the species richness level? This may seem counterintuitive, because at lower species richness the lower Y-axis value should reflect the average biomass of fewer monocultures. Note, however, that the biomass at maximum evenness for a given richness level is derived from all possible species combinations at that richness level. The same should thus be the case for the biomass at minimum evenness at that richness level, which simply corresponds to the mean biomass of all species monocultures. This applies to all levels of  $S$ , hence biomass at minimum evenness always has the same value on the graph (i.e. the biomass at species richness 1).

We will now show that, apart from effects of maximum and minimum evenness, SR-EF curves such as in Fig. 1 also contain information on the effects of a range of intermediate evenness levels. To this end, we calculate the Williams evenness index, one of the most commonly used evenness indices, for a number of different species combinations (Williams 1964):

$$E_{Williams} = E_{1/D} = \frac{1/D}{S}$$

This index is based on Simpson's dominance index, given by:

$$D = \sum_{i=1}^S p_i^2$$

with  $S$  the number of species in the sample and  $p_i$  the probability (relative abundance) of a species in the sample. Assume that, in the pool of 20 species and 1000 individuals referred to above, one species is represented by only one individual and the other 19 species each by about 53 individuals. This case of intermediate evenness ( $E_{Williams} = 0.937$ ) is virtually equivalent to the case of maximum evenness for 19 species, as the difference is only 1 individual on 1000 or 0.1%. The case in question is present in Fig. 1 as a species richness value of 19 and has a biomass value just below the case of maximum evenness for 20 species. The biomass at a species evenness of 0.937 for 20 species is thus virtually equal to the biomass at a species richness of 19. The same reasoning applies for two species out of 20 having one individual each and the other 18 each about 55 individuals ( $E_{Williams} = 0.918$ ), which approximates a species richness value of 18. This evenness value can thus be assigned the biomass corresponding to 18 species on the SR-biomass curve. We can repeat this procedure until the case of minimal evenness discussed before, where 19 out of 20 species each have one individual and the twentieth species has 981 individuals ( $E_{Williams} = 0.052$ ). In other words, in the example above, intermediate evenness values coincide with intermediate biomass, with higher evenness generating higher biomass values. The resulting evenness-biomass curve is

shown as a black line in Fig. 2a. As the curve is based on the species richness-biomass curve in Fig. 1, it consequently contains exactly the same Y-axis values as Fig. 1. Repeating this methodology for all richness levels below the maximum allows us to obtain the effect of species evenness on biomass at every richness level (red to orange lines in Fig. 2a), effectively disentangling what the effects of these two diversity components on biomass would be if they would be jointly varied experimentally. As stated before, the biomass range between minimum and maximum evenness is shown to be greatest for high richness levels, declining increasingly rapidly towards lower richness levels, while the biomass at minimum evenness stays the same over all richness levels (i.e. the average biomass from the monocultures). The effects of SR and SE thus point in the same (positive) direction, and have additive effects on EF when varied together.

The question remains how representative the intermediate biomass values are for other combinations of species relative abundances with the same evenness values. Clearly, not all combinations can be derived from the species richness curve because of the virtually infinite amount of species and abundance combinations at each evenness value. However, in light of this, it is noteworthy that the biomass at a given level of species richness is calculated from all community compositions at that richness level (or a random selection of them). For example, in the first case above, the biomass value at species richness 19 as shown in Fig. 1 represents the experimentally obtained average for all community compositions with 19 species drawn from a total pool of 20 (each with the same abundance of about 53 individuals). Plotting this average biomass on an evenness graph at  $E_{\text{Williams}} = 0.937$ , therefore also represents a variety of cases for this evenness value, rather than just one case, respecting the principle that all species should be made co-dominant in turn. While we cannot exclude that other combinations of species relative abundances at this evenness value will not cancel out and induce some drift from this biomass average, the wide range of evenness cases that can be derived from entire SR-EF curves suggests that resulting species evenness – ecosystem function (SE-EF) curves are good estimates, and experimental data supports that rationale (see later).

Even though SR-EF curves can thus be converted into SE-EF curves, it is important to realize that the resulting relationships might depend on the evenness index used. As there is a myriad of evenness indices (Smith and Wilson 1996), the ensuing relationship with biomass will also vary, an issue also present in experimental assessments of species evenness effects (Weiher and Keddy 1999). As an example, we use

two other traditional evenness indices as described in Smith and Wilson (1996), both based on Shannon-Wiener's  $H'$  diversity index instead of Simpson's dominance:

$$H' = - \sum_{i=1}^S p_i \ln(p_i)$$

where  $S$  again serves as the number of species in the sample and  $p_i$  as the probability of species  $i$  in the sample.

The evenness indices are calculated as follows (Heip 1974, Pielou 1969):

$$E_{Pielou} = J' = \frac{H'}{\ln(S)}$$

$$E_{Heip} = \frac{e^{H'} - 1}{S - 1}$$

The resulting curves are shown in Fig. 2b and c. Whereas the Williams and Heip index both yield the same nonlinear positive pattern as observed in the SR-biomass relationship, at least at high species richness, patterns for the Pielou evenness index turn out quasi-linear, driven by the use of the logarithm of  $S$  (Fig. 2b). Yet all three indices meet the requirements stated earlier: the effects of minimum, maximum and several intermediate evenness levels can be defined based on the richness curve. The obtained SE-biomass curves are in all cases also monotonously positive. Earlier work from Smith and Wilson (1996) has shown that all possible evenness indices are maximal when the species abundances are equal, minimal when species abundances are as unequal as possible, and increase monotonously with increasing equality of species abundances, hence our approach will in this case lead to similar monotonously positive curves for all these possible indices. This confirms previous experimental (Schmitz et al. 2013, Wilsey and Potvin 2000, Zhang et al. 2012) and modelling (Nijs and Roy 2000) studies pointing at uniformly positive effects of evenness on productivity. Notice here that, for every evenness index in Fig. 2, the biomass values (on the y-axis) are exactly the same, because they are derived from the same species richness curve in Fig. 1, yet they are associated with slightly different x-axis values owing to differences in how each evenness index is calculated. For the same reason, SR-EF relationships for ecosystem functions with other shapes than the example on biomass in Fig. 1 will lead to corresponding SE-EF curves that also broadly follow these other shapes. These conclusions comply with earlier work suggesting that species evenness affects ecosystem functioning in much the same way as richness does (Naeem 2009, Wittebolle et al. 2009).

We emphasize here that due to the focus on initial species richness and evenness, our procedure is not influenced by changes in species composition throughout SR-EF experiments. This becomes apparent if



we return to the core of our approach, i.e. that adding one or a few individuals to a set of 1000 would have virtually no effect on ecosystem functioning. Changes that occur within the community of 1000 individuals throughout an original SR-EF experiment, i.e. in the studied ecosystem functions, yet also in species richness, evenness, or even density, can thus be assigned also to the theoretical community with that one or a few additional individuals, given that the latter cannot have a discernable influence. This allows converting the initial richness gradient in an initial evenness gradient even if the community composition changes significantly throughout the experiment. This does however imply that our approach has the same limitations as existing SR- and SE-EF experiments: all experiments looking at the effects of initial richness or initial evenness have to deal with this ‘noise’ created by changes in species composition throughout the experiment while searching for the role of pure diversity effects (unconfounded by species identity) underneath that noise. We do not solve that limitation here, and care should thus still be taken when applying our technique that all species from the species pool are randomised at each richness level and that the ecosystem response is measured before too many changes in species composition have taken place.

Note however that this does not justify the use of realized species evenness or richness (i.e. measures of species composition after the experiment) to construct an SE-EF curve as we are presenting here. One could for example construct such a curve from species-specific biomass values, as often obtained after species richness experiments (e.g. Weigelt et al. 2010). Such realized species evenness levels obtained after an experiment depend on the interaction between the initial diversity and the identity of the present (and dominant) species. Even though realized evenness values often cover a large range, not all species will be equally represented at each evenness level (for example, at low realized evenness levels, only a selection of the most competitive species will be dominant). Constructing an SE-EF curve from realized evenness would thus violate the requirement – as stressed in our procedure above – to have equal representation of all species, and would thus compound effects of evenness with those of species identity. Alternatively, one could consider using SR-EF curves constructed from experimental or natural communities with non-random species loss, i.e. where species have disappeared due to an external driver. The resulting SR-EF curves would however again compound effects of species richness, species evenness and species identity (Leps 2004, Rohr et al. 2016, Schlapfer et al. 2005). Imagine a species-rich community with equal abundances of all species. Exposed to a driver of diversity decline, the community will lose species until a depauperate version of the original community is left with only a few species, or

ultimately even a monoculture of the one species that resists best to the driver in question. In other words, during the degradation process, both species richness and species evenness drop in concert (even though the associated change in EF is typically expressed as a function of richness only). As a result, there are no pure species richness effects from which corresponding species evenness effects can be derived. We thus stress again that our approach is based on sown species richness experiments only.

### Validation

How can we now verify our theory? This requires experiments that vary both richness and evenness (the latter within each richness level). In the following, we apply our technique to the available set of experiments that have assessed a variety of ecosystem properties, processes and indices along both gradients (Dimitrakopoulos 2010, Maestre et al. 2012, Wang et al. 2015, Wilsey and Polley 2004). In Fig. 3, we summarize all ecosystem function responses from these four studies against species evenness (all studies used  $E_{\text{Williams}}$ ). For every panel, we first plotted the observed response against the sown (i.e. experimentally constructed) evenness gradient, using the highest level of species richness in the experiment as an example (red dots in Fig. 3, species richness  $S$  in the bottom right of each graph). Notice that the data in Fig. 3a-f are plotted as averages with error bars, while Fig. 3g-l contain raw data, following availability from these papers. Next, we converted the richness values from the species richness gradient into evenness values according to our methodology. The community biomass at maximum calculated evenness is here thus simply the observed biomass at that richness level, while the value at minimum calculated evenness corresponds to the average community biomass at  $S=1$ . For each intermediate richness level lower than the maximum, by definition characterized by an even distribution of the present species, we theoretically ‘added’ one individual from each missing species to the species pool, until the maximum richness was reached again, and calculated the corresponding evenness. The resulting calculated evenness gradient based on richness, and the associated responses (Fig. 3, black dots), are plotted on the same graph as the sown evenness values (Fig. 3, red dots) and their associated responses.

Now according to our theory, the red and black dots (i.e. the responses to the sown and calculated evenness) should follow approximately the same trend. We can test this assumption for the six datasets with large enough sample size (Fig. 3g-l), by comparing the confidence intervals of linear models containing  $\log(\text{evenness})$  for sown and calculated evenness separately (Supplementary material Table 1). Even though the effect of species evenness on ecosystem functioning itself was not always significant, the

consistent overlap in confidence intervals (see also Supplementary material Table 1) indicates there is no reason to assume the effects of sown and calculated evenness on EF follow a different pattern. Repeating this exercise at lower levels of species richness yielded comparable similarities between the two datasets (not shown). Notice that the response at the highest species evenness (1) has in every case exactly the same value as the response at maximum species richness (Fig. 3), because a fully even system was used to obtain the latter. While these studies thus provide experimental support for our approach, future experiments in which evenness is varied at very high richness could bring additional validation of our technique at such high richness levels.

### Application

We now apply our theoretical approach to a community biomass dataset from a large biodiversity experiment in Jena, Germany, between 2002 and 2008 (Weigelt et al. 2010), visualized in Fig. 4a. Note that we provide an R-script to allow application of the technique to one's own data (Supplementary material). In the Jena-experiment, 82 grassland plots of  $20 \times 20$  m were established, covering a gradient of plant species richness (1, 2, 4, 8, 16, and 60 species) extracted from a pool of 60 species. Every May and August between 2002 and 2008, biomass was harvested from 3–4 subplots of  $0.2 \times 0.5$  m per experimental plot. The authors reported a linear positive relationship between community biomass and the logarithm (with base 2) of initial species richness across the years (see Fig. 4a, fitted with a linear mixed model (black line) with year as a random effect) (Marquard et al. 2009).

This original SR-biomass relationship can now be converted to SE-biomass curves at different levels of species richness (Fig. 4b-d), following our procedure. We used  $E_{\text{Pielou}}$ , as the linearity of the resulting curves facilitates comparisons (see Fig. 2). The community biomass at maximum evenness ( $E_{\text{Pielou}}=1$ ) at each displayed richness level (60 in Fig. 4b, 8 in Fig. 4c and 2 in Fig. 4d) is simply the observed fitted biomass at that richness level, while the value at minimum evenness corresponds to the fitted community biomass at  $S=1$ . To convert the intermediate richness values to evenness, we again theoretically 'added' one individual from each missing species to the originally sown set of individuals, until the maximum richness was reached again; and calculated the corresponding evenness at which the biomass associated with that intermediate richness level should be plotted (Fig. 4b-d).

The resulting SE-biomass relationships confirm the consistent positive effects of evenness on productivity that we showed earlier (see also Schmitz et al. 2013, Wilsey and Potvin 2000, Zhang et al. 2012). Yet we also want to highlight again the clear differences in the slopes of the SE-biomass curves between different

richness levels. Fig. 4b-d reveals indeed that species evenness has larger effects on biomass production when species richness is higher, resulting from the higher realized community biomass at this higher richness. This observation complies with earlier models (Nijs and Roy 2000) and experiments (Schmitz et al. 2013). It also has important real-world consequences: a given reduction in species evenness will have a higher impact on ecosystem functioning in communities with higher species richness, in contrast with the reduced effect of changes in species richness itself at these high richness levels.

We end by using the dataset from Weigelt et al. (2010) as a visualization that relationships between realized species evenness levels based on species-specific biomass and community biomass result in totally different patterns due to the interaction with species identity, as mentioned earlier (Supplementary Material Fig. 1, in contrast to Fig. 4). Such an approach using realized evenness levels illustrates the role of species interactions and shifts in dominance in depauperate communities on ecosystem functioning. It cannot be replaced by our approach, nor replace it, and should not be confused with what we propose here.

### **Conclusion**

In conclusion, our study implies that all published relationships between initial species richness and ecosystem functions contain information on the influences of initial species evenness on those same ecosystem functions, for all assessed richness levels. We have shown how these effects of evenness always have the same direction as those of richness, and how the effect size of evenness increases towards higher richness levels. The latter implies stronger effects of evenness loss in species rich communities. We also demonstrated that these principles apply not only to biomass production (Cadotte et al. 2008, Hector et al. 1999, Marquard et al. 2009), yet also to many other ecosystem processes, like litter decomposition (Dimitrakopoulos 2010), as well as to ecosystem properties such as resistance and resilience (Carvalho et al. 2013, Hector et al. 2001, Naeem et al. 2000). Our approach can thus serve as a fast and easy alternative to further resource-intensive experiments in which evenness is experimentally varied in order to assess its effects on all these ecosystem functions, as these can be deduced from the existing data on species richness effects alone.

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### **Statement of authorship**

JJL and IN developed the concept and wrote the paper, with substantial contribution from HJDB, JL and AM.

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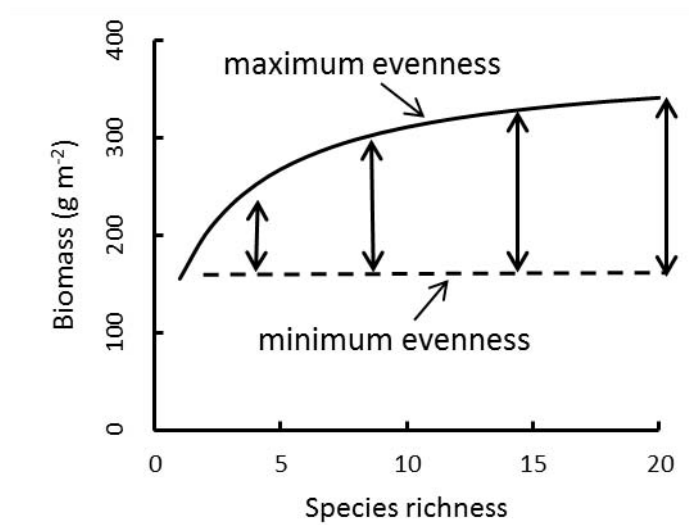
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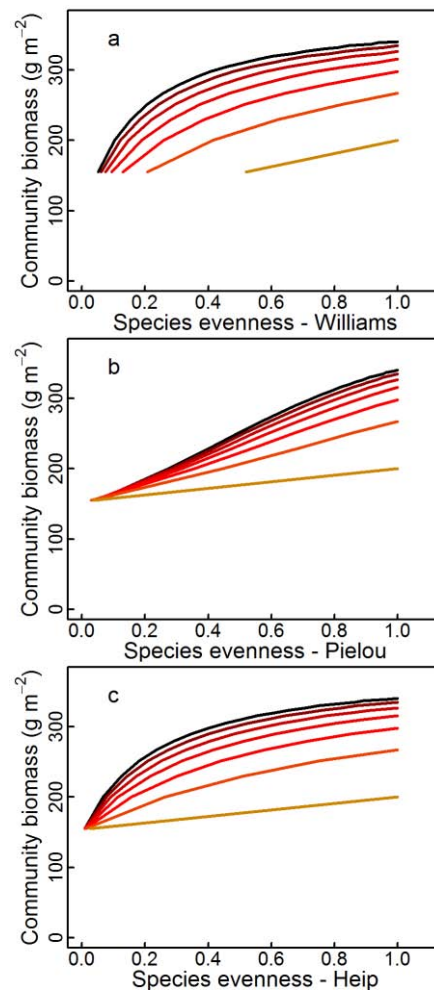


**FIGURE LEGENDS**

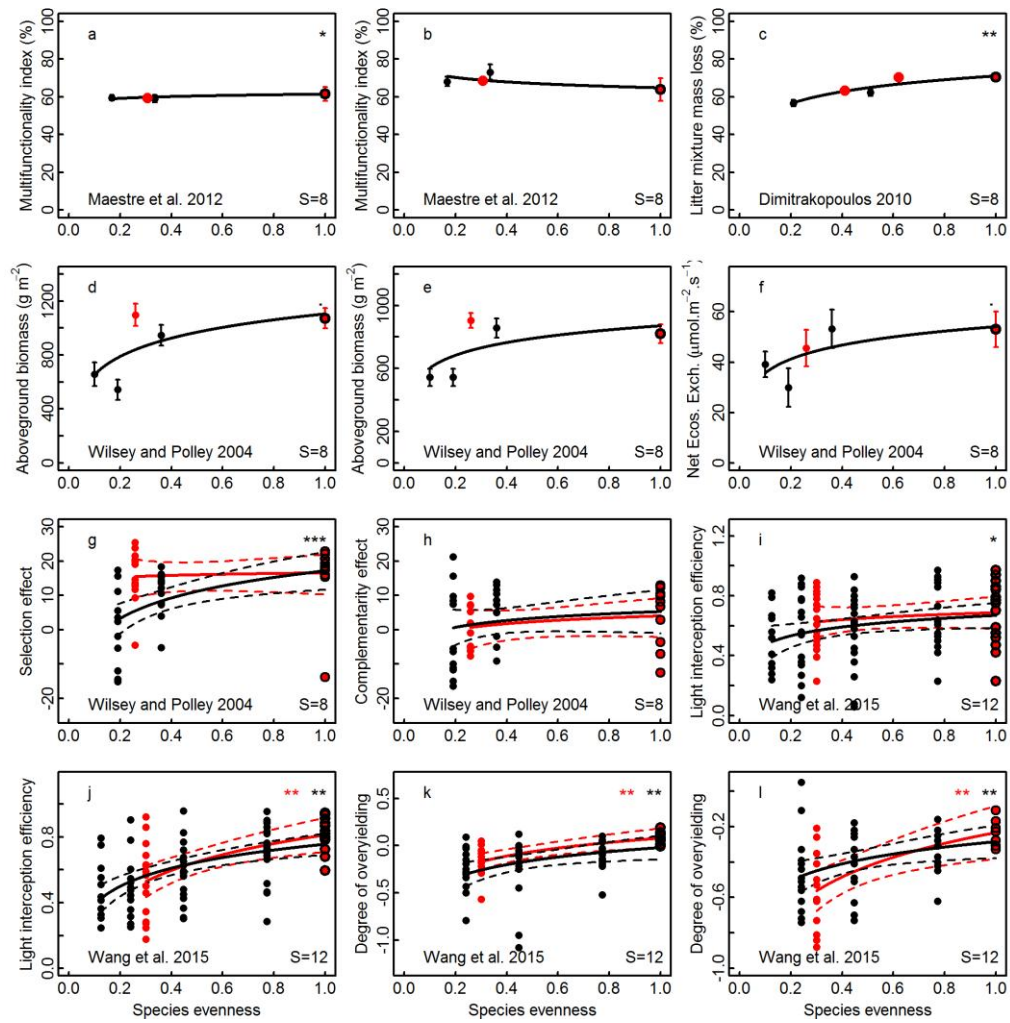
**Figure 1:** Theoretical species richness – community biomass curve and its relationship with maximum and minimum species evenness. The full line shows the community biomass in experiments where all species are equally represented, which corresponds to the biomass at maximum evenness for each richness level. The dashed line indicates the biomass at minimum evenness, i.e. the average biomass of all species monocultures. The double arrows indicate the range between the biomass at maximum and minimum evenness for different richness levels. Biomass values are fictitious.



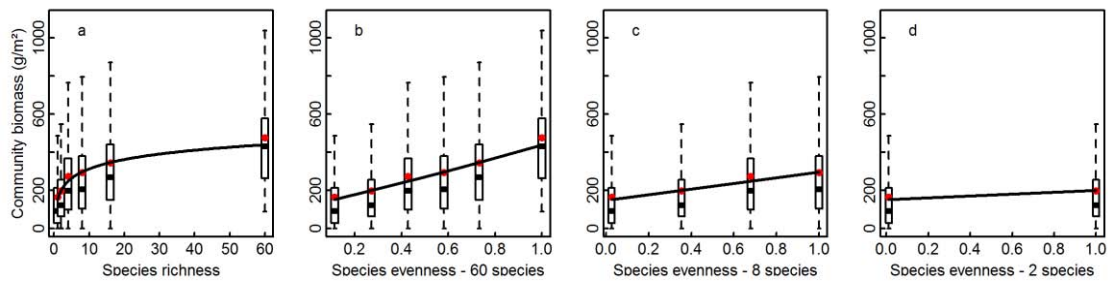
**Figure 2:** Species evenness – community biomass curves at different richness levels (ranging from 2 (orange line) till 20 species (black line) with steps of 3) for 3 different evenness indices, based on the species richness – community biomass curve in Fig. 1.



**Figure 3:** Ecosystem function responses against species evenness ( $E_{\text{Williams}}$ ) from 4 experiments that experimentally manipulated both species richness and evenness. Each response is plotted against the sown (i.e. experimentally created) evenness gradient (red) at a species richness  $S$  (bottom right) and against derived evenness values calculated from the experimentally created species richness gradient (black). For details on calculations, see main text. a and b: multifunctionality index for carbon and nitrogen cycling in the soil at a depth of 0-2 cm (a) and 2-5cm (b) from Maestre et al. (2012), c: decomposition rate (%) in litter bags from Dimitrakopoulos (2010), d and e: peak aboveground biomass ( $\text{g m}^{-2}$ ) from experimental grassland plots in 2001 (d) and 2002 (e) from Wilsey and Polley (2004), f: net ecosystem  $\text{CO}_2$  exchange from the same experimental grassland plots from Wilsey and Polley (2004), data combined over 2001 and 2002, g and h: selection (g) and complementarity (h) effect of aboveground biomass from the same experimental grassland plots from Wilsey and Polley (2004), data combined over 2001 and 2002, i and j: light interception efficiency of experimental plots in 2012 (g) and 2013 (h) from Wang et al. (2015), k and l: degree of overyielding of the light interception efficiency of the same experimental plots in 2012 (i) and 2013 (j) from Wang et al. (2015). Saturating response curves ( $y=\log(x)$ ) were fitted through the combined data for (a-f) and sown (red) and calculated (black) evenness values separately for (g-l) (see Supplementary material Table 1). Confidence intervals from the models overlapped in all cases (g-l), suggesting no significant difference between two types of data could be observed. Significance of the slopes of the evenness effect marked in the top right corner:  $P < 0.001 = ***$ ,  $0.001 < P < 0.01 = **$ ,  $0.01 < P < 0.05 = *$  and  $0.05 < P < 0.1 = .$  For experimental methodology, see the original papers.



**Figure 4:** Community biomass as a function of species richness (a) and evenness (b-d) for data from the Jena-experiment (Weigelt et al. 2010). The saturating response curve  $y=\log(x)$  was calculated based on the original species richness data (a). Species evenness ( $E_{\text{Pielou}}$ ) was then calculated from the species richness gradient at different richness levels (b = 60 species, c = 8 species, d = 2 species), following our theoretical approach (see text), and the community biomass associated with each richness level along the species richness gradient was plotted at the newly calculated evenness level (b-d). Original data shown as boxplots (without outliers), with the average at each level (red dot). For experimental methodology, see Weigelt et al. (2010).



**TABLE LEGEND**

**Table 1:** corrected Akaike information criterion (AICc) for models of ecosystem functioning against the natural logarithm of species evenness for the 12 experimental correlations shown in Fig. 3. The first models (M1) contain only species evenness, the second (M2) contain both species evenness and data origin (true or calculated evenness, see Fig. 3). Due to low sample sizes, the AICc could not be calculated for 2 models (marked as NA). Bold:  $\Delta$ AICc lower than -2, model 1 supported; italics:  $\Delta$ AICc higher than 2, model 2 supported.

Ecosystem function	Reference	AICc M1	AICc M2	$\Delta$ AICc
Multifunctionality index (a)	Maestre et al. 2012	37.385	NA	NA
Multifunctionality index (b)	Maestre et al. 2012	53.166	NA	NA
Litter mixture mass loss (c)	Dimitrakopoulos 2010	42.984	69.891	-26.907
Aboveground biomass (d)	Wilsey and Polley 2004	94.732	122.274	-27.542
Aboveground biomass (e)	Wilsey and Polley 2004	91.565	120.048	-28.483
Net ecosystem exchange (f)	Wilsey and Polley 2004	55.761	85.713	-29.952
Selection effect (g)	Wilsey and Polley 2004	497.338	494.606	2.732
Complementarity effect (h)	Wilsey and Polley 2004	390.557	392.762	-2.205
Light interception efficiency (i)	Wang et al. 2015	-13.729	-12.291	-1.438
Light interception efficiency (j)	Wang et al. 2015	-56.481	-54.315	-2.166
Degree of overyielding (k)	Wanget al. 2015	-3.258	-3.338	0.080
Degree of overyielding (l)	Wang et al. 2015	-30.720	-29.537	-1.183