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The importance of biodiversity and dominance for multiple ecosystem functions in a human-modified tropical landscape

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Abstract

Many studies suggest that biodiversity may be particularly important for ecosystem *multifunctionality*, because different species with different traits can contribute to different functions. Support, however, comes mostly from experimental studies conducted at small spatial scales in low-diversity systems. Here, we test whether different species contribute to different ecosystem functions that are important for carbon cycling in a high-diversity human-modified tropical forest landscape in Southern Mexico. We quantified aboveground standing biomass, primary productivity, litter production, and wood decomposition at the landscape level, and evaluated the extent to which tree species contribute to these ecosystem functions.

We used simulations to tease apart the effects of species richness, species dominance and species functional traits on ecosystem functions. We found that dominance was more important than species traits in determining a species' contribution to ecosystem functions. As a consequence of the high dominance in human-modified landscapes, the same small subset of species mattered across different functions.

In human-modified landscapes in the tropics, biodiversity may play a limited role for ecosystem multifunctionality due to the potentially large effect of species dominance on biogeochemical functions. However, given the spatial and temporal turnover in species dominance, biodiversity may be critically important for the maintenance and resilience of ecosystem functions.

Keywords:

dominance, functional traits, multifunctionality, secondary forest, species richness, tropical forest

Introduction

The world's biodiversity is rapidly declining due to deforestation and habitat fragmentation, with potentially large consequences for the functioning of ecosystems (Bunker et al. 2005, Cardinale et al. 2012, Maestre et al. 2012b). Ecosystem functions can be defined as the stocks and the fluxes of matter and energy over time and space driven by biological activity (Hooper et al. 2005) and biodiversity ('the variety of life') is accepted as one of their major drivers (Balvanera et al. 2006, Midgley 2012). The underlying mechanisms by which diversity drives ecosystem functions remain highly debated (Cardinale et al. 2012). While the niche complementarity hypothesis (high diversity communities make more optimal use of resources and are thus more productive) has received some empirical support (e.g. Cardinale 2011), species still differ in their contribution to ecosystem functioning, as predicted by the sampling effect (Huston 1997). One way of visualizing this is by plotting the cumulative ecosystem function against the cumulative species number, while ranking species in decreasing order of the contribution to the function. This relationship may vary from linear (all species contribute equally) to highly saturating (few species contribute a lot and many species contribute little). Empirical evidence shows that a small subset of species contributes to most of a particular ecosystem function (Balvanera et al. 2005, Bunker et al. 2005, Winfree et al. 2015). This small subset of species often has particular functional trait values to optimally perform those functions (Mouillot et al. 2011): N_2 fixing tree species have, for example, up to nine times faster carbon sequestration rates than non-fixing species (Batterman et al. 2013).

An asymptotic relationship between cumulative species number and ecosystem function suggests that the presence or abundance of species with certain functional traits, rather than high levels of biodiversity, is needed for optimal functioning, as predicted by the mass-ratio hypothesis (Grime 1998). Studies have shown that species differ in multivariate functional trait

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strategies (e.g. Lohbeck et al. 2012), and that distinct trait values optimize different ecosystem functions (Mouillot et al. 2011). Accordingly, it has been proposed that the consideration of multiple ecosystem functions will increase the importance of biodiversity (Hector and Bagchi 2007, Gamfeldt et al. 2008, Zavaleta et al. 2010). Studies on biodiversity and ecosystem *multifunctionality* have been mostly carried out in experimental grasslands and show that species richness promotes ecosystem multifunctionality, often in a linear manner (Hector and Bagchi 2007, Zavaleta et al. 2010, Isbell et al. 2011, Mouillot et al. 2011, Lefcheck et al. 2015). Limited evidence from observational studies shows that such a relationship may not always apply: in drylands only a weak increase in ecosystem multifunctionality was found with species richness (Maestre et al. 2012b), whereas in boreal and temperate production forests a hump-shaped relationship was found (Gamfeldt et al. 2013). In natural ecosystems this relation is more complex because communities do not only differ in species richness, but also in species dominance and composition (Maestre et al. 2012a). Dominant species (in terms of size and/or abundance) contribute disproportionately to ecosystem functions (Smith and Knapp 2003, Dangles and Malmqvist 2004, Winfree et al. 2015). Dominance is typical for natural ecosystems; even in the hyperdiverse Amazon forest only 1.4% of the 16,000 tree species accounts for half of all trees (ter Steege et al. 2013).

Dominance indirectly alters the relationship between species richness and a single cumulative ecosystem function (Hillebrand et al. 2008), from being linear (with low dominance) to being asymptotic (with high dominance), as demonstrated for productivity and decomposition (Dangles and Malmqvist 2004, Kirwan et al. 2007). Similarly, dominance is expected to reduce the effect of biodiversity on ecosystem *multifunctionality*, based on the prediction that the effect of species dominance overrides the effect of species functional traits in determining species' functionality. If that is true, then the same dominant species drive different ecosystem functions

and the effect of species richness on ecosystem multifunctionality is limited (saturating relationship). If instead the effect of species functional traits overrides the effect of species dominance, then different species (with different traits) drive different ecosystem functions and the effect of species richness on ecosystem multifunctionality is strong (linear relationship).

We evaluated the role of species richness, species dominance, and species functional traits for four key ecosystem functions and for multifunctionality in secondary forest that established after crop field abandonment. Most of the world's tropical forests are secondary forests and their importance will continue to increase (Chazdon 2014). It is therefore vital to understand the mechanisms that drive the magnitude and quality of secondary forests' ecosystem functions in human-modified landscapes. We focused on four key ecosystem functions that matter for biogeochemical fluxes and carbon cycling in forests: aboveground standing biomass, primary productivity, litter productivity, and wood decomposition. We asked whether species richness matters for ecosystem multifunctionality and assess the role of species dominance and functional traits in this relationship. Three hypotheses were tested: 1) Few species contribute to most of each ecosystem function, 2) largely the same species account for most of the different functions, 3) a decrease in species dominance will allow different species with different traits to contribute to different functions and, as a consequence, will increase the importance of species richness to ecosystem multifunctionality.

Methods

Research location

We studied tropical secondary forests in Marqués de Comillas, Southern Mexico (16°01'N, 90°55'W). Mean annual temperature is 24 °C and mean annual precipitation is 3000 mm, with a dry period (< 100 mm month⁻¹) from February through April (van Breugel et al. 2006). Small

hills and valleys with sandy and clay soils of low pH (< 5.5) characterize the research area.

Fifteen secondary forest plots (1000 m²) with different fallow ages (< 1-29 yr) were established on abandoned maize fields surrounding the village of Loma Bonita. Each plot consists of two 10 x 50 m subplots; in one all stems with DBH ≥ 1 cm were identified to species level and their DBH recorded, in the other all stems DBH ≥ 5 cm. To enable comparison across size-classes, stems 1 ≤ DBH ≤ 5 cm were duplicated in the analyses.

The area occupied by secondary forests of different ages was quantified by selecting eleven landscapes (1km²) in Marqués de Comillas (933 km²) representing a gradient of forest cover (Pingarroni 2014). In each landscape 30 circular plots (15 m radius) were randomly allocated and land-uses were recorded. When classified as secondary forest, fallow ages were determined based on landowner information. The study landscape composition was approximated by weighting the 15 secondary forest plots according to the representation of their age category in the landscape, where 2 - 4 secondary forest plots together represented each age category (Appendix S1: Table S1). In this study we refer to 'landscape', as the secondary forests scaled to their percent cover in the study region, and to the collective contribution of the 81 focal species in the landscape (for which a range of functional traits were measured locally; for methods see Lohbeck et al. 2012). These species form a representative subsample of all species in the landscape in terms of the biomass they represent (86% of total biomass) and in terms of their range of dominances (Appendix S1: Table S2).

Four key ecosystem functions were assessed that represent major biogeochemical fluxes taking place in forests: *Above-ground biomass* (Mg/ha) was calculated using a generic allometric formula based on the diameter at breast height (DBH), species-specific wood density (mostly local measurements, see Lohbeck et al. 2012) of the stems and the site-specific 'environmental

stress factor' (Chave et al. 2014). *Primary productivity* (Mg/ha/yr) was the net change in standing aboveground biomass over a one-year interval (late 2011/ early 2012 to late 2012/ early 2013).

Litter productivity (Mg/ha/ 2 months) at the plot level was measured by placing seven littertraps (70 x 100cm, at a height of 1.3m) during two months (January-March 2012) at random locations in each site. Each month the litter was collected, dried and weighted. Litter production was measured during the dry season, which is the peak of litter production and may not represent annual litter production, but for species' relative contributions this is unimportant. Plot-level litter production was tightly correlated to the plot biomass ($R^2 = 0.71$, $p < 0.001$, $n = 15$). To estimate the litter produced by each tree, we multiplied the relative biomass of each stem by the plot-level litter production. Doing so, the species-specific litter production was inferred from the plot-level data, assuming that species-litter effects would be reflected in the plot-level litter production.

Wood decomposition (Mg/ha/yr) at the species level was measured for 15 species using a decomposition experiment (litterbag method, 1mm mesh size, 5 replicates per species). Wood samples (15 cm long, diameter 3-5 cm) were incubated in a common garden for 1 year after which the remaining mass was measured. The dry weight before incubation was estimated based on the initial weight and the water content of a representative subsample of the wood. The species-specific proportion of mass lost after one year of incubation was a function of wood density (g cm^{-3} ; % mass loss in one year = $77.4 - 74.2 \times \text{WD}$; $R^2 = 0.51$, $p = 0.003$). The regression equation and species-specific wood density were then used to estimate the wood decomposition rates for the remainder of the species. Subsequently the wood decomposed in the landscape in one year and each species' contribution to that was estimated by multiplying the species-specific wood decomposition rate (proportion of weight loss in a year) by the species-specific mortality (biomass available for decomposition; Mg/ha/yr), derived from the same 2012-2013 time-window. These four ecosystem functions are largely independent at the plot-level;

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only one of the six pairwise correlations between them is significant (Appendix S1: Table S3).

Functions were quantified at the landscape level and for each of the focal species to evaluate species' contributions to the landscape level functions.

Statistical analyses

The cumulative value of each ecosystem function in the landscape was plotted against cumulative species number, with species ranked in decreasing order of impact (positive or negative) on the function. The saturation of this relationship was quantified based on the area under the curve divided by the square area (maximum cumulative ecosystem function value \times 81 focal species), resulting in a metric ranging from 0.5 (linear relationship; all species contribute equally), to 1 (one species contributes the full magnitude of the ecosystem function). We predicted a saturating relationship for each of the 4 ecosystem functions (hypothesis 1). Subsequently, we assessed the overlap in species that comprise at least 50% of the function among the different functions. We predicted that largely the same species contribute to most of the different functions (hypothesis 2). We also tested the concordance in the rank of species contributions across the four functions using Kendall's concordance analysis.

Two complementary simulations were carried out to disentangle the effect of species dominance from the effects of species functional traits on landscape-level functions. To assess the effect of species dominance, we performed a randomization in which all species received a species trait that was randomly picked, without replacement, from the pool of 81 species (randomization R1). This randomized the species traits while conserving the observed species dominances in the landscape, and was repeated 1000 times. To assess the effect of species traits, a second randomization (R2) was carried out in which all individual trees in the dataset received a species trait that was randomly picked from the pool of 81 species, with replacement, and was repeated 1000 times. R2, contrary to R1, breaks the observed dominance distribution in the

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landscape, thereby giving species approximately equal abundances. For each simulation species were ranked in decreasing order of species' contribution to the ecosystem function, and the cumulative ecosystem function was plotted against cumulative species richness, after which the area under the curve was calculated. We expected that R1 would exhibit higher saturation, indicated by larger area under the curve, and R2 would approach linearity, indicated by a smaller area under the curve (hypothesis 3).

We focus on species' contributions to single functions to address the turnover in species importance across functions. This allows us to test the main assumption of the biodiversity-multifunctionality relationship (different species support different functions), and to indirectly assess multifunctionality. In addition, we directly assessed mean multifunctionality by averaging the relative contributions of species to each function (Mouillot et al. 2011). Mean multifunctionality was calculated over three of the four functions, we left out biomass as it was strongly correlated to litter production (Appendix S1: Table S3). Similar to the single functions, mean multifunctionality was plotted against the cumulative species number in which species are ranked in decreasing order of impact on mean multifunctionality. All statistical analyses were carried out using R v. 3.2.4 (R Core Team 2014).

Results

Cumulative ecosystem function showed a strong asymptotic relationship with cumulative species number and this was true for each of the four ecosystem functions considered, as well as for mean multifunctionality (Fig. 1). Only 2 of the 81 species (2.5% of the species evaluated) accounted for half of the total wood decomposition, 5 species (6%) for half of the total standing biomass, 6 species (7%) for half of the total litter production, 10 species (12%) for half of the

primary productivity (see also Appendix S1: Fig. S1), and 7 species (9 %) for half of the mean multifunctionality. Primary productivity needed a higher number of species because species were ordered in decreasing absolute contribution to the function, regardless of whether the effect was positive (growth & recruitment) or negative (mortality). Species that were important for one function tended also to be important for other functions and these were the most dominant species in the landscape. For example, *Trichospermum mexicanum* was the one species that contributed to 50% of ecosystem functioning for all four functions, *Schizolobium parahyba*, *Cordia alliodora*, *Vochysia guatemalensis* and *Ochroma pyramidale* were important for three functions (Appendix S1: Fig. S2). There was a significant concordance in the rank of species contributions across the four functions (Kendall's $W = 0.62$, $P < 0.001$; Appendix S1: Table S4).

When randomizing species traits over the existing dominance structure (R1), the strong saturating relationship between ecosystem function and cumulative species number was maintained (Fig. 2a-d, Appendix S1: Fig. S3), while differences in species traits caused the variation around the curve. The 1000 different R1 simulations showed very high concordance for each of the functions, indicating the order of species functionality hardly changes (Kendall's $W = 0.94$, on average across functions; Appendix S1: Table S4). When randomizing species traits while minimizing species dominance (R2), the relationship became more linear (Fig. 2e-h, Appendix S1: Fig. S3), indicating that species contribute much more equally to each ecosystem function. The range of potential ecosystem function values due to functional trait variability is consistently larger under the existing (unequal) dominance structure of R1 (grey area in Figs 2a-d) compared to the low dominance structure of R2 (grey area in Figs 2e-h). Results show that the species dominance distribution consistently determines the shape of the relation (linear or saturating) between ecosystem function and cumulative species number. The species traits, in

contrast, only determine the variation around the curve and thereby to some extent also the potential absolute value of the function.

Discussion

This study evaluates the importance of biodiversity for multiple ecosystem functions in a tropical human-modified landscape. We found that dominance is potentially more important than species traits in determining species functionality; because of the strong effect of dominance in secondary forests, does only a small subset of the dominant species matter for different functions. We thus found limited support for the increased importance of biodiversity when considering multiple ecosystem functions.

Same dominant species matter for different functions - Cumulative ecosystem function showed a strong asymptotic relationship with cumulative species number and this applied for each of the 4 ecosystem functions considered as well as for mean multifunctionality (Fig. 1, Appendix S1: Fig. S3). Only between 2 and 10 species (2.5- 12% of the total of 81 species) are responsible for 50% of each ecosystem function (Appendix S1: Fig. S1). This small subset largely overlapped among functions (Appendix S1: Fig. S2), and the ranking of species functionality was concordant across functions (Appendix S1: Table S4). So for each ecosystem function in isolation, only few species contributed to most of the function while the many other species contributed little to nothing (cf. Kleijn et al. 2015). This is in line with previous studies showing that only 1% of the 16,000 tree species in the Amazon account for 50% of the carbon storage and biomass productivity (Fauset et al. 2015). Theoretical and experimental advances predict that different species contribute to

different functions, but we found otherwise; the important species largely overlapped among different ecosystem functions (Appendix S1: Fig. S2).

Randomizing species traits over species identity while maintaining the (unequal) dominance structure (R1) resulted in very similar highly saturating relationships between species richness and ecosystem function across the four functions (Fig. 2a-d, Appendix S1: Fig. S3). The ranked species' contributions across simulations were almost identical (Appendix S1: Table S4; average Kendall's $W = 0.94$), indicating that species traits have little effect on these rankings.

Randomizing species traits over each tree, and giving all species near-to-equal abundances (R2), resulted in near-linear simulated relationships between richness and ecosystem function (Fig. 2e-h, Appendix S1: Fig. S3), reflecting a more equal contribution of species to each ecosystem function. Here, species contributions to ecosystem functions no longer depend on relative abundance but are increasingly determined by species traits: the high evenness scenario allows species with deviating traits to drive different ecosystem functions (cf. Hillebrand et al. 2008).

Our results are in line with experimental evidence from soil crust communities (Maestre et al. 2012a) and may partly explain why other observational studies similarly found only a weak link between species richness and multifunctionality in global drylands (Maestre et al. 2012b) and in production forests (Gamfeldt et al. 2013). Dominance was previously shown to alter the relationship between species richness and the single ecosystem functions productivity, decomposition and pollination (Dangles and Malmqvist 2004, Kirwan et al. 2007, Winfree et al. 2015), although some studies found little effect of dominance (Wilsey and Polley 2004, Finn et al. 2013). We show that dominance reduces the effect of species richness on ecosystem functioning in tropical forest, and that this persists when considering multiple ecosystem functions at the landscape scale.

Need to integrate dominance in experimental approaches - Most of our knowledge on the effects of biodiversity on ecosystem multifunctionality comes from grassland experiments. Here typically species richness is manipulated, while reducing inter-plot differences in species composition and dominance. These experimental studies have been fundamental in demonstrating the potential role of species richness in ecosystem functioning and analyzing the underlying mechanisms (e.g. Tilman 2001). However, it is vital to test whether mechanisms found under controlled environments are strong enough to be captured by studies conducted under natural conditions, where species do vary in dominance. In the current study we take such an observational approach and show that species dominance potentially overrules the effect of species richness on multiple ecosystem functions. We argue that our findings need to be further tested experimentally and underline the importance of a new generation of biodiversity experiments that includes variation in species dominance.

Limited set of functions - We used four ecosystem functions that quantify major fluxes in energy and matter, and are of particular importance for climate change mitigation. Such biogeochemical functions dominate the literature on ecosystem functioning (Isbell et al. 2011, Maestre et al. 2012b, Gamfeldt et al. 2013), are of global relevance for the ecosystem services that they underlie, and are thought to respond strongly to changes in biodiversity (MA 2005).

Nevertheless, they represent only a small subset of all functions performed by ecosystems and might be correlated, although in our study that was only the case for the relationship between biomass and litter production (see Appendix S1: Table S3). We treated the functions as additive; landscape functions were predicted based on the effects of the constituent species. Indeed many ecosystem functions are additive (Fox 2005); not only mass-related regulatory functions like biomass and productivity but also functions based on plant-animal interactions like pollination

(Kleijn et al. 2015). By definition dominant species contribute more to additive ecosystem functions (Norberg 2004). However, treating functions as additive ignores the interspecific interactions that are thought to underpin the diversity effect (Finn et al. 2013). Broadening the subset of ecosystem functions to include functions that are not additive, e.g. accumulation of particular nutrients (Lyons et al. 2005) and decomposition of leaf-litter mixtures (Handa et al. 2014), may generate different results.

Diversity matters for maintenance of multifunctionality - Results obtained in this study show that the effect of dominance on species' contributions to ecosystem functions is large and thereby reduces the importance of biodiversity for ecosystem multifunctionality, at a given spatial scale and at a given moment in time. However, at the same time, we show that any species could potentially matter for ecosystem functioning if it reaches high dominance. Thus species that are seemingly redundant now, could become important in the future when disturbances cause populations of dominant species to collapse and rare species to fill the niches that come available (Walker et al. 1999). In fact this continuous re-assembly of communities is characteristic for secondary forests (Lohbeck et al. 2014). Testing effects of spatio-temporal complementarity of species is vital to assess effects of biodiversity loss on *maintenance* of ecosystem multifunctionality: although biodiversity may not matter so much for ecosystem multifunctionality in a tropical forest landscape at a given moment in time, biodiversity (and locally rare species) may be critically important for ecosystem stability and resilience across temporal and spatial scales (Walker et al. 2004, Jucker et al. 2014, Hautier et al. 2015, Isbell et al. 2015).

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Figure 1. Landscape-level cumulative ecosystem function (percentage of the maximum value) against ranked cumulative species number for each of the ecosystem functions: biomass, primary productivity, litter productivity, and wood decomposition, and for mean multifunctionality. The strong saturating nature of each of the curves indicates that few species contribute a lot to the ecosystem function whereas most species contribute little to nothing. See also Appendix S1: Figs S1 and S2. Cumulative productivity descends below zero, and increases somewhat erratically due to mortality.

Figure 2. The cumulative contribution of individual species to the cumulative value of different ecosystem functions: a,e) above-ground biomass, b,f) primary productivity, c,g) litter productivity, d,h) wood decomposition. Graphs in the left column show the scenarios using method 1 (R1; randomizing species traits, maintaining the dominance structure) and graphs in the right column show the scenarios using method 2 (R2; randomizing species traits, minimizing dominance). The red line is the observed trend (see Fig. 1, Appendix S1: Fig. S2), the black line

is the mean of the 1000 simulations, the grey area is the range of variation generated by the simulations.

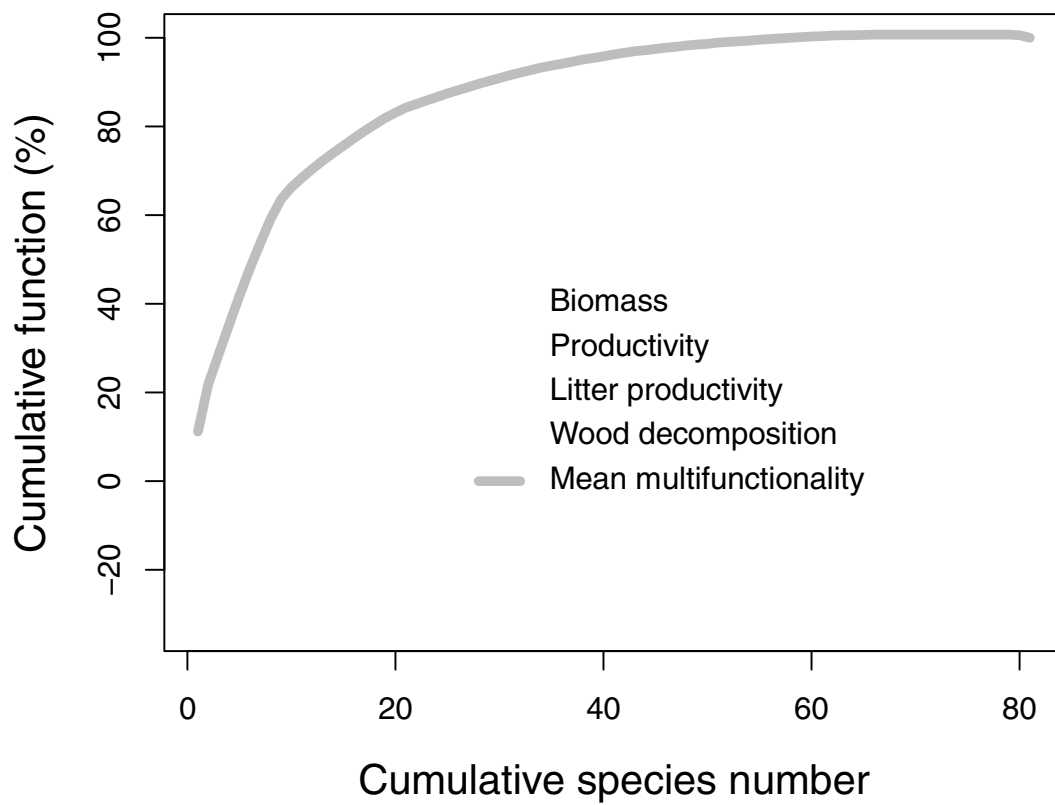


Figure 1

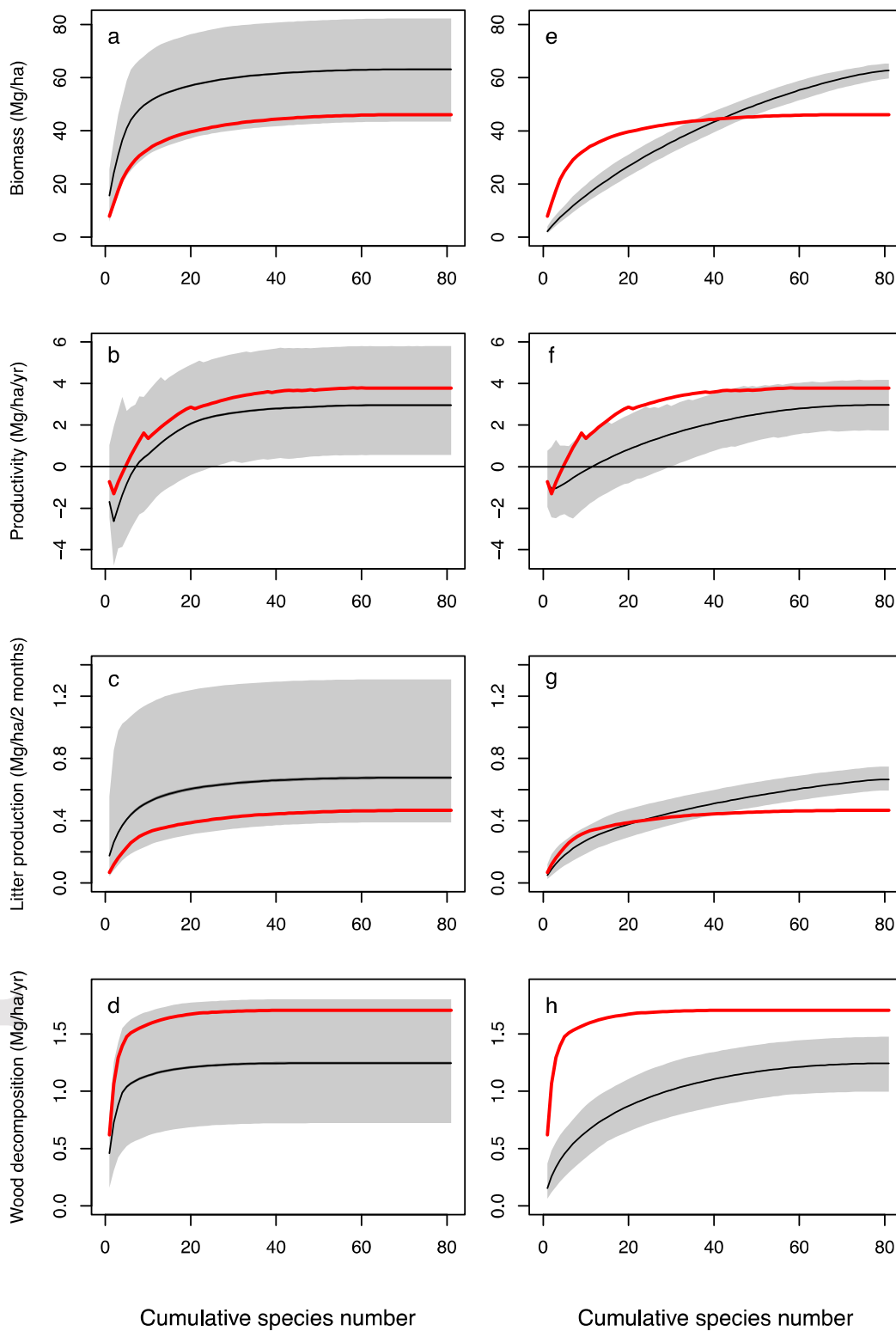


Figure 2