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LETTER

Tree species richness promotes productivity in temperate forests through strong complementarity between species

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Abstract

Understanding the link between biodiversity and ecosystem functioning (BEF) is pivotal in the context of global biodiversity loss. Yet, long-term effects have been explored only weakly, especially for forests, and no clear evidence has been found regarding the underlying mechanisms. We explore the long-term relationship between diversity and productivity using a forest succession model. Extensive simulations show that tree species richness promotes productivity in European temperate forests across a large climatic gradient, mostly through strong complementarity between species. We show that this biodiversity effect emerges because increasing species richness promotes higher diversity in shade tolerance and growth ability, which results in forests responding faster to small-scale mortality events. Our study generalises results from short-term experiments in grasslands to forest ecosystems and demonstrates that competition for light alone induces a positive effect of biodiversity on productivity, thus providing a new angle for explaining BEF relationships.

Keywords

Biodiversity, competition, complementarity, ecosystem functioning, forest succession model, forests, productivity, species richness, trees.

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INTRODUCTION

As species extinction rate is accelerating, it is increasingly recognised that a crucial objective of ecological research is to better understand how species diversity affects the functioning of ecosystems (Naeem *et al.* 2009). The relationship between plant richness and productivity, a key ecosystem process (Chapin *et al.* 2002), has been widely studied in the last two decades using three distinct approaches: sowing experiments (Hooper *et al.* 2005; Balvanera *et al.* 2006; Cardinale *et al.* 2007); observations in natural systems (Caspersen & Pacala 2001; Vila *et al.* 2007; Paquette & Messier 2011); and theoretical models (Bolker *et al.* 1995; Tilman *et al.* 1997; Loreau 1998a,b). Many experiments on the relationship between biodiversity and ecosystem functioning (BEF) were carried out in the last two decades (Hector *et al.* 1999; Hooper *et al.* 2005), usually showing that plant productivity increases with increasing species richness, often levelling off at high richness. However, this response pattern is not general, for instance it varies with study location (Hector *et al.* 1999; Hooper *et al.* 2005). Although experiments may provide causal information on the relationship between diversity and productivity, they have been criticised because their random species assemblages may inherently be artificial and too different from assemblages in natural ecosystems (Grime 2002; Lepš 2004; Thompson *et al.* 2005; Duffy 2009). Furthermore, the vast majority of experiments have focused on artificial grasslands (Hooper *et al.* 2005; Cardinale *et al.* 2007) because such ecosystems are convenient to manipulate and yield results within a reasonable timeframe. There is considerable debate whether the results from short-term (usually a few years, slightly above a decade at best) grassland experiments may merely reflect transient dynamics (Thompson *et al.* 2005), possibly underestimating long-term effects (Cardinale *et al.* 2007; Marquard *et al.* 2009).

Although forests are terrestrial ecosystems of key importance at regional to global scales (e.g. for carbon storage; Chapin *et al.* 2002), they have not received much attention to date regarding BEF patterns. Diversity experiments in forests are indeed difficult to implement because of the size and much slower development of trees. However, recently tree seedlings have been planted at different richness levels and compositions (Scherer-Lorenzen *et al.* 2007), and first results from tropical experiments suggest positive tree diversity effects on timber yield in the short term (Potvin & Gotelli 2008). Still, the effects of changes in tree species diversity on forest productivity have more often been inferred from observations in natural ecosystems (Vila *et al.* 2007; Paquette & Messier 2011). Yet, observed diversity–productivity relationships necessarily include multiple sites, are affected by different environmental conditions and thus depend on the geographical scale and ecological organisation level that is considered (Waide *et al.* 1999; Mittelbach *et al.* 2001). Therefore, although almost all studies using observations in natural ecosystems have shown a positive BEF relationship, they have failed to depict consistent causal mechanisms.

As both experimental approaches and observations in natural ecosystems have limitations, theoretical approaches have been employed to advance the controversy in the BEF field (Tilman *et al.* 1997; Loreau 2010). These theoretical studies have revealed that species richness does not necessarily enhance ecosystem processes (Loreau 1998a,b), but when it does, this is due to the combination of two types of effects (Loreau *et al.* 2001). 'Selection' (also called 'Sampling') effects are due to species-specific impacts on ecosystem processes (i.e. increasing species richness can promote a mixture's productivity because it increases the probability of including the most productive species that ultimately will dominate the community's response). 'Complementarity' effects enhance an ecosystem process such as productivity through interspecific interactions (e.g. facilitation) or niche partitioning, thus leading to a more efficient use of available resources.

We explore an alternative approach to study the response of forest productivity to changes in tree species richness using a process-based forest succession model featuring five key advantages:

1. The model has been developed and validated independently from efforts focusing on diversity–productivity patterns (Bugmann 2001a,b).
2. In contrast to models from theoretical ecology (Tilman *et al.* 1997; Loreau 1998a,b), it deals with real species that are characterised by specific autecological traits and trade-offs (Bugmann 2001a,b).
3. It can be used to simulate forest dynamics at the centennial time scale, allowing us to test for long-term effects, thus (i) avoiding the bias that may be induced by early successional biodiversity effects (Caspersen & Pacala 2001) and (ii) dealing with realised species richness, rather than initial species richness.
4. Simulations allow for exploring a much larger number of species combinations than any real experiment.
5. The model allows us to elucidate the underlying causal processes.

We present the results of virtual biodiversity experiments performed at a broad range of sites using 30 European tree species, and we focus on the long-term relationship between productivity and realised species richness.

MATERIAL AND METHODS

We performed simulations with a forest succession model, differing in species richness and composition (from 1 to 30 European tree species) and covering a time period of 2000 years, at 11 sites in central Europe located along a strong climatic gradient.

Forest succession model

We used ForClim v2.9.6 (Bugmann 1996; Bugmann & Solomon 2000; Didion *et al.* 2009), which had been developed for simulations over a wide range of environmental conditions. ForClim is based on a minimum number of ecological assumptions, with low parameter requirements. Following the standard approach of gap models (Botkin *et al.* 1972), the establishment, growth and mortality of trees on multiple forest patches are simulated while considering abiotic and biotic limitations to establishment and growth. Forest properties at a larger spatial extent are derived by averaging the properties simulated at the patch scale (Shugart 1984; Bugmann 2001a,b).

In ForClim, trees are established with a diameter at breast height of 1.27 cm as a function of species-specific responses to winter temperature, light availability at the forest floor, growing degree-days and browsing pressure (Bugmann 1994). In principle, all species (from the species pool chosen) are available for establishment; in other words, there is a constant seed rain in the patches and no dispersal limitation. Actual tree growth (i.e. stem diameter increment at breast height) is calculated by modifying the optimum growth rate according to abiotic or biotic conditions (growing degree-days, soil moisture and nitrogen status, crown length, and inter and intraspecific competition), which finally leads to changes in species composition. In the current version, the model concentrates on competition for light. Community dynamics arise in the model via the amount of light that is available to each tree, which depends on self-shading as well as shading by taller trees in the patch, thus rendering tree height an important variable. Light intensity across the canopy is calculated using the Beer–Lambert law for the absorption of light travelling through the leaf layers of every patch. Other resources are affecting species performance, such as nitrogen availability that varies across sites, but this resource itself is a constant at the site level in the model. To calculate weather-dependent factors, mean monthly temperatures and monthly precipitation sums are simulated. The model is further constrained by soil water holding capacity, which is important for calculating soil water balance and a drought index.

From stem diameter at breast height, the sizes of other tree compartments (e.g. foliage, roots) and total aboveground biomass are estimated using allometric equations, which partly respond to changing competition and thus to diversity changes (Bugmann 1994; Didion *et al.* 2009). Species coexistence in forest gap models is brought about by two main mechanisms: first, trade-offs evident from the life-history strategies, such as high rates of colonisation often being tied to low shade tolerance, or a typically short lifespan of early successional, fast-growing trees; and second, the fact that cyclical succession is occurring on each individual patch, such that species with different properties are able to dominate during different parts of the cycle.

Tree mortality is stochastic and it has two components: (1) a 'background' mortality that is constant across time, and (2) a growth-related mortality. Large-scale disturbances (e.g. windthrow, wildfires) are not considered here. The background mortality depends on species' maximum longevity, whereas the growth-related mortality is an integral proxy for stress conditions (i.e. tree vigour). As competition affects individual tree growth, it has an indirect effect on mortality rates via the growth-related mortality. A detailed description of the model is available elsewhere (Bugmann 1996; Bugmann & Solomon 2000; Didion *et al.* 2009); species parameters are provided in Appendix S1.

ForClim has evolved from a simulator of forests in the Swiss Alps to a general model that is applicable to temperate forests of central Europe (Bugmann & Cramer 1998), eastern North America (Bugmann & Cramer 1998), the Pacific Northwest of the USA (Bugmann & Solomon 2000), northeastern China (Shao *et al.* 2001) and the Colorado Front Range of the Rocky Mountains (Bugmann 2001a,b). To our knowledge, ForClim is the only succession model that has been demonstrated to be applicable 'out of the box' (i.e. without any re-parameterisation) across widely different climates while still keeping a species resolution, thus supporting its generality. Using such a model to explore the diversity–productivity relationship differs from previous modelling studies (Tilman *et al.* 1997; Loreau 1998a,b) in two key regards: (1) we used a multi-trait model that takes into account observed trade-offs in species biology (e.g. growth/shade tolerance), as the ForClim parameters are mostly derived from observable and measured traits; and (2) the model has originally not been developed to study diversity–productivity questions, and can thus be viewed as an independent tool.

Simulations

The accuracy of ForClim in Europe has been shown by its ability to reproduce vegetation patterns along a broad environmental gradient (Didion *et al.* 2009) spanned by 11 sites with contrasting temperature and precipitation conditions (Table S2 in Appendix S1). We used these 11 sites to run virtual experiments. Each simulation lasted

2,000 years, starting from bare ground, so that the forests simulated over 200 patches of 1/12 ha (16 ha in total) for each site reached a pseudo-equilibrium in terms of species composition and total biomass (while gaps still randomly occur in the forest due to the nature of cyclical succession on each patch).

Number of simulations with different tree species richness

At each site we ran simulations that differed in their original species composition, ranging from 1 to 30 European tree species for which ForClim had been parameterised (cf. Table S1). However, it was not feasible to simulate all possible combinations of species, as this would represent

$$\mathrm{N} = \sum_{k=1}^{30} \binom{30}{k} \approx 1.07 \times 10^9 \text{ simulations for each site.}$$

We therefore chose to limit the simulation runs for each richness level (i.e. number of species k) to 500. For $k = 1$ and $k = 29$ we ran simulations corresponding to the

$$\binom{30}{1} = \binom{30}{29} = 30 \text{ possible combinations for each site,}$$

whereas, for $k = 2$ and $k = 28$ we ran simulations corresponding to the full

$$\binom{30}{2} = \binom{30}{28} = 435 \text{ possible combinations.}$$

For the other richness levels ($k = \{3, 4, \ldots, 27\}$), the total number of possible combinations was too large, and therefore we ran 500 simulations randomly drawn from all possible combinations of species, respectively.

Biodiversity and ecosystem functioning experiments are usually evaluated based on an analysis of variance of productivity measured in the plots (Hector *et al.* 1999; Marquard *et al.* 2009). However, it is normally impractical to sow all possible species combinations at each richness level. In order to circumvent this difficulty and to deal with the runtime problem in the simulations described above, we decided to consider an (unbiased) 95%-confidence interval of the median, which would be obtained for the productivity across

$$\binom{30}{k} \text{ combinations for a given initial species richness } k \text{ in our simulations.}$$

This method consists of assessing an interval that covers the true median of a population using a subsample that depends on the size and on the confidence coefficient chosen (here 95%) (Mood & Graybill 1963; Rice 1995). This nonparametric approach was employed across all levels of species richness at all sites (Fig. 1b).

Thus, overall we ran

$$\binom{30}{1} + \binom{30}{2} + \sum_{k=3}^{27} 500 + \binom{30}{28} + \binom{30}{29} + \binom{30}{30}$$
$$= 13\,431 \text{ simulations for each site,}$$

differing in initial species composition from 1 to 30 European tree species. This yielded a total of 147 741 simulations across all sites. To be consistent with earlier experimental studies, we also present the classical analysis of variance in the simulated productivity, which also allows testing for composition and interaction terms.

Simulation output

We define 'realised species richness' as the species richness at the end of the simulation. We consider that a species was present if its biomass represented more than 1% of total aboveground biomass. Productivity was obtained by averaging the yearly productivity of 10 years at a 100-year distance (1100, 1200, …, 2000) to minimise temporal autocorrelation.

To test for the robustness of our model regarding recruitment rates, we performed additional simulations with increased or decreased recruitment rates. These results yielded the same pattern as the ones presented in this study, demonstrating that our results are robust to changes in recruitment rates.

Identification of selection and complementarity effects

We quantified the net biodiversity effect (ΔY) in simulations with more than one species in the input as the difference between the simulated productivity of a multi-species forest and its expected productivity. This reflects the null hypothesis that there is no selection

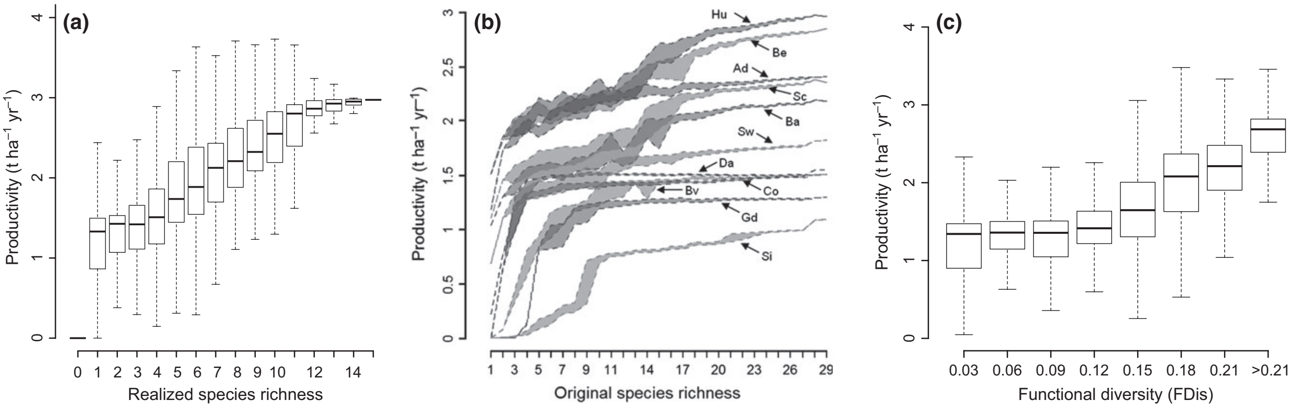

Figure 1 Forest productivity increases with increasing species richness and functional diversity. (a) Box plot of simulated productivity across all sites as a function of realised species richness (at the end of the simulation); n = 147 741. (b) Estimate of the median of productivity against original species richness for each of 11 sites. Shaded areas between dashed lines represent a 95% confidence interval of the true median of productivity (see Material and methods section). Shades of various colours were used simply to better distinguish the sites. *Ad*: Adelboden, *Ba*: Basel, *Be*: Bern, *Bv*: Bever, *Co*: Cottbus, *Da*: Davos, *Gd*: Grande Dixence, *Hu*: Huttwil, *Sc*: Schaffhausen, *Sw*: Schwerin, *Si*: Sion. (c) Box plot of simulated productivity across all sites as a function of function dispersion (*FDis*) index (at the end of the simulation); n = 147 741. For the sake of readability, *FDis* values were grouped in eight classes (e.g. the class '0.03' gathers all *FDis* values lower than 0.03).

or complementarity effect relative to the simulated productivity of monospecific forests (Loreau & Hector 2001). These calculations were carried out based on the relative abundance (in terms of biomass) of the species at the end of the simulation. We then partitioned the signal into the selection (*SE*) and complementarity (*CE*) effects following Loreau & Hector (2001). We further divided ΔY, *SE* and *CE* by the expected forest productivity based on monocultures [i.e. similar to the D index proposed by Loreau (1998a,b)] to allow for intersite comparisons. For the analyses involving these effects, values were square-root transformed to meet the assumptions of linear regression while preserving positive and negative signs (Loreau & Hector 2001). We used the maximum productivity resulting from all simulations of each site as a proxy of site fertility. We used Pearson correlations to determine the relationship between the mean of both effects and site fertility, and between the regression slope and site fertility.

Sensitivity analysis and additional simulations and analyses

In ForClim species are defined by parameter values, thus any effect related to species diversity must be related to the diversity in parameter values. Therefore we performed a sensitivity analysis of species-specific parameters to elucidate the relative contribution of the diversity in each parameter to the biodiversity effect we observed. We focused on three parameters linked to growth and competition (maximum tree height *kHMax*, growth rate parameter *kG* and shade tolerance of adult trees *kLa* – see Table S1). The parameters *kAMax* (species-specific maximum age reached by trees) and *kS* (relating to the height-diameter allometry) were also tested, but they affected the pattern only weakly. These results are therefore not reported here.

We ran simulations with all 30 species at the site Bern (2000 years over 200 patches), with all species having the same value of the tested parameter at a time. We calculated the net biodiversity effect of these simulations (hereafter named ΔY_{test}), which is the difference between the simulated productivity of the multi-species forest and its expected productivity based on the simulated productivity of the monocultures (using the monocultures simulated with the modified parameter values to achieve a fair comparison).

Then, we used the following index to quantify the difference between ΔY_{test} and the original net biodiversity effect (i.e. with the original diversity in parameter values), hereafter named ΔY_{obs}:

$$D_{\Delta Y} = \frac{\Delta Y_{test}}{\Delta Y_{obs}} \times 100.$$

Thus, the weaker $D_{\Delta Y}$, the larger the importance of the diversity in the values of the studied parameter in promoting difference in productivity between diverse forests and monocultures. For each of the 'target' parameters (i.e. *kHMax*, *kG* and *kLa*), we repeated this analysis with different values to cover the range of values of the parameter.

Furthermore, to explore the pathways by which the diversity in parameter values affects forest productivity, we did the same kind of sensitivity analysis for mean values of leaf area index (LAI) and for the coefficient of variation of LAI (i.e. variability of LAI over time for a same simulation). We calculated the same indices as used for the net biodiversity effect:

$$D_{\Delta LAI} = \frac{\Delta LAI_{test}}{\Delta LAI_{obs}} \times 100 \quad \text{and} \quad D_{\Delta LAI} = \frac{\Delta CV(LAI)_{test}}{\Delta CV(LAI)_{obs}} \times 100,$$

where ΔLAI_{test} is the difference between the simulated LAI of the multi-species forest and its expected LAI based on the simulated monocultures, and $\Delta CV(LAI)_{test}$ is the difference between the CV(LAI) of the simulated multi-species forest and its expected CV(LAI) based on the simulated monocultures. ΔLAI_{obs} and $\Delta CV(LAI)_{obs}$ are the original diversity effect on LAI (i.e. with the original diversity in parameter values) and the original diversity effect on CV(LAI), respectively.

Thus, the weaker D_{LAI} and the weaker $D_{CV(LAI)}$, the larger the importance of the diversity in the values of the studied parameter in promoting a difference in LAI and in CV(LAI), respectively, between diverse forests and monocultures.

Finally, to further highlight the causal processes driving the net biodiversity effect produced by the model, we carried out additional analyses focusing on the comparison between the most diverse forest at each site and the monocultures (detailed in Appendix S4).

Statistical analyses

We carried out a classical ANOVA in simulated productivity, testing for site location, realised species richness, composition, and interactions terms. Realised species richness was used in this analysis (overall, results were similar with initial species richness). To help elucidating the functional mechanisms driving possible biodiversity effects, we used a continuous functional diversity index [i.e. the functional dispersion index (*FDis*, Table 1)] because it is a multi-traits index, and is mathematically independent of species richness (Laliberté & Legendre 2010). *FDis* values were calculated with all species-specific ForClim parameters (see Appendix S1). Species richness was square-root transformed to meet the assumptions of the analyses. Species richness was tested against the richness-by-site term, and functional diversity against the functional diversity-by-site interaction. Site differences, functional diversity-by-richness, richness-by-site interactions, and the functional diversity-by-site interaction were tested against the site–species richness–functional diversity interaction term.

Table 1 Summary of the analysis of productivity simulated in the virtual experiments with ForClim (*top*), and summary of the analysis of median productivity per level of richness and site (*down*)

Source of variation	d.f.	MS	*F*	*P*
Productivity				
Site	10	4241.1	96.39	< 0.001
√(Species richness)	1	1065.3	16.24	< 0.001
FDis	1	4033.9	25.79	< 0.001
√(Species richness) × *FDis*	1	173.5	3.94	*n.s.*
Site × √(Species richness)	10	65.6	1.49	*n.s.*
Site × *FDis*	10	156.4	3.55	*n.s.*
Site × √(Species richness) × *FDis*	10	44.0	220.00	< 0.001
Residuals	145 998	0.2		
Median estimate				
Site	10	10.4	400.20	< 0.001
√(Species richness)	1	26.9	1031.73	< 0.001
Site × √(Species richness)	10	0.2	6.46	< 0.001
Residuals	308	0.03		

Top: We used realised species richness and the functional diversity index *FDis* (functional dispersion, Laliberté & Legendre 2010 and see Material and methods section). *Down*: the non-biased estimate of median productivity we used necessarily returns one value per input richness level, which only allows testing for original species richness and site effects. All effects were tested against overall residuals. Type I sum of squares were used in both analyses, d.f., degrees of freedom; MS, mean squares.

The site–species richness–functional diversity interaction was tested against the overall residuals.

Further, an ANOVA was performed using the median estimate of productivity (as described above). The method we used to calculate the non-biased estimate of median productivity refers to initial richness (as the point of this method is to assess the true median across all possible combinations for a given richness from a sample of 500 simulations of similar richness).

The relationship between net biodiversity, selection, and complementarity effects on the one hand and realised species richness on the other hand was tested using a linear regression model at both the intersite and intrasite levels. To test for the link between diversity effects and functional diversity, linear regressions of net biodiversity, selection and complementarity effects against *FDis* were calculated at both the intersite and intrasite levels, with emphasis on the simulations with maximum species richness at each site.

RESULTS

Forest productivity at pseudo-equilibrium increased strongly with both realised species richness and functional trait diversity (Fig. 1a, Table 1), but it varied significantly across sites, ranging from 1.1 to 2.97 t ha^{-1} year^{-1} for simulations with 30 species (i.e. the highest richness tested). A positive biodiversity–productivity relationship was also evident when considering initial species richness, and it was further confirmed by the unbiased estimate of the median (see Material and methods section). The shape of the relationship varied across sites, but it consistently reached an asymptote at high species richness (Fig. 1b, Table 1 and Fig. S1 in Appendix S2). Saturation, defined as 90% of the productivity obtained in the simulation with 30 species, occurred at lower richness at sites with low maximum productivity (Fig. 1b). Productivity increased with functional dispersion (Fig. 1c and Table 1), showing that the positive trend between species richness and productivity is strongly related to an increase in functional diversity.

In 93.1% of the simulations, mixtures showed higher productivity than the average of the monoculture productivities (non-transgressive overyielding; Loreau & Hector 2001; Hector *et al.* 2002; Table S3 in Appendix S2). Nevertheless, diverse forests achieved greater productivity than the most productive monospecific forest (transgressive overyielding) in only 10.9% of simulations, which is similar to patterns observed in experiments (Cardinale *et al.* 2007); however, large differences were evident across sites. It is noteworthy that the species forming the most productive monoculture was never the most dominant species in the most diverse forest, except at one site (see Appendix S3).

The net biodiversity effect (i.e. the difference between the simulated productivity of a multi-species forest and its expected productivity based on the simulated monospecific forests, under the null hypothesis that there is no selection or complementarity effect; Loreau 1998a,b; Loreau & Hector 2001) calculated with realised abundance at the end of the simulation was positive in 85% of simulations, increasing with realised species richness (slope = 0.059, $P < 0.001$, Fig. 2a). Thus a strong overyielding pattern was present in most cases. To explain it, we partitioned the selection and complementarity components of the net biodiversity effect (Loreau 1998a,b; Loreau & Hector 2001), which showed striking results: both effects range from positive to negative, but the selection effect was negative in 36% of simulations across all sites whereas the complementarity effect was negative in 11% of simulations only; the complementarity effect was stronger than the selection effect in 80% of simulations (Table S2). The selection effect increased weakly with realised species richness (slope = 0.020, $P < 0.001$, Fig. 2b, Table S3 in Appendix S1). In contrast, complementarity increased 2.5 times more strongly with realised species richness (slope = 0.052, $P < 0.001$, Fig. 2c). This pattern was robust, as it was found at 9 of 11 sites (Figure S1 in Appendix S2).

Also, the net biodiversity was strongly positively related to functional diversity (*FDis*) across sites (slope = 1.67, $F_{1,144754}$ = 55850, $P < 0.001$, $r^2 = 0.28$) as well as within sites. The complementarity and selection effects were also related to *FDis*, although the relationship was much stronger for complementarity (slope = 1.33, $F_{1,144754}$ = 47680, $P < 0.001$, $r^2 = 0.25$) than for selection (slope = 1.67, $F_{1,144754}$ = 5327, $P < 0.001$, $r^2 = 0.04$; Fig. 3). Overall, this

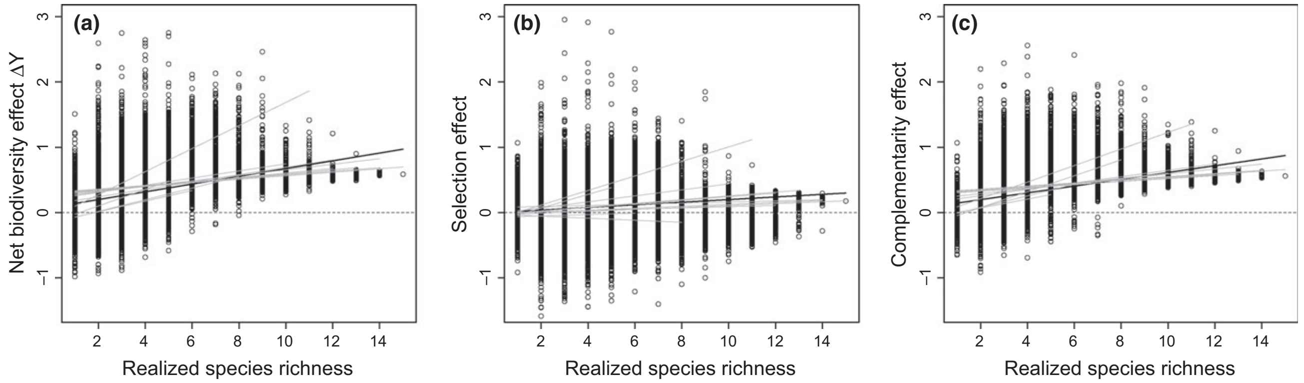

Figure 2 Net biodiversity (a), selection (b) and complementarity (c) effects as a function of realised species richness across all sites. The effects were calculated following the original method (Loreau & Hector 2001), but divided by the expected forest productivity based on monocultures (Loreau 1998a,b) to allow for intersite comparisons. Values are square-root transformed to meet the assumptions of the analysis while preserving positive and negative signs. Black lines are from the linear regression model with all sites, with (a) slope = 0.059, $P < 0.001$; (b) slope = 0.020, $P < 0.001$; and (c) slope = 0.052, $P < 0.001$ (n = 144 969 for a, b and c). Grey lines are from linear regression models for each site (n = 11, details in Table S3). Note that realised richness is shown in this figure, thus there are simulations with $n > 1$ species at the beginning that result in forests with only one species at the end. In such cases ($n = 1$ in the figure), it is still possible to calculate the effects (a, b, c) by comparing simulated productivity to expectations from monocultures (defined as simulation with one species at the beginning of the simulation).

confirms the strong importance of functional diversity for explaining why productivity increases with increasing species richness.

Analysing the influence of fertility in the simulations with 30 species at each site showed that complementarity was positively related to site fertility (assessed as the maximum productivity resulting from all simulations at the site) ($r = 0.86$, $P < 0.001$), while no relationship was found between the selection effect and site fertility ($r = -0.36$, $P = 0.27$). However, the slope of a linear regression between realised richness and the complementarity effect at the site level became steeper as fertility decreases ($r = -0.78$, $P < 0.01$), whereas no relationship was found for the selection effect ($r = -0.43$, $P = 0.19$) (Figure S2 in Appendix S2). In other words, the richness-complementarity slope was lower at the most fertile sites than in poor sites, but the absolute values of complementarity remained larger at the most fertile sites.

DISCUSSION

Positive biodiversity effect driven by complementarity

The positive relationship between tree diversity, both in terms of species richness and functional trait diversity, and long-term productivity as well as the saturation behaviour (Fig. 1) that are evident from our simulations are consistent with short-term experimental results from herbaceous communities (Hector *et al.* 1999; Hooper *et al.* 2005). Thus, our results strongly support the idea that the positive biodiversity effects highlighted in experiments are neither transient (Hector *et al.* 2007) nor limited to short-lived species. Particularly, our results are consistent with the increasing relative importance of complementarity over time relative to selection as found by Cardinale *et al.* (2007).

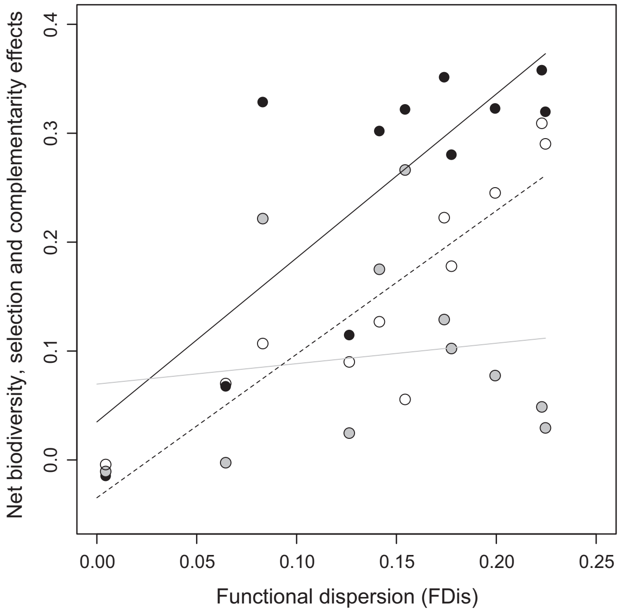

Figure 3 Net biodiversity (black dots), selection (open dots) and complementarity (grey dots) effects as a function of functional dispersion (*FDis*) index for the simulation with an original richness of 30 species considering all sites together ($n = 11$). The effects were calculated following the original method but divided by the expected forest productivity based on monocultures, and values are square-root transformed to meet the assumptions of the analysis while preserving positive and negative signs. Black plain line: linear regression model for net biodiversity effect against *FDis* (slope = 2.62, $P < 0.005$); grey plain line: linear regression model for selection effect against *FDis* (slope = 1.30, $P = 0.162$); dashed line: linear regression model for complementarity effect against *FDis* (slope = 2.33, $P < 0.001$).

The simulations further show that environmental conditions affect the richness-productivity relationship (Fig. 1b and Table 1) as well as the relative importance of the complementarity and selection effects, as evident from the large intersite differences (Table 1 and Figs S1 and S2). Our results suggest that site fertility promotes absolute values of complementarity (Fig. S2a), which corroborates within-site experimental results (Dimitrakopoulos & Schmid 2004; Weigelt *et al.* 2009). In addition, we can confirm theoretical expectations (Bertness & Callaway 1994) regarding the higher importance of complementarity in harsh environments, as the loss of a species affects complementarity more strongly at poor than at fertile sites (Fig. S2b); yet, this prediction is still a hotly debated issue in BEF research (Warren *et al.* 2009; Weigelt *et al.* 2009).

Underlying mechanisms

Our results show that competition for light alone is sufficient to entail a positive effect of biodiversity on productivity (Fig. 1) because of complementarity effects (Fig. 2). Yet, hypotheses about positive complementarity effects usually assume that species exploit different resources (Tilman *et al.* 1996). How can this strong biodiversity effect thus be explained, as it involves only one resource? A key advantage of the use of a mechanistic model is that we can diagnose *a posteriori* the cause of the simulated BEF patterns, as follows. In the model, an individual needs to pass abiotic filters (soil and climate conditions) to grow at a given site, independently from the presence of other species. All species that passed these filters compete for one resource (light) with various efficiencies, mediated by environmental conditions, but there is no direct positive (facilitative) effect built into the model. To quantify how productivity was impacted by species and functional diversity (i.e. diversity in tree characteristics), we performed a sensitivity analysis of species-specific parameters, as exemplified here for the site Bern. This analysis showed that removing the diversity of shade tolerance values across species reduced the biodiversity effect (most diverse forest vs. monocultures) by more than 70% on average, whereas removing the diversity in maximum height and growth rate reduced the effect by 70 and 60%, respectively (Fig. 4). Thus the diversity in these three parameters appears to be a crucial driver of the positive BEF effect. Note that the importance of diversity in height of trees for productivity is consistent with observations in natural forests (Ruiz-Jaen & Potvin 2011).

We explored potential causes underlying the simulated effect of species richness on productivity (Fig. 5) by performing systematic, targeted simulation studies. We found that the positive BEF relationship is driven primarily by the shading regime (i.e. vertical stand structure) that results for a given species assemblage. This regime is an emergent property of the heights of the trees in a stand, and as we consider a dynamic system, we can only discuss an 'average' or 'typical' shading regime for a stand at pseudo-equilibrium. Each tree in this type of stand is growing according to this shading regime (based on current light availability) and according to its intrinsic properties (shade tolerance, growth rate). The shading regime is the result of the heights of trees and of the species composition of the stand – both of which in turn are related to the past shading regime.

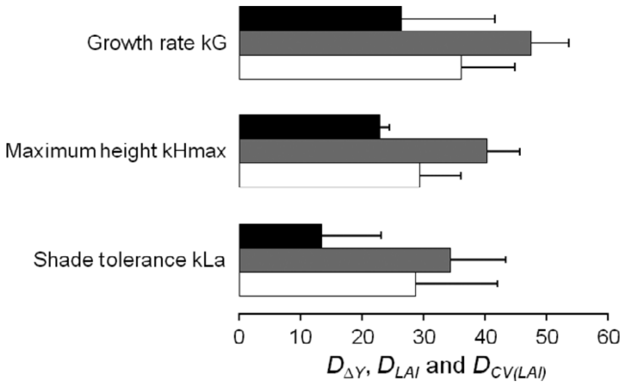

Figure 4 $D_{\Delta Y}$, D_{LAI} and $D_{CV(LAI)}$ indices calculated from the sensitivity analysis to the diversity in parameter values for the site Bern, for shade tolerance of adult trees (*kLa*), maximum height (*kHmax*) and growth parameter (*kG*) (see Material and methods section). Those indices represent the percentage of the original effect of diversity on the simulated productivity, LAI, or CV(LAI) that is achieved when a target parameters is held constant. The lower the index ($D_{\Delta Y}$, D_{LAI} or $D_{CV(LAI)}$), the stronger the diversity effect. For each index, the values are averaged across several fixed values for each parameter (see Material and methods section): for *kLa*, five parameter values were tested by setting parameters equal across all species (*kLa* = 1, 3, 5, 7, 9); for *kHmax*, five values (*kHmax* = 15, 25, 35, 45, 55); and for *kG*, three values (*kG* = 100, 200, 300).

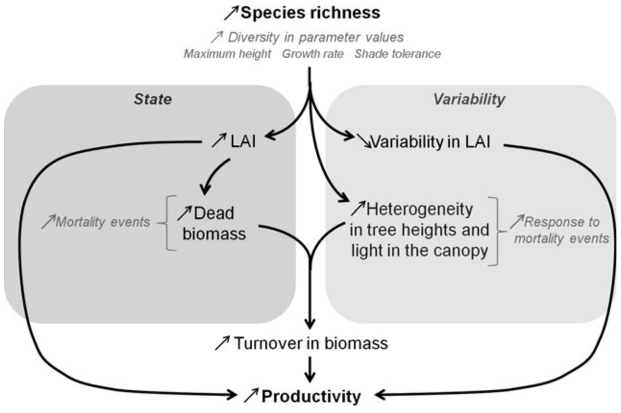

Figure 5 Summarised explanatory diagram showing the main underlying mechanisms driving the mean biodiversity effect in ForClim. The mechanisms can be divided into two categories: those affecting the mean values of some forest characteristics ('state'); and those affecting the variability of these characteristics ('variability'). The detailed evidence for these mechanisms is provided in Appendix S4.

These positive and negative feedbacks render the search for a mono-causal explanation, a hopeless venture. However, to disentangle the underlying mechanisms, we provide a framework below that enables one to follow along the main processes involved in the simulated dynamics.

We found that increasing species richness enhances forest productivity through its impact on (1) the mean values of some forest characteristics and (2) their variability, as explained briefly below (cf. Fig. 5). A comprehensive discussion is available in Appendix S4.

First, regarding the mean state of the simulated forest, higher species richness leads, on average, to a larger LAI because of higher diversity in species trait values. We verified that the most diverse forest has a higher LAI than expected from monocultures, and that LAI increased positively with *FDis* (Appendix S4). The importance of functional diversity in promoting LAI was confirmed by the sensitivity analysis showing that removing the diversity of shade tolerance, maximum height and growth rate across species strongly reduced the difference in mean LAI between the most diverse forest and monocultures (Fig. 4; as explained further above). We hypothesised that increasing the functional diversity increases the complementarity of light niches that can be filled, which leads to a larger leaf cover in the forest and thus a larger LAI. We further showed that this pattern leads to increased productivity because of an increased potential to produce new biomass at the stand level. Also, a higher LAI in more diverse forests leads to an increased frequency of mortality events, thus endogenous disturbances (single-tree mortality) cause more gaps in the vertical structure of diverse forests. This is consistent with the fact that in the model the survival of a tree is affected by the amount of light it receives, thus a more diverse forest necessarily experiences increased mortality rates.

Second, regarding the variability of the characteristics of the simulated forest, we found that more diverse forests feature a less variable LAI over time. In fact, CV(LAI) decreased with increasing *FDis* (Appendix S4). The role of functional diversity in creating this pattern was further confirmed by the sensitivity analysis, which showed that removing the diversity of parameter values across species strongly reduced the difference in CV(LAI) (Fig. 4). Consistent with the stimulation of LAI, we found that a stronger complementarity of light niches (i.e. larger functional diversity) across species led to a more stable leaf cover in the forest and thus a lower CV(LAI) across years. We further showed that this larger stability in LAI led to a higher productivity. We also found that more diverse forests feature a more rapid response to mortality events. Diverse forests had, on average, more small and fewer tall trees compared with the monocultures. Thus, interspecific competition tends to shape a forest with a very different vertical structure compared with forests that feature intraspecific competition only. The structure of diverse forests renders them more reactive to changes in light conditions, as increasing light conditions have a stronger stimulating effect on growth for smaller than for taller trees (Moore 1989). We further verified that mixtures respond by a more rapid recovery (in terms of productivity) to disturbances (here, mortality events) than monocultures, showing that mixtures produce more biomass after a mortality event than expected from the monocultures. This is due to the fact that in the simulated diverse forests, trees better exploit total available light and fill gaps left by dead trees faster because they comprise species with diverse shade tolerances and growth abilities, resulting in larger heterogeneity in tree height and leaf display (Appendix S4). This decrease of the variability of light availability in diverse forests with increasing richness is also consistent with the lower CV(LAI) in the most diverse forest compared with monocultures. The emergent effect of the change in the mortality regime and in the response to mortality events is a stimulation of biomass turnover and thus of productivity in diverse forests (Fig. 5; and see Appendix S4 for a detailed justification of the steps presented in Fig. 5).

Thus, we provide evidence for a cascade of mechanisms to explain the biodiversity effect on productivity, taking into account the effect of diversity on both mean values and variability of forest characteristics. Obviously, our model-derived explanation (Fig. 5) should be tested using field data. Nevertheless, our findings provide a significant step towards disentangling the underlying mechanisms of the biodiversity effect on forest productivity.

Lastly, it is worth noticing that our findings suggest that competitive processes for one resource alone (i.e. light) are sufficient to induce a positive biodiversity effect. Our results indicate that diversity can promote a more efficient resource use for a different reason than in Loreau's model (1998), as (1) our model is based on the highly asymmetric competition for light and (2) it uses observed species-specific trade-offs. Obviously, our results do not exclude that positive biodiversity effects may occur via complementarity in exploiting different resources, either symmetrically or asymmetrically (Tilman *et al.* 1996). Although ForClim is a well-established and thoroughly validated model, one should be aware of the general constraints inherent to all modelling approaches and derived conclusions. For instance, ForClim considers only competition for light, but it is conceivable that additionally competition for nutrients (e.g. soil nitrogen content) may affect the effect of biodiversity on productivity (Tilman *et al.* 1997; Loreau 1998a,b). Therefore, our findings provide a sufficient, but not obligatory explanation for a positive biodiversity effect.

CONCLUSIONS

Beyond the ability to elucidate causal processes, the use of a mechanistic forest model to explore the effect of species diversity on ecosystem functioning leads to three major conclusions.

First, our analyses suggest that tree diversity strongly influences primary productivity in European temperate forests across a wide range of sites with different climates through a strong complementarity effect. It emerges from species-specific constraints alone in combination with competitive processes.

Second, the species richness-forest productivity relationships simulated here are consistent with experimental results (Hooper *et al.* 2005) and they also match theoretical conjectures (Tilman *et al.* 1997) about the saturation of the relationship in the long term.

Third, our approach offers the potential to consider the effects of climate change on both diversity and ecosystem functioning (Naeem & Wright 2003), as the model we used takes into account the impact of climate on the establishment, growth and survival of trees. Our study thus provides a framework for disentangling the role of diversity as a crucial driver for productivity in forests and to explore the mechanisms driving the pattern, thus adding a puzzle piece towards predictive BEF research (Naeem & Wright 2003; Hillebrand & Matthiessen 2009).

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AUTHOR CONTRIBUTIONS

The authors declare no conflict of interest. X.M., L.F. and H.B. designed the research, X.M. conducted the research, and X.M., L.F., M.S.-L. and H.B. contributed to the analyses and interpretation of the results and wrote the manuscript. All authors contributed substantially to revisions.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Supplementary Tables S1, S2, S3 and S4.
Appendix S2 Supplementary Figures S1 and S2.
Appendix S3 Evidence regarding the impact of species' traits on the productivity of monocultures and on the difference between species-specific productivity in monocultures vs. the mixture (with 30 species in input) for each site.
Appendix S4 Evidence for the processes driving the emerging biodiversity effect in the simulations, including additional analyses and results.

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