

LETTER

Temporal stability in forest productivity increases with tree diversity due to asynchrony in species dynamics

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Abstract

Theory predicts a positive relationship between biodiversity and stability in ecosystem properties, while diversity is expected to have a negative impact on stability at the species level. We used virtual experiments based on a dynamic simulation model to test for the diversity–stability relationship and its underlying mechanisms in Central European forests. First our results show that variability in productivity between stands differing in species composition decreases as species richness and functional diversity increase. Second we show temporal stability increases with increasing diversity due to compensatory dynamics across species, supporting the biodiversity insurance hypothesis. We demonstrate that this pattern is mainly driven by the asynchrony of species responses to small disturbances rather than to environmental fluctuations, and is only weakly affected by the net biodiversity effect on productivity. Furthermore, our results suggest that compensatory dynamics between species may enhance ecosystem stability through an optimisation of canopy occupancy by coexisting species.

Keywords

Asynchrony, biodiversity, ecosystem functioning, ecosystem predictability, forests, gap model, insurance hypothesis, productivity, stability, structural equation model.

Ecology Letters (2014) 17: 1526–1535

INTRODUCTION

Concerns about current biodiversity loss have led to explore the role of biodiversity for ecosystem functioning (Loreau *et al.* 2001) and services (Gamfeldt *et al.* 2013). Even though the most studied relationship has been the effect of species richness on ecosystem productivity, changes in biodiversity have also been recognised for long to affect the stability of ecosystem properties (Givnish 1994; Johnson *et al.* 1996). There are several aspects of ecological stability, such as resistance, resilience or persistence of ecosystem properties, reviewed elsewhere (Ives & Carpenter 2007; Griffin *et al.* 2009). Here we focus on the temporal stability of community productivity (Lehman & Tilman 2000; Hector *et al.* 2010). We also explore the effect of species richness on the predictability of community productivity (McGrady-Steed *et al.* 1997) by evaluating the variability in primary production across all possible species compositions with a given species richness. We specifically aim at testing the ‘insurance hypothesis’ (Yachi & Loreau 1999), which states that biodiversity should ‘insure’ ecosystems against declines in their functioning (*e.g.* biomass production) because more species provide a higher guarantee that some will maintain functioning, and improving our knowledge on underlying mechanisms.

There was a long-standing controversy about the relevance and direction of the relationship between diversity

and ecosystem stability (May 1972; Ives *et al.* 1999; Ives & Carpenter 2007). As nicely summed up in other studies (Hughes & Roughgarden 1998; Loreau & de Mazancourt 2013), the debate was partly solved by findings from biodiversity and ecosystem functioning (*BEF*) experiments that were carried out in the last two decades. These experimental results showed that diversity may destabilise individual species dynamics by increasing competitive interactions, while reducing the variability in biomass production of the whole community, thus increasing temporal stability at the ecosystem level (Tilman *et al.* 2006; Proulx *et al.* 2010). However, large uncertainties remain regarding our understanding of the putative stabilising role of competitive interactions in communities, and the mechanisms underlying the diversity–stability relationship (Isbell *et al.* 2009; Loreau 2010).

It appears intuitive that interspecific competition should stabilise the community by enhancing negative covariation in the relative abundances of the constituent species, thus leading to compensatory dynamics between species (Lehman & Tilman 2000; Gonzalez & Loreau 2009). However, it has been shown analytically that most of the time competition should have a destabilising role at the ecosystem level (Loreau & de Mazancourt 2013), although it would have no effect in the case of symmetrical communities in which all species have the same competitive characteristics. Thus, asymmetry between competing species

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should be a key component to explain diversity–stability patterns. Although pioneering work has shown that strong asymmetry in interspecific competitive traits may be destabilising at the community level (Hughes & Roughgarden 1998), other studies have confirmed the expected pattern, focusing on either asymmetry in species' responses to environmental conditions (Ives *et al.* 1999; Loreau & de Mazancourt 2008) or in species' growth rates (Fowler *et al.* 2012; Loreau & de Mazancourt 2013).

To clarify the role of asymmetry between species, Loreau & de Mazancourt (2013) identified three main mechanisms linked to interspecific differences that may drive the stabilising effect of diversity in ecosystem properties (although they are not exclusive): (1) differences in species' intrinsic responses to environmental fluctuations, (2) differences in the speed at which species respond to disturbances and (3) reduction in the strength of competition. Mechanisms (1) and (2) involve temporal complementarity between species, conferred by the asynchrony in species' responses as the averaging of asynchronous population fluctuations reduces the variability in productivity at the community level (Loreau & de Mazancourt 2008; Hector *et al.* 2010). Mechanism (3) relies on the functional complementarity between species, which occurs when the productivity of a diverse community shows higher productivity than expected from monocultures (*overyielding*, Loreau & Hector 2001). Such an effect can increase the temporal stability in productivity of the community as it leads to a greater increase in the mean relative to the variability (Lehman & Tilman 2000). Identifying and disentangling the relative effects of these three mechanisms is often not straightforward in empirical diversity–stability studies. However, de Mazancourt *et al.* (2013) recently proposed a new framework to quantify these effects, by deriving the properties of individual species in monocultures and applying them to mixed communities.

Another frontier in the diversity–stability field lies in the generality of the relationship over time and across ecosystems (Griffin *et al.* 2009). In fact, BEF-experiments for terrestrial ecosystems have mostly focused on artificial grasslands because they can be carried out on the short term, during a few years on average (Hooper *et al.* 2005; Cardinale *et al.* 2009). The validity of these experimental results on the long term has been questioned (Duffy 2009; Marquard *et al.* 2009) as well as their transferability to other ecosystems – such as forests (Scherer-Lorenzen *et al.* 2005). The existence of a diversity–stability relationship has been poorly explored in forests because of the long-term monitoring required. Furthermore, the very few studies that explored this question (DeClerk *et al.* 2006; Lebourgeois *et al.* 2013; Perot *et al.* 2013) could necessarily not explore a wide range of environmental conditions and species richness.

Linking theory-based expectations and supposed underlying mechanisms with experimental results is thus a key requirement in the BEF field (Griffin *et al.* 2009; de Mazancourt *et al.* 2013), especially in forest communities in which experimentation is difficult. This task can benefit from a novel approach recently proposed through the use of process-based forest succession models to carry out virtual BEF-experiments with tree species (Morin *et al.* 2011), in which community composition and forest productivity are emergent properties

based on environmental filtering and competition in the long term. A modelling approach necessarily brings some limitations regarding the fact that the results rely on the basic principles embedded in the model, but it also has several advantages. First, it renders the study of adult-tree communities possible, for which obtaining long-term data is exceedingly difficult. Second, we emphasise that (1) this approach deals with species that are characterised by observed autecological traits and trade-offs (Bugmann 2001) and thus allows to use a trait-based approach, (2) a much larger number of species combinations can be explored than in any real experiment, (3) forest dynamics can be simulated in the long term (centennial time scale), thus avoiding the bias due to transient effects (Duffy 2009) or induced by early successional biodiversity effects (Caspersen & Pacala 2001) and allowing to deal with realised richness and (4) this approach allows for quantifying the three main mechanisms supposed to drive ecosystem stability: (1) the overyielding effect, (2) the asynchrony in species responses to environmental fluctuations and (3) the asynchrony in species dynamics independent of environmental fluctuations.

Through extensive simulations, this approach has shown that tree species richness promotes average productivity in European temperate forests, mostly through strong complementarity between species, demonstrating that competition for light alone may induce a positive effect of biodiversity on average productivity (Morin *et al.* 2011). This biodiversity effect emerged because increasing species richness promotes higher diversity in shade tolerance and growth ability, which results in forests exhibiting a faster turnover in biomass. This framework seems promising for a next step, *i.e.* exploring the effect of biodiversity on the variance in productivity.

Provided that diversity has an effect on the temporal variance of community productivity, a corollary question is whether diversity has also an effect on the variability in productivity across all possible species compositions with a given species richness (McGrady-Steed *et al.* 1997). In other words, is the productivity of a community more predictable when richness increases? If so, biodiversity would 'insure' ecosystems against a decline in their functioning because more species provide a higher guarantee that some will maintain functioning (McGrady-Steed *et al.* 1997). This question has been rarely addressed to date (Naeem & Li 1997), but virtual BEF-experiments can provide productivity data for a large number of species combinations, and they appear particularly suitable to test for this pattern.

We thus tested several facets of the diversity–stability relationship and its hypothesised causal processes using virtual BEF-experiments, considering combinations of 30 European tree species and a wide range of environmental conditions. More specifically, we aimed to test the following hypotheses:

- (1) the variability in mean productivity across stands of different species composition decreases with increasing species richness and functional diversity;
- (2) the temporal stability in productivity increases with increasing species richness and functional diversity at the community level, while it decreases at the species level;
- (3) the effect of diversity on temporal stability is mostly caused by the asynchrony in species responses to environ-

mental fluctuations and in species dynamics independent of environmental fluctuations, but not by an overyielding of productivity.

MATERIAL AND METHODS

Following the same methodology as in Morin *et al.* (2011), we simulated virtual biodiversity experiments with 30 species (trees and shrubs), at various sites along a strong climatic gradient, using a forest succession model.

Forest succession model and simulations

We used FORCLIM v2.9.6 (Didion *et al.* 2009), a model based on a small number of basic ecological assumptions (Botkin *et al.* 1972; Bugmann 2001), *i.e.* (1) the forest stand is abstracted as a composite of many small patches of land (800 m²), each patch having its own dynamics, (2) patches are horizontally homogeneous, *i.e.* tree position within a patch is not considered, (3) the leaves of each tree are located in an indefinitely thin layer at the top of the stem and (4) successional processes can be described on each of those patches separately, *i.e.* there are no interactions between patches. From these assumptions, the model follows the standard approach of gap models: the establishment, growth, and mortality of trees on the multiple forest patches are simulated, deriving stand properties at a larger spatial extent by averaging the properties simulated at the patch scale (Bugmann 2001), and considering abiotic and biotic limitations to establishment and growth (specifically, growing degree-days, soil moisture and nitrogen status as well as light availability at the height of the tree crown, *i.e.* the outcome of inter- and intra-specific competition). A detailed description of the model is available in several publications (Bugmann 1996; Bugmann & Solomon 2000; Didion *et al.* 2009); species parameters are provided in Table S1 (Appendix S1).

Exploring the diversity–stability relationship with a forest succession model differs from previous modelling studies (Yachi & Loreau 1999; Lehman & Tilman 2000) because we used a multi-trait model that takes into account the observed trade-offs in species biology (*e.g.* growth/shade tolerance). Indeed, FORCLIM parameters are mostly derived from observable and measured traits. Note that other competitive processes that are likely to affect community composition and ecosystem functioning, *e.g.* competition for nutrients, are not explicitly taken into account in our simulations. This work is thus a theoretical study testing how diversity can stabilise communities driven by competition for light, which undoubtedly is a key process of forest community dynamics.

Similarly to Morin *et al.* (2011), we performed simulations with FORCLIM to conduct virtual experiments during 2000 years, with various diversities (1–30 European species) at 11 sites in central Europe, distributed along a strong climatic gradient (see Appendix S1–S2 for a description of the simulations and site conditions). To be sure that the simulated forests were at pseudo-equilibrium, we considered the last 1000 years. For each simulation, we collected the realised species richness (*i.e.* final richness after 2000 years), relative abundance and mean productivity of each species. Mean

productivity values were calculated by averaging the yearly productivity (newly accumulated biomass) of 10 years sampled every 100-year to minimise temporal autocorrelation (*i.e.* years 1100, 1200, ..., 2000).

Effect of biodiversity on the predictability of productivity

To test whether the predictability of forest productivity increased with increasing species richness (*SR*), we calculated the coefficient of variation in mean productivity across simulated forests with the same species richness (CV_{af}). If CV_{af} decreases, predictability increases. To go beyond species richness, and to explore the possible functional role of diversity in promoting stability of productivity, we used a continuous functional diversity index: functional dispersion ($FDis$). This index is preferable over other functional diversity indices because it is a multi-traits index and is mathematically independent of *SR* (Laliberté & Legendre 2010). $FDis$ values were calculated for all simulated forests, using all FORCLIM species parameters.

We tested whether CV_{af} decreased with realised *SR* and $FDis$ using simple linear models, both across sites and for each site separately. CV_{af} data were log-transformed for the analyses. Note that $FDis$ could only be calculated for communities with $SR > 2$.

Effect of biodiversity on temporal stability

Temporal stability (*TS*) was quantified using a classically accepted indicator (Lehman & Tilman 2000): $TS = \mu/\sigma$, where μ and σ are respectively the mean and the standard deviation of the yearly productivity of the 10 years sampled every 100-year. We tested whether *TS* at the community level increased with realised *SR* and with $FDis$, using a simple linear model, both across sites and for each site separately.

We also evaluated whether the stability at the species level decreased with *SR*, using a simple linear model of the averaged $TS_{species}$ across all species of the community against realised *SR*. *TS* values were log-transformed.

Relative importance of mechanisms involved in temporal stability

Following Loreau & de Mazancourt (2013), we calculated three variables from the simulations to test for the relative involvement of the underlying processes driving temporal stability: (1) asynchrony in species responses to environmental fluctuations, (2) asynchrony in species dynamics independent of environmental fluctuations and (3) net biodiversity effect on productivity (*i.e.* a proxy quantifying the reduced competition due to interspecific interactions relative to intraspecific interactions).

The net biodiversity effect (ΔY) was calculated in communities with more than one species at the end of the simulation, as the difference between the simulated productivity of a multi-species forest and its expected productivity (Loreau & Hector 2001; Morin *et al.* 2011, and for details see Appendix S2).

It was not possible to directly and independently separate the asynchrony in species responses to environmental fluctuations and the asynchrony in species dynamics (which in this case

reflects species responses to competition for light and small disturbances independent of environmental fluctuations) from the model outputs, as both act simultaneously. The community synchrony in species productivity can be assessed through various metrics (see Appendix S3). Here we used Loreau & de Mazancourt's (2008):

$$\varphi_C = \frac{\sigma_C^2}{(\sum_{i=1}^n \sigma_i)^2}$$

where σ_C^2 is the variance in productivity at the community level, and σ_i is the standard deviation in productivity of species i in a community with n species. φ_C is bounded by zero and one. Then, following de Mazancourt *et al.* (2013), we used the simulations of monospecific forests to assess the synchrony in species responses to environmental fluctuations (φ_E). All simulations performed for one site use the same climate time series, which allows for calculating φ_E by comparing the response of monospecific forests to fluctuations in climate (Appendix S2). Finally, we assessed the synchrony in species dynamics independent of environmental fluctuations (φ_D) by fitting a linear model between φ_C and φ_E , and using its residuals as a proxy for φ_D . It is important to acknowledge that we used both φ_E and φ_D in the analyses (*i.e.* synchrony measures), and thus caution should be taken in the interpretation as we actually discuss the role of asynchrony.

Analyses

Linear models – We fitted linear models of ΔY , φ_D and φ_E separately against SR . Then we fitted multiple regression models of TS against ΔY , φ_D and φ_E to quantify the relative importance of these effects in driving the stability of the communities, for each site. Normality of the residuals was checked using Q–Q plots.

Structural Equation Modeling (SEM) – To go further in understanding the role of the three putative drivers of stability across all sites, we used SEM because this method can deal with correlated explanatory variables and highlights causal links. To understand what facets of functional diversity are involved in enhancing stability, we explored whether the mean and variance of some key traits in the communities were significantly important to explain how functional diversity affects TS . We thus used community-weighted means (CWM , Diaz *et al.* 2007) and community-weighted variances (CWV , Sonnier *et al.* 2010) of three traits (maximum height, growth rate and shade tolerance) as supplementary biotic drivers (see Appendix S2 for more details).

RESULTS

Biodiversity increased the predictability of forest productivity

CV_{af} decreased strongly with realised species richness (Fig. 1-a) and functional trait diversity (Fig. 1-b) across sites. These effects were corroborated at the site level for the vast majority of the 11 sites, with the exception of one and three sites for realised species richness and functional diversity respectively (Table S3). Thus, the productivity of simulated forests is more

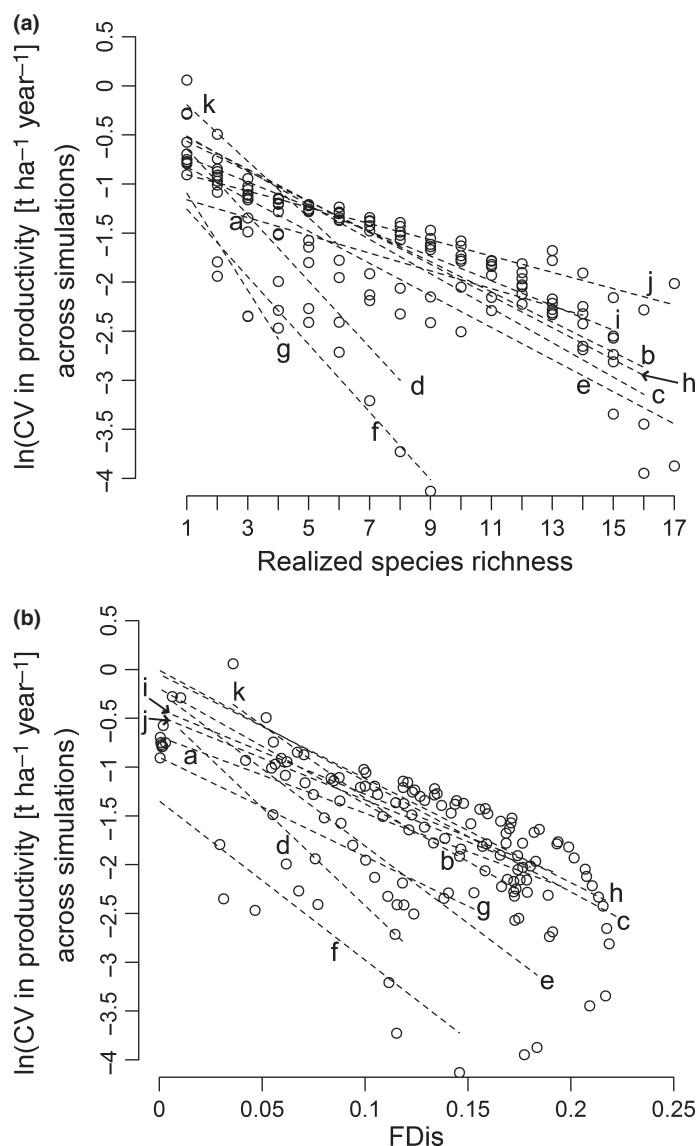


Figure 1 Predictability of forest productivity across simulated forests decreases with increasing species richness and functional diversity. (a) CV of productivity across simulated forests with same realised SR (at the end of the simulation) against species richness; $n = 135\ 115$. CV of simulated productivity were log-transformed. Slope_{all sites} = -0.020 (SE ± 0.001); $r^2_{\text{all sites}} = 0.52$; $F_{1,134} = 133.3$, $P < 0.001$ (model details shown in Table 1). (b) CV of productivity across simulated forests with same SR (at the end of the simulation) against mean functional dispersion ($FDis$) ($FDis$ values are averaged for each realised SR value); $n = 135\ 115$. CV of simulated productivity were log-transformed. Dashed lines represent the regression lines per site (model details shown in Table 1). Slope_{all sites} = -1.90 (SE ± 0.04); $r^2_{\text{all sites}} = 0.38$; $F_{1,134} = 127.0$, $P < 0.001$. Slope values in Table S3. Sites: (a)-Adelboden; (b)-Basel; (c)-Bern; (d)-Bever; (e)-Cottbus; (f)-Davos; (g)-Grande Dixence; (h)-Huttwil; (i)-Schaffhausen; (j)-Schwerin; (k)-Sion.

predictable with increasing SR and increasing functional diversity.

Effect of biodiversity on temporal stability

The temporal stability of forest productivity increased significantly with realised SR (Fig. 2-a, slope = 0.061 [CI: 0.060 –

0.062], $F_{1,135114} = 8501$, $P < 0.001$) and FD is (Fig. 2-b, slope = 0.210 [CI: 0.207–0.213], $F_{1,121924} = 5668$, $P < 0.001$) across sites. Thus, stability increases by 6.29% on average for each species added. These effects are conserved at the site level for all sites for realised SR , with all slopes being signifi-

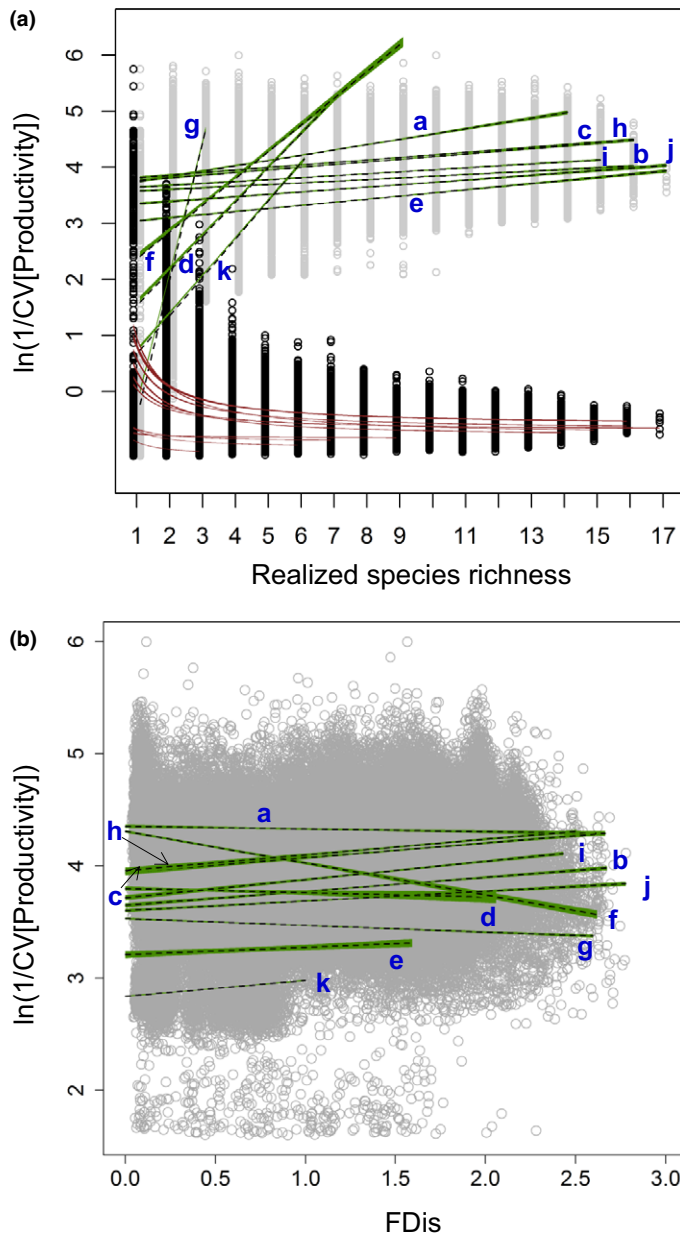


Figure 2 Temporal stability of forest productivity against increasing species richness and functional diversity. (a) Ecosystem temporal stability of productivity (TS) and average species temporal stability against realised species richness. Grey open circles: community TS ($n = 135\ 115$); regression lines (dashed lines) and its 95% confidence interval (green) are shown for each site. TS data have been log-transformed. Black open circles: species temporal stability ($TS_{species}$) averaged for each simulation ($n = 135\ 115$); regression curve (dashed lines) and 95% confidence interval (red) are based on a fit of $\ln(TS_{species})$ against SR_{site}^i for each site. Slope and b_{site} values in Table S4. (b) Community temporal stability of productivity against FD_{is} for each site ($n = 121\ 925$). Regression lines (dashed lines) and its 95% confidence interval (green) are shown for each site. Slope values in Table S5. Site correspondence (letters) as in Figure 1.

cantly positive (Fig. 2-a, Table S4). For functional diversity, the relationship is significantly positive for only seven sites (Fig. 2-b, Table S4). Thus, the temporal stability in forest productivity is more consistent with increasing species richness, while its dependency on functional diversity varies across sites.

Regarding the average temporal stability at the species level, the simulations show a decreasing trend with increasing species richness for each site (Fig. 2-a and Table S5). These results thus confirm that SR can have a stabilising effect at the community level, but a destabilising effect at the species level.

Relative importance of mechanisms involved in temporal stability

Relationships with species richness

First we verified that ΔY , φ_D and φ_E were all related to species richness. These results show that ΔY was positively related to SR (as shown in Morin *et al.* 2011), while the relationship was significantly negative for φ_D and φ_E for each site (Table S6). Thus, the net biodiversity effect, the asynchrony in species responses to environmental fluctuations, and the asynchrony in species dynamics independent of environmental fluctuations all increase with increasing SR .

Relationships with temporal stability

Multiple regressions at each site showed that the variance explained in TS by the three drivers ranged between 17 and 43% (Table 1). For each site, φ_D was a significant explanatory variable at all sites, while this was the case at 10 and 9 sites for φ_E and ΔY respectively. φ_D was the most important driver of TS at all sites, as it represented more than 74% of the explained variance at all sites but one (61% in Sion). φ_D was always negatively related to TS (Table 1 and Fig. 3), while this was the case at only seven sites for φ_E , while ΔY was positively related to TS at five sites. These results thus suggest that the asynchrony in species dynamics independent of environmental fluctuations is the strongest driver promoting temporal stability of ecosystem productivity.

The performance of the SEM is acceptable [CFI = 0.94, Fig. 4; a model is regarded as acceptable if its CFI exceeds 0.93 (Byrne 1994)], with a strong explanatory power on TS ($r^2 = 0.54$) regarding the large number of simulations ($n = 120\ 908$). To build this SEM we started from the full model, but we had to remove the variables with weak effects to obtain a non-rejected model according to the CFI. The selected model only includes CWV and CWM in shade tolerance. This analysis confirms that asynchrony in species dynamics independent of environmental fluctuations is the strongest driver of TS , with a positive effect (as φ_D is strongly and negatively related to TS). SR directly affects TS negatively in the model, which means that the positive effect of SR on TS previously shown in this study actually relies on the indirect effect of SR on functional diversity, and especially on the variance in shade tolerance. CWV and CWM in shade tolerance are the only diversity variables affecting φ_D , with negative effects, which means that asynchrony in species dynamics increases with increasing variance of shade tolerance in the community.

Table 1 Multiple regression model temporal stability against φ_D , φ_E and ΔY , for each site.

Sites	φ_D		φ_E		ΔY		Expl. Var.			
	Est.	SE	Est.	SE	Est.	SE	r^2	φ_D	φ_E	ΔY
Adelboden	-1.99 ***	0.03	-0.23 ***	0.02	-0.11 ***	0.03	0.30	0.30	0.01	0.00
Basel	-1.30 ***	0.02	0.06 ***	0.01	0.09 ***	0.02	0.23	0.23	0.00	0.00
Bern	-2.11 ***	0.03	-0.21 ***	0.02	0.07 .	0.04	0.26	0.25	0.01	0.00
BeverS	-1.94 ***	0.03	0.26 ***	0.02	-0.17 ***	0.02	0.41	0.39	0.01	0.00
Cottbus	-0.64 ***	0.01	-0.20 ***	0.01	-0.22 ***	0.01	0.26	0.19	0.02	0.05
Davos	-2.00 ***	0.03	0.61 ***	0.04	0.13 **	0.04	0.42	0.38	0.03	0.00
GrandeDixence	-1.91 ***	0.04	-0.68 ***	0.04	-1.78 ***	0.18	0.30	0.27	0.02	0.01
Huttwil	-2.20 ***	0.03	-0.13 ***	0.02	0.22 ***	0.05	0.29	0.28	0.01	0.00
Schaffhausen	-1.77 ***	0.03	-0.08 ***	0.01	-0.12 ***	0.03	0.31	0.31	0.00	0.00
Schwerin	-1.02 ***	0.02	0.04 **	0.01	0.14 ***	0.02	0.17	0.17	0.00	0.00
Sion	-0.70 ***	0.01	-1.62 ***	0.03	-1.00 ***	0.03	0.43	0.27	0.06	0.11

The three last columns indicate the percentage of variance explained by each variable in the models. *Est.*: coefficient value; *SE*: standard error. (***) significance at the 0.0001 threshold; (**): significance at the 0.001 threshold; (*): significance at the 0.01 threshold; (.): significance at the 0.1 threshold.

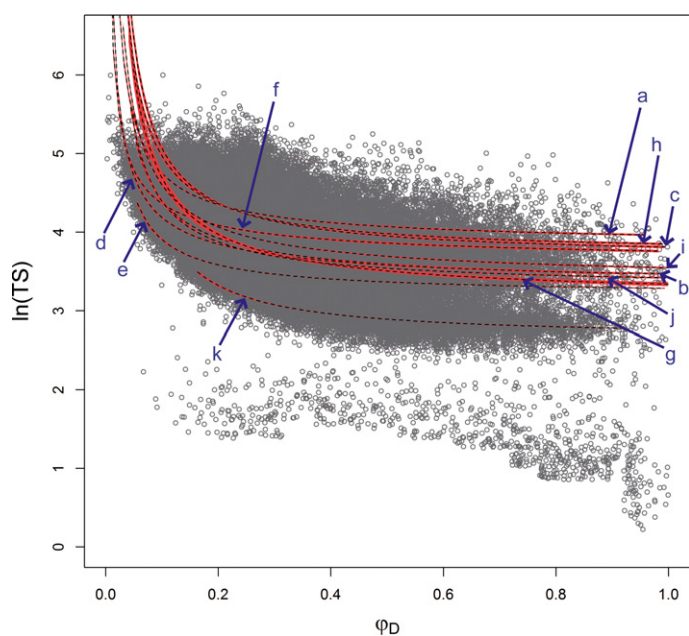


Figure 3 Temporal stability of forest productivity decreases with φ_D , thus increases with asynchrony in species dynamics independently to environmental fluctuations. Data of temporal stability are log-transformed. Regression curves (dashed lines) and its 95% confidence interval (red) are shown for each site, they are based on a fit of $\ln(TS)$ against $\varphi_D^{a_{site}}$ for each site. a_{site} values are shown in Table S8 in Appendix S1. $n = 120\,906$. Site correspondence as in Figure 1.

Based on these results, we aimed to go further to better understand how asynchrony in species dynamics may enhance temporal stability. Three main factors should be involved in φ_D : synchrony in species response to competition (*i.e.* response to shading), synchrony in species response to the creation of a forest gap (*i.e.* change in the light regime) and demographic stochasticity. Synchrony in species response to competition and in species response to gaps are closely related as they both depend on how growth is affected by light conditions, and thus these two effects cannot be separated, hereaf-

ter named φ_{CG} Demographic stochasticity may also be involved in φ_D , as a change over time in the number of trees in a community necessarily affects community productivity over time. Thus, we carried out an additional analysis, testing whether the effect of φ_D on TS was due to demographic stochasticity or φ_{CG} (see Appendix S3 for details). The results showed that asynchrony in species response to competition and to gaps was the main driver of the effect of species diversity on temporal stability. We further showed that φ_{CG} is significantly and negatively related to both mean LAI and CV_{LAI} of the simulated forests for all sites (Appendix S3 and Table S7), suggesting that a greater asynchrony in species response to competition and to gaps leads to a greater cover of leaf layers and to stronger stability in this cover over time.

DISCUSSION

Our study yielded three main results, as the simulation experiments showed that (1) increasing diversity (both species richness and functional diversity) increases the predictability of forest productivity, (2) temporal stability increases with increasing species richness and (3) this is mostly due to the asynchrony between species-specific responses to competition for light in mixed forests.

Diversity enhances the predictability of forest productivity

The increased predictability can be simply related to the saturating response of ecosystem properties to increasing diversity shown in grassland experiments (Cardinale *et al.* 2009) and confirmed by virtual forest experiments (Morin *et al.* 2011). The greater the diversity, the larger the chance to sample productive species and/or positively interacting species, and thus the larger the probability to reach high levels of productivity. However, because the maximum productivity that is achievable has an upper limit, species-rich communities reach more similar productivity than species-poor ones. Nevertheless, this finding shows that communities with more species and larger functional diversity are more likely to reach a predictable pro-

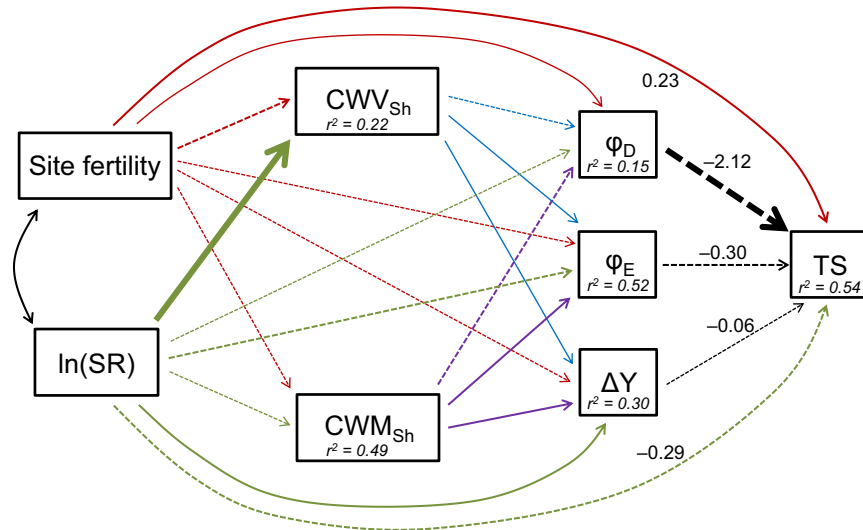


Figure 4 Results of the SEM analysis for temporal stability. Arrows represent causal paths. Solid and dashed arrows correspond to positive and negative respectively. All paths shown are significant, and the thickness of the arrows is proportional to the strength of the related effect. For the sake of clarity, only coefficients for the paths linking *TS* are shown (coefficients values are presented in Table S9 in Appendix S1) and error paths are not presented. The part of variance explained for each dependent variable in the model is shown inside their respective box. Model's CFI = 0.94. *SR*: species richness; *Site Fertility*: maximum productivity simulated in the site; CWM_{Sh} : community-weighted mean of shade tolerance of species in the community; CWV_{Sh} : community-weighted variance of shade tolerance of species in the community; ϕ_D : synchrony in species' demographic response to competition; ϕ_E : species' response to environmental fluctuations; ΔY : net biodiversity effect; *TS*: temporal stability.

ductivity, while uncertainty on the level of productivity is higher in species-poor forests.

Diversity has a stabilising impact at the community level but a destabilising impact at the species level

The strong positive diversity–stability relationship that we found in the simulated forests is consistent with short-term experimental results from herbaceous communities (Hooper *et al.* 2005; Tilman *et al.* 2006; Isbell *et al.* 2009). As for the relationship between species richness and mean productivity (Morin *et al.* 2011), we found large variability in the range of this positive effect across sites, because the wide range of abiotic conditions affects the number of species that can persist in one site as well as the maximum level of productivity reachable. Nevertheless, the trend remains valid within each site. Our results also showed that diversity promotes instability at the species level, confirming theoretical expectations (Ives & Carpenter 2007; Loreau & de Mazancourt 2013) and experimental findings (Tilman *et al.* 2006). Although it would be beneficial to test and corroborate the pattern found at the community level in natural or experimental forests (Scherer-Lorenzen *et al.* 2007; Potvin & Dutilleul 2009), the present finding suggests that diversity promotes stability of ecosystem processes also in the long term, and that such a pattern is not valid for grasslands only (Duffy 2009).

The stabilising impact of diversity depends on asynchrony in species dynamics and environmental fluctuations

Our results support the biodiversity insurance hypothesis, which has been invoked to explain the positive impact of

diversity on temporal stability of ecosystem processes (Naeem & Li 1997), stating that many species provide a higher likelihood that some will maintain functioning even if others fail (Yachi & Loreau 1999). Similar to Yachi & Loreau (1999), our findings highlight the role of asynchrony of species responses to environmental fluctuations and, to a lesser extent, overyielding in stabilising community productivity. However, the pattern we found is mainly due to a different process than the ones proposed by Yachi & Loreau (1999). In our study, diversity enhances stability through compensatory dynamics between species, mostly caused by the asynchrony in species dynamics, independent of environmental fluctuations. Thus, the stabilising effect promoted by diversity arises from interactions between species rather than from their different responses to environmental conditions.

It is noticeable that our simulations show that diversity has a strong effect on both mean productivity (see Morin *et al.* 2011) and temporal stability (the present study). As mentioned above, the diversity effect on mean productivity was strongly associated with a high overyielding effect. However, overyielding was found to drive temporal stability only weakly (Fig. 3b). Thus, the effects of diversity on productivity and on stability appear to be independent, as they are not driven by the same mechanism, which is in line with a recent meta-analysis on experimental studies (Cardinale *et al.* 2013).

Furthermore, temporal asynchrony is not implemented *a priori* in FORCLIM, it is a property that emerges from the model simulations (Grimm *et al.* 2005). These results were not predictable *a priori* because negative feedback loops play a major role in forest successions and are therefore explicitly considered in gap models like FORCLIM. A former paper showed that the positive impact of diversity on productivity

can arise from such negative feedback loops, involving counter-intuitive processes, such as increasing mortality rates with increasing diversity (Morin *et al.* 2011). As the model reflects long-term dynamics based on small-scale disturbances triggered by tree mortality and spatial variability in light conditions, our analyses elucidated that such dynamics lead to increasing stability with increasing asynchrony between species dynamics.

The limits of these findings should, however, not be ignored. First, the model concentrates on competition for light alone, mediated by soil and climatic conditions (Morin *et al.* 2011), but it could be expanded to disentangle the effects of competition for several resources (water, nutrients...). Our results showed that site conditions affect community stability, although not as strongly as in grasslands (Leps 2004). Second, the simulation results featured weak interannual variability at the site level, and we should thus be cautious regarding predictions (Fowler *et al.* 2012). Another limitation lies in the difficulty to directly test our results against field data, as comparative study plots of different diversity at the same site have rarely been established, or are necessarily spanning a lower range of tree diversity (Baeten *et al.* 2013). Still, the strength of the trend evident from our findings calls for a test by proper experiments or field sampling (*e.g.* time series of forest inventories).

Underlying mechanisms from the model's principles

We highlighted the importance of diversity in some species traits to promote asynchrony in species dynamics, especially variance in shade tolerance, as key causal processes underlying temporal stability of forest productivity. As competition for light is the only competitive process at play in the model, this finding could be interpreted as follows. In natural forests, dynamics are driven by small disturbances (death of trees), creating gaps in the canopy and inducing strong changes of light availability. A community with species having contrasted strategies regarding shade tolerance is thus more likely to include coexisting species showing a greater asynchrony in species response to changes in local light conditions.

However, how may asynchrony in species response to these small disturbances enhance temporal stability? While demographic stochasticity plays a minor role, our results highlight two closely related processes: asynchrony in species response to competition for light *and* to changes in the light regime (*i.e.* creation of a gap). In fact, in communities showing great asynchrony in these properties, we can expect that any gap is filled more quickly than in communities with weaker asynchrony, because of a stronger ability to respond fast to local disturbances while maintaining long-term productivity, as previously shown (Morin *et al.* 2011). Shade-intolerant species usually grow fast and have a fast response to forest gaps (Bazzaz 1979), but they lead to unstable ecosystem properties if they grow alone, because their dynamics strongly depend on disturbances. Shade-tolerant species alone grow too slowly to respond fast enough to forest gaps. Thus, only a mixture of species with various light foraging strategies can exhibit both fast responses to small disturbances *and* greater stability. We

further showed that forests with larger asynchrony in species dynamics occupy on average more canopy layers with less variability over time. Thus, a greater asynchrony in species responses to changes in the light regime allows forest communities to respond faster to small canopy gaps *and* to have larger and more stable LAI, which results in a greater temporal stability in productivity.

CONCLUSION

Linking theoretical and empirical work is necessary to better understand the effect of biodiversity on the stability of ecosystem functioning (Griffin *et al.* 2009). The present study was based on virtual experiments using a well-established and thoroughly field-validated model, constituting significant progress in this direction. Our results showed that variability in productivity between forest stands decreases as species richness and functional diversity increase; temporal stability increases with increasing diversity due to compensatory dynamics across species; and this pattern is mainly driven by the asynchrony of species dynamics. Recent theoretical works have suggested that asynchrony in species responses may either stabilise or destabilise the biomass production of an ecosystem (Fowler *et al.* 2012; Loreau & de Mazancourt 2013). Here, we illustrated with a process-based model based on competition for light that diversity strongly affects temporal stability through asynchrony in species responses to small disturbances, leading to an optimisation of canopy occupancy by coexisting species. These findings represent an important step towards a better understanding of the role of asynchrony in diversity–stability relationships.

ACKNOWLEDGEMENTS

We thank H. Jactel, G. Kunstler, M. Loreau and F. Valladares for helpful discussions and comments on earlier versions of the manuscript, and O. Gimenez and P. Garcia Palacios for their statistical advice on SEMs. We also thank T. Dray, A. Rossberg, and D. S. Srivastava, as well as two anonymous referees for their constructive comments and suggestions on previous version of the manuscript. This study was mainly funded by a grant from the EU 7th FP project BACCARA (contract no. 226299) and ETH Zürich, and also benefited from the ANR project BioProFor (contract no. 11-PDOC-030-01) and the Biodiversa project EC21C (contract no. 12-ANR-EBID-0005-01).

AUTHORSHIP

The authors declare no conflict of interest. XM, LF and HB designed the research, XM conducted the research, and XM, LF, CdM, MSL and HB contributed to the analyses and interpretation of the results and wrote the manuscript. All authors contributed substantially to revisions.

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Editor, Marcel Rejmanek
Manuscript received 3 June 2014
First decision made 5 July 2014
Manuscript accepted 15 August 2014