

Species interactions increase the temporal stability of community productivity in *Pinus sylvestris*–*Fagus sylvatica* mixtures across Europe

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Summary

1. There is increasing evidence that species diversity enhances the temporal stability (TS) of community productivity in different ecosystems, although its effect at the population and tree levels seems to be negative or neutral. Asynchrony in species responses to environmental conditions was found to be one of the main drivers of this stabilizing process. However, the effect of species mixing on the stability of productivity, and the relative importance of the associated mechanisms, remain poorly understood in forest communities.

2. We investigated the way mixing species influenced the TS of productivity in *Pinus sylvestris* L. and *Fagus sylvatica* L. forests, and attempted to determine the main drivers among overyielding, asynchrony between species annual growth responses to environmental conditions, and temporal shifts in species interactions. We used a network of 93 experimental plots distributed across Europe

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to compare the TS of basal area growth over a 15-year period (1999–2013) in mixed and monospecific forest stands at different organizational levels, namely the community, population and individual tree levels.

3. Mixed stands showed a higher TS of basal area growth than monospecific stands at the community level, but not at the population or individual tree levels. The TS at the community level was related to asynchrony between species growth in mixtures, but not to overyielding nor to asynchrony between species growth in monospecific stands. Temporal shifts in species interactions were also related to asynchrony and to the mixing effect on the TS.

4. Synthesis. Our findings confirm that species mixing can stabilize productivity at the community level, whereas there is a neutral or negative effect on stability at the population and individual tree levels. The contrasting findings regarding the relationships between the temporal stability and asynchrony in species growth in mixed and monospecific stands suggest that the main driver in the stabilizing process may be the temporal niche complementarity between species rather than differences in species' intrinsic responses to environmental conditions.

Key-words: asynchrony, mixed-species forests, niche complementarity, organizational levels, overyielding, plant–plant interactions, temporal variability

Introduction

Mixed-species stands may provide many forest functions and services more effectively than monocultures (Gamfeldt *et al.* 2013; van der Plas *et al.* 2016). The often higher level and stability of productivity in mixed forests is of interest for many functions and services, as well as being a precondition for the promotion of mixtures in forestry practice. There is strong evidence that mixed-species stands often produce greater yields than monocultures (Piotto 2008; Paquette & Messier 2011; Vilà *et al.* 2013; Pretzsch *et al.* 2015; Liang *et al.* 2016) and improve the stability of productivity in various ways (Pretzsch, Schütze & Uhl 2013; Jucker *et al.* 2014; de Dios-García, Pardos & Calama 2015; Metz *et al.* 2016). However, some studies with opposite findings in productivity (Chen *et al.* 2003; Cavard *et al.* 2010) and stability (Grosiord *et al.* 2014; Merlin *et al.* 2015) highlight the importance of considering the complementarity of the corresponding species assemblages (Toigo *et al.* 2015) as well as the underlying site conditions with their specific growth limiting factors (Forrester 2014).

The term 'stability' in ecosystems encompasses several concepts, such as resistance, resilience or temporal stability (TS) of productivity, which address the diversity–stability relationship (McCann 2000; Ives & Carpenter 2007). The temporal variability is usually measured by the coefficient of variation or its inverse, i.e. the TS, which depends on the mean and standard deviation (SD) (Tilman, Lehman & Bristow 1998). Beyond the statistical theory which predicts a rise in the community stability when species diversity increases (McCann 2000), i.e. the averaging effect, different biological mechanisms have been identified as possible causes of increasing the TS with regard to plant or tree species diversity. These include overyielding, species asynchrony and species interactions (Hector *et al.* 2010; Loreau & de Mazancourt 2013; Blüthgen *et al.* 2016). Overyielding means

higher productivity in mixtures than a weighted average of the corresponding monospecific systems caused by species interactions, which may lead to a stabilizing effect by a higher mean if the SD remains constant (Tilman 1999). Species asynchrony occurs when the temporal responses of the species to environmental variations are not perfectly positively correlated. This mechanism has been reported as a key factor in the TS (Loreau & deMazancourt 2008; Hector *et al.* 2010), in accordance with the insurance hypothesis (Yachi & Loreau 1999). Differences in species' intrinsic response to environmental fluctuations may influence species asynchrony in more diverse communities, but species interactions can also trigger species asynchrony by compensatory dynamics between species (Tilman, Lehman & Bristow 1998; Morin *et al.* 2014). Temporal shifts in species interactions were also found to reduce the temporal variability in mixed forests communities (del Río, Schütze & Pretzsch 2014). The above-mentioned species interactions may involve the TS as a consequence of their effect on overyielding, but at the same time overyielding may be linked to species asynchrony (Allan *et al.* 2011). These direct and indirect relationships make it difficult to disentangle the key mechanisms and therefore the relative importance of the different mechanisms on the diversity–stability relationship is still poorly understood (Loreau & de Mazancourt 2013).

In general, diversity has been found to have a stabilizing effect on productivity at the community level, but a destabilizing effect at the population levels by increasing competitive interactions (Hector *et al.* 2010; Gross *et al.* 2014). However, contrasting results have been obtained at the population level (Jiang & Pu 2009), even among the few studies undertaken in forest communities (Jucker *et al.* 2014; Morin *et al.* 2014). This trade-off between the effects at different organizational levels might be crucial in ecosystems with few species, where the species-specific dynamic can be of major importance, as in many European temperate mixed forests comprising only

two or three tree species. Contrasting diversity–stability relationships might also be expected along ecological gradients, with the relative importance of different mechanisms varying along the gradients (Hallett *et al.* 2014; Xu *et al.* 2015).

The number of studies concerning the relationship between diversity and TS of productivity based on empirical data in forests (DeClerk, Barbour & Sawyer 2006; Jucker *et al.* 2014) is far fewer than in grasslands communities. This is due to the inherent arduousness involved in carrying out experiments with tree species, due to their long life span, as well as the difficulties of conducting observational studies in natural ecosystems, where many uncontrollable factors interact. In this study, we focus on two tree species, *Pinus sylvestris* L. and *Fagus sylvatica* L., growing in monospecific and mixed stands across a large range of their distribution. This design allowed us to infer the general effect of this admixture on the TS of productivity while considering the large spatial variability in site conditions across Europe. This mixture was selected because it includes a combination of species with different functional traits which can trigger species complementarity, including an early and a late-successional species, a light-demanding as opposed to a shade-tolerant species, and a conifer with a broad-leaved species. The mixture between *P. sylvestris* and *F. sylvatica* was found to show significant mixing effects in terms of productivity and structural heterogeneity (Pretzsch *et al.* 2015, 2016). It may serve as a model system for other widespread species combinations of comparable functionally dissimilar species.

Our main objective was therefore to explore whether mixing species of contrasting traits increases the TS of productivity at different organizational levels and, if so, to elucidate the main underlying mechanisms in order to better understand the interspecific dynamics of the *P. sylvestris*–*F. sylvatica* and comparable mixtures. In our two monospecific and mixed stands, the community, population and individual levels are represented by the stand, species and tree levels, respectively. The main hypotheses were that: (i) productivity varies less through time in mixed than in monospecific stands at the community level but not at the population and individual tree levels; (ii) in this model mixture, the dynamics of species interactions is one of the drivers that stabilizes productivity due to the dissimilar functional traits of these species; and (iii) the spatial variation among sites in terms of the mixing effect on the TS of productivity can be partially explained by site environmental conditions.

Materials and methods

FIELD DATA AND STUDY DESIGN

The study data came from a transect of plots in mixed and monospecific forest stands of *P. sylvestris* (Scots pine) and *F. sylvatica* (European beech) located along an environmental gradient. The transect was established voluntarily and nationally funded by members of the COST Action FP1206 EuMIXFOR (see www.mixedforests.eu). The study design was based on the ‘triplet’ concept (Pretzsch *et al.* 2014), i.e. at each location, three plots were established, one in

a mixed-species stand and two in the respective monocultures; the three plots being located in similar site conditions (soil and topographic conditions) in order to allow meaningful comparisons between mixtures and monocultures. A total of 31 triplets (93 plots) were set up across the main distribution area of this mixture in Europe (Fig. 1), covering a large environmental gradient, mainly determined by water supply. Climate data were collected from all available meteorological stations in the proximity of each triplet (see Table S1, Supporting Information for more detailed information about climate and site conditions).

The three plots for each triplet were installed in even-aged, fully stocked forest stands of similar age in which thinning treatments had not been recently applied (for details see Table S2 and Pretzsch *et al.* 2015, 2016). The mixed plots represent tree-wise mixtures with species proportions that range from 27% to 73% of pine, although in most of them the proportion is around 50% (in terms of basal area). Plots are rectangular varying in size from 0.02 to 1.30 ha, with larger variation among triplets than within triplets (Table S1). On each plot, the tree species, tree diameter, total height and height to the crown base were recorded for all trees. In a subsample of 20 trees per plot and species, the two increment cores were extracted at a stem height of 1.30 m for a tree ring analysis. Annual growth series were cross-dated and the arithmetic means of the annual ring widths of the two cores were used for further analysis. A description of the main stand characteristics is provided in Table S2.

PRODUCTIVITY DATA AT DIFFERENT ORGANIZATIONAL LEVELS

Community level

In contrast to other studies which focused on above-ground biomass growth when studying diversity–productivity and/or diversity–stability relationships in forests (Paquette & Messier 2011; Jucker *et al.* 2014, 2016), we used stand basal area growth per hectare (BAI) as a proxy to represent community productivity. Calculation of stand biomass growth would have required height–diameter functions and tree biomass allometric functions for all sites. However, it is well known that such calculations could lead to additional uncertainty, especially in mixed stands (Toigo *et al.* 2015) as the respective functions are commonly derived from monospecific stands data. Using these functions may have caused biased estimations of biomass growth as mixing tree species can modify tree allometry (Pretzsch 2014; Forrester *et al.* 2016) as well as between-tree growth partitioning (Binkley *et al.* 2003; Pretzsch & Schütze 2014), suggesting the need of specific functions for mixtures (Forrester & Pretzsch 2015; del Río *et al.* 2016).

Our study focused on the TS and overyielding during the 15-year period prior to the inventory (1999–2013). This period was chosen because it covers sufficient years to provide meaningful information on temporal variability in growth, while avoiding bias from tree mortality or tree removal which could have interfered with the results because mixing may change species-specific mortality rates (Zhao *et al.* 2006; Condés & del Río 2015).

Stand basal area was calculated as the sum of the cross-sectional area (at 1.30 m above-ground level) of all the trees measured at a given time. Stand basal area increments per year were determined based on cored trees and non-cored trees. In the case of sampled trees, we used tree ring series to reconstruct tree diameters over bark for each of the 15 years of the study period. To estimate the diameter increments of non-cored trees, we fitted diameter increment functions for each plot and species per year, based on diameter increments and tree diameters of cored trees

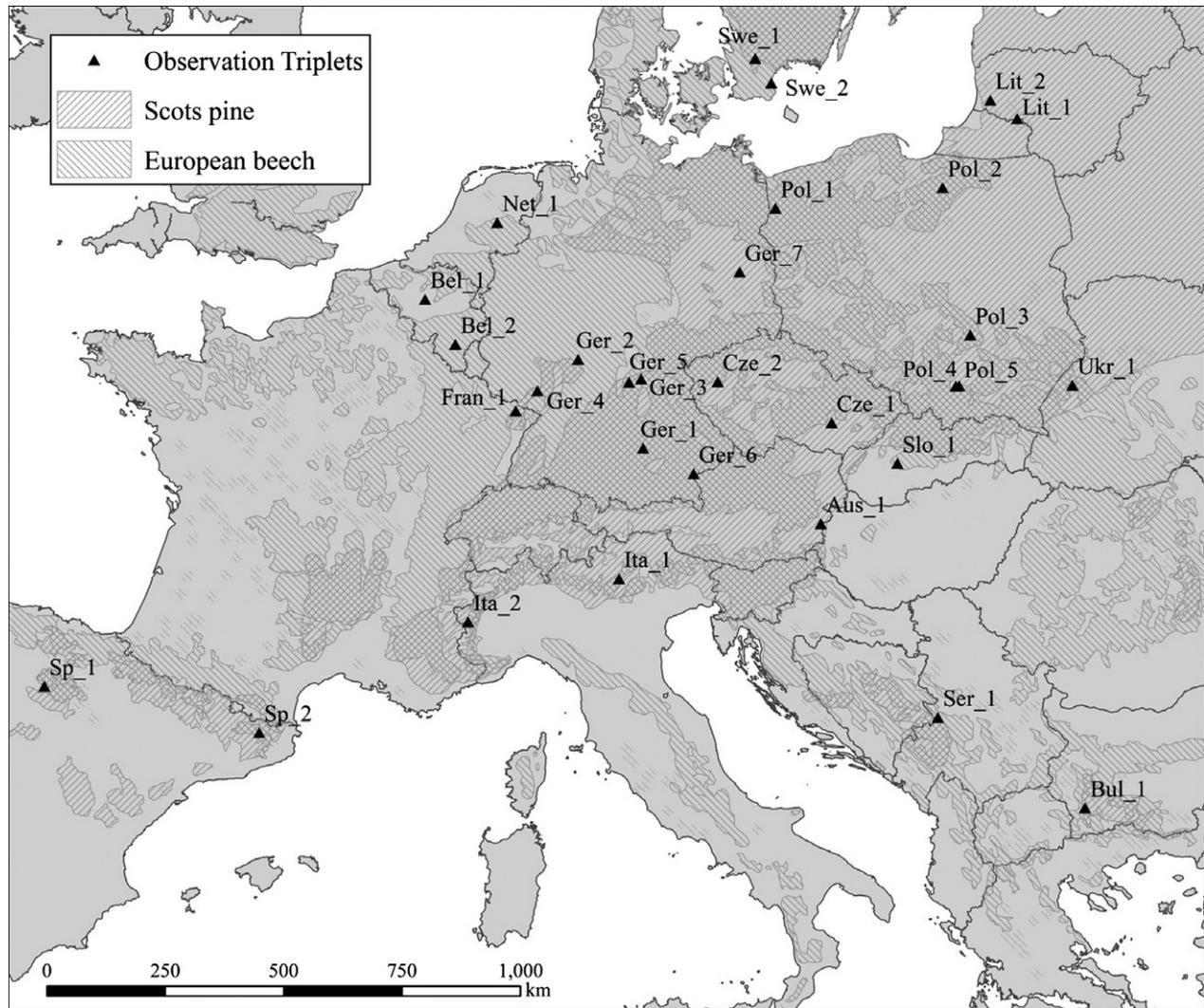


Fig. 1. Location of the 31 triplets of monospecific and mixed stands of Scots pine and European beech over the distribution of *Pinus sylvestris* and *Fagus sylvatica* according to EUFORGEN (<http://www.euforgen.org/distribution-maps/>).

[31 triplets \times 4 (two tree species in mixed and monospecific stand) \times 15 years = 1980 functions for the studied period 1999–2013]. We used log–log models ($\ln(id) = a_0 + a_1 \times \ln(d)$), where id was the tree diameter increment for that year (cm year^{-1}) and d was the tree diameter at breast height (cm).

Population level

To study the productivity at the population level, we additionally calculated the annual basal area increment (BAI_t) per species in the mixed plots. In order to compare species behaviour in mixed and monospecific stands, we scaled up the species-specific basal area increment series in mixed stands to 1 ha using species basal area proportions. As species proportion can change from 1 year to another due to the different annual basal area increments between species, we calculated species proportions per year using the estimated annual basal area per species.

Individual tree level

At the individual tree level, we used the measured tree ring widths from cored trees transformed to the individual tree basal area

increments. As the tree growth response to variability in environmental conditions and to intra- and interspecific competition depends on the trees' social status (Martín-Benito *et al.* 2008; Zang, Pretzsch & Rothe 2012; del Río, Condés & Pretzsch 2014), we only used dominant and co-dominant trees (1691 trees) in this study, selected from the diameter and height distributions per species and plot.

DATA EVALUATION AND ANALYSIS

TS at different organizational levels

Temporal stability at the different organizational levels was calculated as the inverse of the coefficient of variation for the 15-year study period, i.e. the ratio of mean basal area increment to its SD. This measure of the temporal variation is often preferred to the coefficient of variation, because the latter decreases with stability and when the stability increases it approaches zero (Lehman & Tilman 2000). Statistics of the mean, SD and TS of the annual basal area increment at the different organizational levels are presented in Table S3.

The effect of mixing species on TS of productivity at the community and population levels was analysed using a mixed linear model including the species composition of the plot as a fixed factor. At the community level, we first compared mixed vs. monospecific stands, and in a second step, we considered species identity of monospecific plots. Data were ln-transformed to reduce heteroscedasticity in residuals.

$$\ln(\text{TS}_{ij}) = (a_0 + a_{0j}) + a_1 \cdot \text{composition} + \epsilon_{ij} \quad \text{eqn 1}$$

where TS_{ij} was the temporal stability of the annual basal area increment for the plot i in the triplet j ; composition was a dummy variable with two levels, mixed and monospecific, or three levels, mixed, monospecific pine and monospecific beech; a_0 and a_1 were parameters to be estimated. We included a random effect (a_{0j}) due to the hierarchical structure of the data to account for possible correlation of the three plots within a triplet. Covariates potentially influencing the TS as species abundance or proportion, climatic attributes (Table S1) and their interaction with species composition were tested. At the tree level, we fitted a similar model but taking also the effect of tree size on TS into account.

In order to study the effect of mixing on the TS at the different organizational levels, we first defined the mixing effect on the TS as the ratio of the TS in mixed stands to the TS in monospecific stands ($\text{TS}_{\text{mixed}}/\text{TS}_{\text{mono}}$), and then we analysed the correlation between the ratios at the community, population and individual tree levels.

Overyielding

The over- or underyielding values per triplet at the community level were estimated using the ratio of productivity (RPP) (Harper 1977), $\text{RPP} = \sum \text{BAI}_{i,\text{mix}}/\text{BAI}_{i,\text{mono}}$, where $\text{BAI}_{i,\text{mix}}$ is the observed basal area increment (i.e. productivity) of species i in the mixed stand and $\text{BAI}_{i,\text{mono}}$ is the basal area of species i in the monospecific stand. $\text{BAI}_{i,\text{mix}}/\text{BAI}_{i,\text{mono}}$ quantified the required land area of monospecific stand to produce the same basal area for species i . If $\text{RPP} > 1$, the mixed stands was more efficient in terms of productivity than the monospecific stands, i.e. there was overyielding; if $\text{RPP} < 1$, there was underyielding (see del Río *et al.* 2016). We estimated the RPP per year and triplet for the 15-year study period and then averaged them per triplet.

To estimate the overyielding at the population level, we used the relative productivity per species (RP_i) (Pretzsch *et al.* 2013; del Río *et al.* 2016), i.e. the ratio of the observed productivity of species i in the mixed stand (up-scaled to one hectare) to the observed productivity of the respective species in the monocultures, $\text{RP}_i = (\text{BAI}_{i,\text{mix}}/m_i)/\text{BAI}_{i,\text{mono}}$, where m_i was the species proportion estimated by the proportion of species i in the stand basal area for a given year. As for RPP, the RP_i ratios were estimated per year and later averaged for the 15 years in order to consider the possible influence of temporal changes on species proportion. We tested whether the mean RPP and RP_i were significantly different from one, i.e. significant over- or underyielding, using a t -Student test. The possible relationship between overyielding and TS at the different organizational levels was assessed through simple linear models. At the community level, we studied the possible influence of RPP on the temporal stability in mixed stands (TS_{mixed}) and on the mixing effect ($\text{TS}_{\text{mixed}}/\text{TS}_{\text{mono}}$). At the population level, we related the RP_i to the mixing effect, i.e. ratio of TS at the population level.

Species asynchrony

Asynchrony in species responses to environmental conditions in mixed stands, hereafter called species asynchrony, was estimated by the coefficient of correlation between the basal area growth series of

the two species growing in mixed stands (r_{mixed}); a value of -1 means complete asynchrony between species' growth responses and $+1$ indicates complete synchrony. This approach was similar to that proposed by Gross *et al.* (2014), although in its simplest version of a mixture composed of only two species. Additionally, we studied the correlation between the basal area increment series of the two species growing in the monospecific stands (r_{mono}), as this correlation might express the differences or the similarity in the dependence of the two species on interannual environmental conditions without the potential effect of species interactions on this dependence, i.e. asynchrony of the species' intrinsic response to environmental fluctuations (Loreau & de Mazancourt 2013). Species asynchrony was estimated at the community level by stand basal area increment series of the two species. At the tree level, species asynchrony was studied by the species-specific mean tree basal area increment series.

We explored the role of species asynchrony in TS in a similar way to that for overyielding, i.e. using linear models for relating TS_{mixed} and the ratios of $\text{TS}_{\text{mixed}}/\text{TS}_{\text{mono}}$ to r_{mixed} and r_{mono} at the different organizational levels. Furthermore, we tested whether there was any relationship between species asynchrony and overyielding.

Temporal shifts in species interactions

To study the interannual variation in species interactions in terms of productivity as a function of annual growing conditions, we used a similar approach to that used in del Río *et al.* (2014). Species interactions were studied through the comparison of the annual productivity in mixed stands ($\text{BAI}_{\text{mixed}}$) to the corresponding reference productivity (BAI_{ref}) assuming that there was no mixing effect, i.e. the two species grow similarly in the mixture and in the monocultures. The reference productivity was calculated as the sum of the productivities of the two species in monospecific stands multiplied by their proportion in the mixed stand ($\text{BAI}_{\text{ref}} = \sum \text{BAI}_i \cdot m_i$) (Pretzsch *et al.* 2013; del Río *et al.* 2016). When the annual basal area increment in the mixed stand was higher than the reference basal area increment, there was a positive species interaction or overyielding; whereas when it was lower, this indicated a negative interaction or underyielding. In this section, the aim was to study the temporal variation in species interactions independently from its net effect or overyielding. Therefore, we standardized the observed and reference basal area increment series by dividing them by the mean and we built the respective basal area growth indices series ($\text{IBAI}_{\text{mixed}}$ and IBAI_{ref}) to remove the net overyielding effect for the 15 year period (see Fig. S1). The comparison of the standardized series provided the interannual variation in species interactions in terms of basal area increment.

A year was considered to have favourable growing conditions when the IBAI was high and unfavourable when the IBAI was low. To test whether annual species interactions in terms of basal area increment vary depending on growing conditions, we fitted a linear model relating the two growth indices ($\text{IBAI}_{\text{mixed}} = f(\text{IBAI}_{\text{ref}})$). The slope of this model reflected whether the interannual shifts in species interactions in terms of basal area increment depended on annual growing conditions expressed as growth rates. A slope higher than 1 meant that species interaction was greater (more positive or less negative) than the mean in high-growth years, and lower (less positive or more negative) than the mean in low-growth years, whereas a slope lower than 1 meant the opposite (see Fig. S1). Therefore, the slope was used as an index to express the shifts in species interactions with interannual growing conditions. As the two variables ($\text{IBAI}_{\text{mixed}}$, IBAI_{ref}) were assumed to be measured with the same error and as we were interested in the slope and not in predicting

$IBAI_{mixed}$, we used a major regression to estimate the slope per triplet and then explored if the slope estimates were related to TS_{mixed} and TS_{mixed}/TS_{mono} .

Results

TEMPORAL STABILITY AT THE DIFFERENT LEVELS: COMMUNITY, SPECIES AND INDIVIDUAL TREE LEVEL

Community level

Temporal stability of the annual stand basal area increment was on average 15% lower in the monospecific than in the mixed stands ($P = 0.010$), the estimated mean being $TS = 4.99$ and 5.90 respectively. When the composition of monospecific stands was considered, the TS in monospecific European beech stands was 17% lower (estimated mean 4.88) than the mixed stands ($P = 0.012$), whereas for Scots pine the mean was 13% lower (5.10) ($P = 0.0434$) (Table S4). We tested the possible influence of climatic variables and species proportion but found no significant relationships. When analysing the mean and the SD of stand BAI, there were no statistical differences between compositions.

Population level

There were no statistical differences between the TS of annual basal area growth in mixed (expanded to hectare) and in monospecific stands at the population levels (Table S4). However, for pine, both the mean and the SD of the annual basal area increment were significantly lower in mixed than in monospecific stands (21% and 27%, respectively), whereas for beech the mean and the SD were significantly higher in mixed than in monospecific stands (41% and 56%, respectively). Climatic variables and species proportion did not explain TS variability for either of the two species.

Individual tree level

Temporal stability in the annual tree basal area increment was significantly different between the trees on the pure and mixed plots for pine ($P < 0.001$), being greater in

monospecific stands (Table S4). The inclusion of the tree size or site covariates did not improve the basic model. The increase in TS in monospecific stands was due to a higher mean tree BAI, as the differences between monospecific and mixed stands were only significant for the mean ($P < 0.001$) and not for the SD. For beech, there were no differences in tree TS between mixed and monospecific stands, but the tree size had a significant effect on tree TS (Table S4). Both the mean and the SD were significantly higher in the mixed compared to the monospecific stands.

Overall effect

The results showed that at the community level the mixture increased the stability of productivity, but this effect disappeared at the population level while at the tree level the opposite effect was observed in the case of pine. The stability was lower at the population level than at the community level, particularly for beech (Fig. 2a). The observed mean ratios TS_{mixed}/TS_{mono} at the community level were 1.31 and 1.28 for beech and pine, respectively, whereas at the population level, they were not significantly different from one. There was a positive correlation (r) between the mixing effect on stability at the two levels for both species ($r = 0.763$, $P < 0.0001$ for pine; $r = 0.716$, $P < 0.0001$ for beech). Interestingly, there was no correlation between the effects of mixing on stability at the tree level with the corresponding effects at the community (Fig. 2b) and population levels.

OVERYIELDING

The mean RPP of all triplets was 1.12 and it was statistically different from 1. This indicated that there was a general overyielding in stand basal area growth although the variability among triplets was large with some triplets showing underyielding (Fig. S2a). The RPP was not related to any of the site variables analysed, or to the TS in mixed stands. Also, overyielding was not related to any of the mixing effects of the TS at the community level (ratio of the TS in mixed stands to monospecific stands) (Fig. S2a).

At the population level we found overyielding in the case of beech ($RP_{be} = 1.49$) and underyielding for pine ($RP_{pi} = 0.87$), both significantly different from one (note that

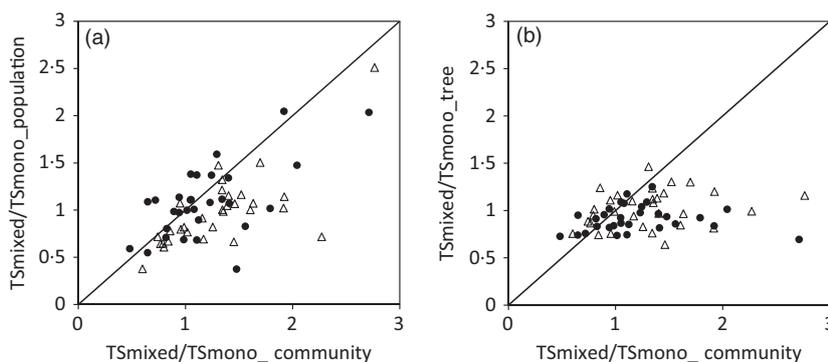


Fig. 2. Relationship between the mixing effects on temporal stability in basal area increment (TS_{mixed}/TS_{mono}) at the different organizational levels for *Fagus sylvatica* (white triangles) and *Pinus sylvestris* (black circles); (a) population vs. community levels; (b) individual tree vs. community levels.

there was no correlation between the RP_i of the two species). The $TS_{\text{mixed}}/TS_{\text{mono}}$ ratio at the population level (i.e. mixing effect on stability) was negatively related to the relative productivity by species (RP_i) for pine (Fig. 2b). This suggested that underyielding was linked to higher stability for pine at the population level, but it is important to highlight the absence of differences between mixed and monospecific stands in the TS at this level.

SPECIES ASYNCHRONY

The mean coefficient of correlation between the basal area increment series of beech and pine in the mixed stand ($r_{\text{mixed}} = 0.37$) indicated that there was synchrony in species responses to variation in environmental conditions in mixed stands at the community level. However, there was a high variability among triplets ranging from -0.84 to 0.89 (Fig. 3). The observed high negative values revealed the presence of a high species asynchrony at the community level for some triplets. The respective mean correlation in monospecific stands (r_{mono}), i.e. the species' intrinsic response to environmental variations, was similar at 0.37 with a narrower range (from -0.39 to 0.87). The latter indicated that in some triplets the two species used the annually available site resources differently, whereas in other cases, the response to the interannual fluctuations in environmental conditions was quite similar. However, the relationship between r_{mixed} and r_{mono} was not significant (Fig. S3), reflecting that the mixture might change the species-specific responses to annual environmental conditions. The values of the correlation coefficient between the species' basal area increments were not significantly related to any site characteristics.

The TS of community productivity in mixed stands (TS_{mixed}) could partially be explained by the species

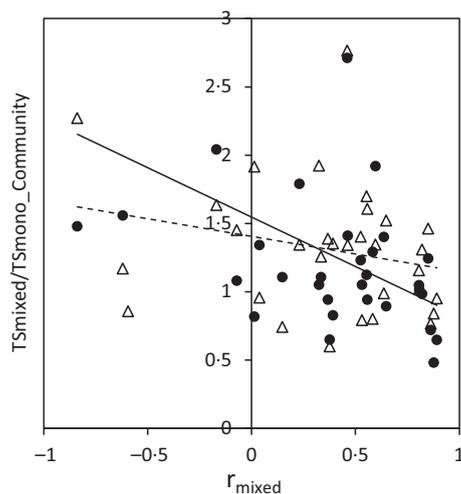


Fig. 3. Relationship between the mixing effect on stability ($TS_{\text{mixed}}/TS_{\text{mono_pine}}$) and the species asynchrony expressed by the coefficient of correlation between species increments (r_{mixed}) for *Fagus sylvatica* (white triangles) and *Pinus sylvestris* (black circles). Straight lines are the linear trend lines, dashed for beech (NS) and solid for pine ($TS_{\text{mixed}}/TS_{\text{mono_pine}} = 1.55 - 0.72 \cdot r_{\text{mixed}}$; $R^2 = 0.25$; $P = 0.004$).

asynchrony in mixed plots (Fig. S4a) ($R^2 = 0.40$, $P < 0.001$). For coefficients of correlation higher than 0.6 , the TS_{mixed} decreased notably, being always under the mean TS (6.08). Therefore, when the species asynchrony was lower, the stability in the mixture was lower. However, this relationship was not significant when considering the correlation in monocultures (asynchrony in species' intrinsic response to environmental variations) (Fig. S4b). The mixing effect on stability at the community level (ratio $TS_{\text{mixed}}/TS_{\text{mono}}$) increased in the case of pine when the species asynchrony in mixed stands was higher ($R^2 = 0.25$, $P = 0.004$), but this effect was not significant for beech (Fig. 3).

Overyielding (RPP) was inversely related to species asynchrony in mixed stands (r_{mixed}) at the community level ($R^2 = 0.20$, $P = 0.011$) (Fig. 4). However, this relationship was not significant when relating RPP to the coefficient of correlation in monocultures (r_{mono}).

At the individual tree level, the mean correlation between the mean tree basal area growth series of beech and pine was 0.41 in mixtures, varying from -0.65 to 0.91 , whereas the respective mean correlation in monocultures was 0.32 with a narrower range (from -0.35 to 0.77). In contrast to the results observed at the community level, the coefficients of correlation in mixed and monospecific stands were correlated ($r = 0.43$, $P = 0.0161$). The coefficients of correlation at the tree level and at the community level were positively correlated in mixed stands ($r = 0.58$, $P < 0.0005$) and in monocultures ($r = 0.74$, $P < 0.0001$). The asynchrony at the tree level was not related to the TS at the individual tree and species levels.

TEMPORAL SHIFTS IN SPECIES INTERACTIONS

The results of the major regression per triplet, relating the observed and reference stand basal area growth indices, indicated that the slope was statistically different from one

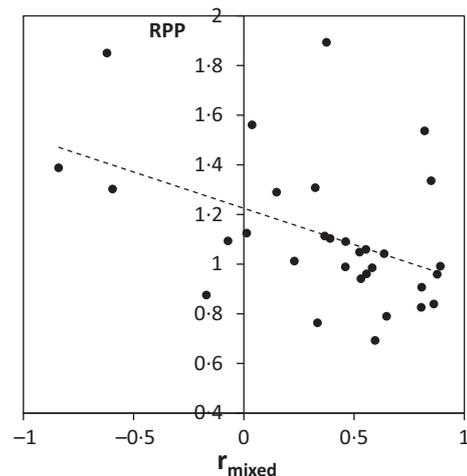


Fig. 4. Relationship between the overyielding (RPP) and the coefficient of correlation between species increments in mixed stands (r_{mixed}) ($RPP = 1.23 - 0.29 \cdot r_{\text{mixed}}$; $R^2 = 0.20$; $P = 0.011$).

for nine out of the 31 triplets ($P < 0.05$), four having a slope higher than one and five with a slope lower than one (Table S5). The relationship between the temporal stability in mixed stands (TS_{mix}) and the slope values was negative ($R^2 = 0.21$, $P = 0.010$) (Fig. S5). As with other variables, site characteristics were not significant. The slopes were also negatively related to the mixing effect on stability ($TS_{\text{mixed}}/TS_{\text{mono}}$). Figure 5 shows that lower slopes were linked to those triplets where the TS was higher in mixed than in monospecific stands and this is particularly notable for pine ($R^2 = 0.53$, $P < 0.001$ for pine; $R^2 = 0.32$, $P = 0.001$ for beech). Thus, the change in temporal variation of productivity in mixed stands compared to monocultures was linked to a temporal variation in species interaction. This interaction was more positive (or less negative) in low-growth years and more negative (or less positive) in high-growth years. In triplets where the stability was higher in monospecific stands, the slopes tended to be greater than one, which meant more positive interactions in high-growth years and more negative interactions in low-growth years.

The slopes explained part of the variability in the coefficient of correlation between the basal area increment series of beech and pine in the mixed stand or species asynchrony (r_{mixed}) ($R^2 = 0.16$, $P = 0.027$) (Fig. S6). These positive relationships suggest that part of the asynchrony observed in mixed stands might be caused by temporal changes in species interactions.

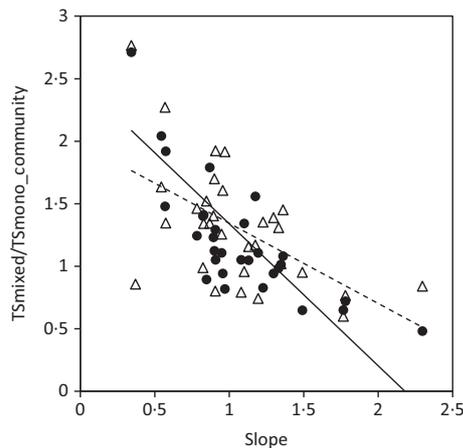


Fig. 5. Relationship between the mixing effects on temporal stability in basal area increment ($TS_{\text{mixed}}/TS_{\text{mono}}$) at the community level and the slope of the major regression between observed and reference stand basal area growth indices in mixed stands ($IBAI_{\text{mixed}} = a + b \cdot IBAI_{\text{reference}}$; see text and Fig. S1 for additional information) for *Fagus sylvatica* (white triangles) and *Pinus sylvestris* (black circles). The slope is an index of the temporal shifts in species interactions depending on growth rates; slopes lower than 1 indicate more positive (or less negative) interactions in years of low growth. Straight lines are the linear trend lines, dashed for beech ($TS_{\text{mixed}}/TS_{\text{mono_beech}} = 1.98 - 0.64 \cdot \text{Slope}$; $R^2 = 0.32$; $P = 0.001$) and solid for pine ($TS_{\text{mixed}}/TS_{\text{mono_pine}} = 2.48 - 1.14 \cdot \text{Slope}$; $R^2 = 0.53$; $P < 0.001$).

Discussion

DRIVERS OF THE TS AND THE LEVEL OF PRODUCTIVITY

Overyielding

Overyielding was found to contribute to the stabilization of productivity in different types of communities (Isbell, Polley & Wilsey 2009; Hector *et al.* 2010; Jucker *et al.* 2014). Our analysis showed a significant overyielding at the community level, but it was not linked to the TS of productivity (Fig. S2). This result for our two species mixture contrasts with the findings of Jucker *et al.* (2014) for tree mixtures of two to four species. Based on long-term simulations, Morin *et al.* (2014) reported that the TS was weakly driven by overyielding, which is in line with our results. However, it is important to consider that the stabilizing effect of overyielding may increase with species diversity, and may therefore have a relatively small effect in two-species mixtures, such as in our case (Hector *et al.* 2010).

Species asynchrony

The important role of species asynchrony in community stability has been highlighted recently in many studies (Roscher *et al.* 2011; Blüthgen *et al.* 2016). The results from our study indicated that asynchrony in species growth in mixed stands, which can be interpreted as a temporal niche complementarity (Loreau 2010, p. 132), was an important driver of the TS (Figs 3 and S4a). However, it should be noted that in our case, species asynchrony in monospecific stands was not related to stability (Fig. S4b). This indicated that intrinsic species-specific responses to environmental fluctuations observed in monospecific stands are not necessarily a good indicator of the stabilizing effect that emerges when species are mixed (Gross *et al.* 2014). The mixing of Scots pine and European beech changed the intrinsic species responses to yearly environmental variations at the community level in comparison to monospecific stands. Previous studies concerning forests have reported changes in the growth response to extreme droughts between mixed and monospecific stands (Lebourgeois *et al.* 2013; Pretzsch *et al.* 2013), although the results depended on species composition (Grossiord *et al.* 2014; Merlin *et al.* 2015). Nevertheless, those studies were either mainly based on tree level growth analyses or made no attempt to link the tree and community level analyses.

The species asynchrony–overyielding relationship (Fig. 4) contradicted the hypothesis stated by Jucker *et al.* (2014), who argued that species asynchrony might not influence overyielding because it would require a rapid response in forest dynamics to environmental conditions. Our results suggest, however, that asynchrony in species annual growth, expressing temporal niche complementarity, might be an important mechanism driving overyielding in this mixture. Nevertheless, both studies did not consider the diversity effect on mortality. This may influence overyielding, as well as TS,

because significant effects of mixing species on tree mortality, self-thinning lines and stand density indices have been reported previously (Binkley 1984; Binkley *et al.* 2003; Woodall, Miles & Vissage 2005; Condés & del Río 2015; Pretzsch & Biber 2016).

Temporal shifts in species interactions

We found the higher TS in mixed stands to be linked to inter-annual shifts in species interactions that mitigated the growth responses to environmental fluctuations in mixed stands in comparison to monospecific ones (Figs 5 and S5). That is, the temporal variation in niche complementarity between species may be one of the main factors underlying the increase in TS. These results provide empirical support of the simulation-based findings of Morin *et al.* (2014), which pointed out the greater importance of species interactions as opposed to species-intrinsic differences in responses to environmental conditions.

TEMPORAL STABILITY AND OVERYIELDING AT DIFFERENT LEVELS

The different stabilizing effects of species mixing at the different organizational levels were in accordance with theory-based expectations (Tilman 1999; Loreau & de Mazancourt 2013) and showed that the general pattern found in diversity–TS relationships at the community level also occur in the case of mixed forests with two species. Generally, species diversity increases the TS of productivity at the community level, but a high variability in this effect was reported at the population level (Jiang & Pu 2009). We found a stabilizing effect at the community level, but a neutral effect at the population level. The lack of any destabilizing effect at the population level might be explained by the slower dynamics of forests, requiring long periods before any change in relative species abundance occurs, this factor plays an important role in diversity–population stability (Roscher *et al.* 2011). Accordingly, a negative diversity effect on population stability was found by Morin *et al.* (2014) based on long-term simulations from a process-based succession model.

Mixing species resulted in a destabilizing effect on individual pines, whereas in the case of beech, a neutral effect was found. The differences between the population and individual tree level responses for pine may be due to the fact that only dominant and co-dominant trees were explored at the tree level. Thus, a stabilizing effect might be expected in suppressed trees, highlighting the importance of considering tree social status. Our results also indicated that the differences in species asynchrony in growth responses to environmental fluctuations between mixed and monospecific stands were lower at tree than at the community level. These results underlined the need for further studies at the community level and the importance of linking both levels. An important finding was that mixing effects that were evident at the mean tree or population levels do not necessarily have any far-reaching

relevance at the community level. Studies that apply an individual tree level approach may overlook any compensation effects at the population or community levels and lead to questionable predictions when the results from individual dominant trees are scaled up to the community level responses. It is important to underline the possible mixing effect on size distributions (Pretzsch & Schütze 2014, 2015), which can cause the contrasting effects at different levels, and contribute to misleading results if not taken into account when up-scaling.

Moreover, both the overyielding of mixed-species stands at the community level and the differences in growth stability at the community, population and individual tree levels point to a multiplicative character of mixing effects. Thus, modelling approaches should not simply derive mixed stand dynamics from the weighted mean of the respective monocultures but reproduce the spatial and temporal interspecific interactions between the combined species (Pretzsch, Forrester & Rötzer 2015).

ENVIRONMENTAL DRIVERS

The experimental design of our study was originally developed to examine whether the temporal variability of productivity in monocultures and mixed-species stands depended on the site-specific water availability (Pretzsch *et al.* 2015). Many dendrochronological studies suggest that trees at drought prone sites may frequently suffer water limitation and therefore present more distinct fluctuations between high- and low-growth years (Fritts 2001). However, we found no significant effect of precipitation or the de Martonne aridity index on the TS of productivity. This finding may be due to other environmental factors which could modify the effect of water availability and confound any productivity–water relationship. Indeed, the high variability in species asynchrony observed in monospecific stands along the transect at both the community and mean tree levels (r_{mono} from negative values to almost 1), suggested that different environmental factors might be influencing species-specific growth at the different sites. Similarly, species over- or underyielding (RPP_i) were not correlated, indicating that different environmental factors influence the mixing effect for each species.

Few studies have quantified the effects of European beech and Scots pine interactions on water, light or nutrient availability, uptake or use efficiencies. Water-related interactions may play a role as a result of interspecific differences in interception (Nihlgård 1970; Augusto *et al.* 2002; Staelens *et al.* 2006; Gerrits, Pfister & Savenije 2010; Van Nevel 2015), the isohydric behaviour of pine vs. the anisohydric behaviour of beech (Hartmann 2011) and contrasting vertical root distributions and litter layers (Bonnemann 1939; Knapp 1991; Heinsdorf 1999), which may influence the vertical profile of water availability and uptake. The seasonality of resource use by a given species can also be modified by mixing, as shown for transpiration and light (Forrester *et al.* 2010; Sapjanskas *et al.* 2014). Further studies on the water and nutrient pools and fluxes might be required to determine their contribution

to the temporal niche complementarity effects shown here for the mixture of pine and beech.

Concluding remarks

Spatial and temporal species' complementarity in structure or functioning seems to be essential to increase the level and stability of productivity in mixed compared to monospecific stands. In our two-species mixture, species asynchrony in growth response to environmental fluctuations in mixed stands was shown to increase both the level and stability of productivity. This mechanism, together with the temporal shifts in species interactions suggested the important role of temporal niche complementarity in the stabilizing process. We found that this stabilizing effect did not depend on the site water supply or humidity, suggesting that the stabilization resulted from various complementarity effects together. This species assemblage may provide a model example for other widespread species combinations regarding the degree of spatial and temporal complementarity. Other common conifer-broadleaved mixtures of early and late-successional species or shade intolerant and tolerant species may behave similarly in terms of the level and the TS of productivity.

Author's contributions

M.R. and H.P. conceived the ideas and designed methodology; all authors, except D.F., contributed to data collection; M.R. and R.R. analysed the data; M.R., H.P., R.R., K.B., L.C., D.F., Q.P., H.S. and A.B. contributed to the results interpretation and discussion; M.R. and H.P. led the writing of the manuscript; All authors contributed critically to the drafts and gave final approval for publication.

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Data accessibility

Data available from the Dryad Digital Repository <http://dx.doi.org/10.5061/dryad.fq4tk> (del Río et al. 2017).

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Supporting Information

Details of electronic Supporting Information are provided below.

Table S1. Overview of the 31 mixed *Pinus sylvestris*–*Fagus sylvatica* triplets included in this analysis.

Table S2. Stand characteristics of monospecific and mixed-species stands of the triplets.

Table S3. Description of the mean, SD and stability of the annual basal area increment at the different organizational levels observed in monospecific and mixed-species stands.

Table S4. Fixed effect results at the community level, population level and the individual tree level for the prediction of the temporal stability, mean and SD of the annual basal area increment.

Table S5. Estimates of the slope of the major regression between observed and reference stand basal area growth indices in mixed stands.

Fig. S1. Example of the process of standardization and analysis of temporal variation in species interactions.

Fig. S2. Relationship between the mixing effect on stability and the overyielding.

Fig. S3. Relationship between the coefficient of correlations of species stand basal area at the community level in mixed and monospecific stands.

Fig. S4. Relationships between the temporal stability of the stand basal area increment in mixed stands and the species asynchrony in mixed and monospecific stands.

Fig. S5. Relationship between the temporal stability of the stand basal area increment in mixed stands and the slope of the major regression between observed and reference stand basal area growth indices in mixed stands.

Fig. S6. Relationship between the species asynchrony in mixed stands and the slope of the major regression between observed and reference stand basal area growth indices in mixed stands.