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

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Running headline:
Species interactions enhance stability in mixed forests

**Abstract**

1. There is increasing evidence that species diversity enhances the temporal stability of community productivity in different ecosystems, although its effect at population and tree levels seems to be negative or neutral. Asynchrony between species was found to be one of the main drivers of this stabilizing process. However, scarce research in this area has been undertaken in forest communities, so determining the effect of species mixing on the stability of forest productivity as well as the identity of the main drivers involved still poses a challenging task.
2. We investigate the way in which mixing species influences the temporal stability of productivity in *Pinus sylvestris* L. and *Fagus sylvatica* L. forests, and attempt to determine the main drivers. We used a network of 93 experimental plots distributed across Europe to compare the temporal stability of basal area growth over a 15-year period (1999-2013) in mixed and monospecific forest stands at different organizational levels, namely community, population and individual tree levels. Overyielding, asynchrony between species, and species interactions were explored as possible drivers of temporal stability of productivity.
3. Mixed stands showed a higher temporal stability of basal area growth than monospecific stands at community level, but not at population or individual tree levels. Asynchrony between species growth in mixtures was related to temporal stability, but neither overyielding nor asynchrony between species growth in monospecific stands were linked to temporal stability. Therefore, species interactions modify between-species asynchrony in mixed stands. Accordingly, temporal shifts in species interactions were related to asynchrony and to the mixing effect on temporal stability.
4. Synthesis. Our findings confirm that species mixing can stabilize productivity at community level whereas there is a neutral or negative effect on stability at population and individual tree level. The contrasting findings as regards the relationships between temporal stability and species asynchrony in mixed and monospecific stands suggest that the main driver in the stabilizing process is the temporal niche complementarity between species rather than differences in species specific responses to environmental conditions.

**Keywords**

Temporal variability; mixed-species forests; plant-plant interactions; overyielding; asynchrony; niche complementarity; organizational levels;

## Introduction

Mixed-species stands are widely thought to provide many forest functions and services more effectively than monocultures (Hector & Baghi 2007; Gamfeldt *et al.* 2013; van der Plas *et al.* 2016). The superior level and stability of productivity in mixed forests is of interest for most functions and services, as well as being a precondition for the promotion of this alternative in forestry practice. Much evidence exists 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) although contradictory findings of underyielding (Chen et al 2003; Carvard *et al*. 2010) discourage generalization. Many studies show that mixing may improve different aspects related to the stability of productivity (Jucker *et al.* 2014; Pretzsch, Schütze & Uhl, 2013; de Dios-García, Pardos & Calama, 2015; Metz *et al.* 2016), but again, the findings of other research suggest the opposite (Grossiord *et al.* 2014; Merlin *et al.* 2015). Among the probable reasons for these varying and seemingly inconsistent findings are differences in the complementarity of the analyzed species assemblages (Toïgo *et al.* 2015) as well as the underlying site conditions with their specific growth limiting factors (Forrester 2014). Findings may also differ depending on the level of analysis, as mixing effects in forest communities are frequently studied at stand, species, or individual tree level; the results not necessarily being the same (Forrester & Pretzsch 2015). The conservation and management of productive, stable, and resource-use efficient mixed-species stands requires an improved understanding of the mechanisms involved, which could also contribute towards theory development and greater generalization with regard to these forests.

The term ‘stability’ in ecosystems includes several concepts such as resistance, resilience or temporal stability of productivity, all of which address diversity-stability relationships (McCann 2000; Ives & Carpenter 2007). In the case of forests, temporal variability of community productivity is an important ecological property because stability of productivity is an indicator of sustainability of both forest functioning and the delivery of ecosystem services (Blüthgen *et al.* 2016). Temporal variability is usually measured by the coefficient of variation or its inverse, i.e temporal stability then depends on the mean and standard deviation (Tilman, Lehman & Bristow 1998). Different statistical and biological mechanisms have been identified as possible causes of increasing temporal stability as regards species diversity. These include overyielding, species asynchrony and species interactions (Hector *et al.* 2010, Loreau & Mazancourt 2013; Blüthgen *et al.* 2016). Overyielding means higher productivity in mixtures than in the corresponding monospecific systems, which may lead to a stabilizing effect by a higher mean if other factors remain constant (Tilman 1999). Species asynchrony exists when the temporal responses of the species are not perfectly positively correlated. Such increases in the variability of responses may result in a reduction in the community variability. Asynchrony of species-specific responses to environmental fluctuations has been reported as a key factor in temporal stability (Loreau & de Mazancourt 2008; Hector *et al.* 2010), in accordance with the insurance hypothesis (Yachi & Loreau 1999). However, species interactions can also trigger species asynchrony by compensatory dynamics between species (Tilman, Lehman & Bristow 1998; Morin *et al.* 2014), which might result in less variation at community level (Loreau & de Mazancourt 2013). Species interactions may also involve temporal stability as a consequence of their effect on overyielding, and 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 community level, but a destabilizing effect at population levels by increasing competitive interactions (Hector *et al.* 2010; Gross *et al.* 2014). However, contrasting results have been obtained at population level (Jiang & Pu 2009), even among the scarce 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 interest, as in many European temperate mixed forests comprising only two or three species.

Diversity- roductivity relationships in forests have been found to depend on environmental gradients (Pretzsch *et al.* 2010; Toïgo *et al*. 2015; Jucker *et al.* 2016), since the result of the interactions among species changes depending on the growing conditions (Forrester, 2014; Forrester & Bauhus, 2016). The growth response of tree species to climatic conditions as well as temporal variation in climate-growth relationships also vary considerably among sites (Lloyd & Fastie 2002; Tardif *et al*. 2003). Therefore, differences in diversity-stability relationships might also be expected along ecological gradients, with the relative importance of different mechanisms varying along the gradients (Hallet *et al*. 2014; Xu *et al.* 2015).

The number of studies concerning the relationship between diversity and temporal stability of productivity based on empirical data in forests 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 often uncontrollable factors interact. In a recent study, Jucker *et al.* (2014) analysed several monospecific and mixed forests of 16 target species in Europe (Jucker *et al.* 2014) and found a positive effect of species diversity on the stability of wood productivity. However, a previous study found the opposite for conifer mixed forests in Sierra Nevada, California (DeClerck, Barbour & Sawyer 2006). Therefore, further research is required to elucidate the mixing effect on temporal stability of productivity and the underlying mechanisms for different forest species assemblages and sites.

In this study we focus on two tree species, *Pinus sylvestris* L. and *Fagus sylvativa* L., growing in mono-specific and mixed forests across a large range of their distribution. This design allows us to infer the general effect of this admixture on the temporal stability 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 highly complementary traits, 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. Actually, the mixture between *P. sylvestris* and *F. sylvatica* was found to shown 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 spatial and temporal complementarity in traits.

The main hypotheses in this study are that: (*i*) temporal stability of productivity is higher in mixed than in mono-specific stands at community level but not at population and individual tree levels; (*ii*) in this model mixture, the dynamics of species interactions is one of the drivers in stabilizing productivity due to the complementary traits of these species; and (*iii*) the mixing effect on temporal stability depends on site conditions. Our main objective is therefore to explore whether mixing species of contrasting traits increases the temporal stability of productivity at different organizational levels and if so, to elucidate the main underlying mechanisms in order to better understand the inter-specific dynamics of the *P.sylvestris - F.sylvatica* and comparable mixtures.

## MATERIAL AND METHODS

### Field data and study design

The study data come from a transect of plots in mixed and monospecific forest stands of *P. sylvestris* (Scots pine) and *F. sylvatica* (European beech) 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 main aim of the initiative was to study the variability of over-yielding, structural properties and stability under different environmental conditions in monocultures and mixtures (see for example Pretzsch *et al.* 2015; 2016). 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, with similar site conditions (soil and topographic conditions) in order to allow meaningful comparisons between mixtures and monocultures. A total of 31triplets (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 gathered from all available meteorological stations in the proximity of each triplet (see Table S1 in Supporting Information for 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 18% to 72 % of pine, although in most of them the proportion is around 50%. Plots are rectangular with varying sizes from 0.02 to 1.55 ha. In each plot, the tree species, tree diameter, height and height to the crown base were recorded for all trees. In a sub-sample of 20 trees per plot and species two increment cores were extracted at a stem height of 1.30 m for 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 in mixed and monospecific stands are provided in Table S2.

### Productivity data at different organizational levels

*Community level*

As a proxy to represent community biomass productivity we use stand basal area growth per hectare, as it is closely linked to measured variables in the field. In contrast to other studies which focused on aboveground biomass growth when studying diversity- roductivity and/or diversity-stability relationships (Paquette & Messier 2011; Jucker *et al*. 2014, 2016), we relied on basal area growth. 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 at least in mixed stands (Toïgo *et al.* 2015) as the respective functions were derived from data of monospecific stands. Using these functions may had caused biased estimations of biomass growth as mixing tree species can modify tree allometry (Pretzsch 2014) 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; Río *et al.* 2016).

Our study focuses on the temporal stability and over-yielding 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, whilst avoiding bias form unknown tree mortality or tree removal which could have interfered the results as mixing may change species-specific mortality rates (Zhao *et al*. 2006; Condés & Río 2015).

Stand basal area was calculated as the sum of the cross sectional area (at 1.3 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 (31 triplets * 4 (two tree species in mixed and monospecific stand) * 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 is the tree diameter increment for that year (cm $year^{-1}$) and d is the tree diameter at breast height (cm).

*Population level*

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

*Individual tree level*

At individual tree level we used the measured tree ring widths from cored trees transformed to individual tree basal area increments. As the tree growth response to variability in environmental conditions and to intra- and inter-competition level depends on tree social status (Martín-Benito *et al*. 2008; Zang, Pretzsch & Rothe 2012; Río, Condés & Pretzsch 2014) we used only dominant and codominant trees (1691 trees), selected through the diameter and height distributions per species and plot.

**Data evaluation and analysis**

*Temporal Stability at different organizational levels*

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

The effect of mixing species on temporal stability of productivity at community and population level was analyzed using a mixed linear model including the species composition of the plot as a fixed factor. First we compared mixed vs monospecific stands, and in a second step we considered species identity of monospecific plots. Data were log-transformed to correct heteroscedasticity in residuals.

$$\mathrm{Ln}(TS_{ij}) = (a_0 + a_{0j}) + a_1 \cdot \text{composition} + \varepsilon_{ij} \quad \text{eqn 1}$$

where $TS_{ij}$ is the temporal stability of the annual basal area increment for the plot *i* in the triplet *j*; composition is a dummy variable with two levels, mixed and monospecific, or three levels, mixed, monospecific pine and monospecific beech; $a_0$ and $a_1$ are 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 TS included climatic attributes and their interaction with species composition were tested. At tree level we fitted a similar model but taking also the effect of tree size on temporal stability into account.

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

*Overyielding*

The over- or under-yielding values per triplet were estimated using the ratio of productivity (RPP) (Harper, 1977), $RPP=\sum P_{i,mix}/P_{i,mono}$, where $P_{i,\,mix}$ is the observed productivity (i.e. basal area increment) of species *i* in the mixed stand and $P_{i,\,mono}$ is the productivity of species *i* in the monospecific stand. 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 population level we used the relative productivity per species ($RP_i$) (Pretzsch *et al.* 2013; 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 monoculture, $RP_i=(P_{i,\,mix}/m_i)/P_{i,mono}$, where $m_i$ is the species proportion estimated by the proportion of species *i* in the stand basal area for a given year. As for RPP, $RP_i$ 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 under-yielding, using a t-student test, and the possible relationship between overyielding and temporal stability at different levels through simple linear models. At community level we studied the possible influence of RPP on the temporal stability in mixed stands ($TS_{mixed}$) and on the mixing effect ($TS_{mixed}/TS_{mono}$). At population level we related the $RP_i$ to the mixing effect, i.e. ratio of TS at population level.

*Asynchrony*

To estimate the species asynchrony we used the coefficient of correlation between the growth series of the two species growing in mixed stands ($r_{mixed}$); a value of -1 means complete asynchrony between species' growths and +1 indicates complete synchrony. This approach is 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 monocultures ($r_{mono}$), as this correlation might express the differences or the similarity in the dependence of the two species on inter-annual environmental conditions, i.e. the asynchrony of the intrinsic response of each species 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 tree level it was studied by species specific mean tree basal area increment series.

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

*Temporal variation in species interactions*

To study the inter-annual variation in species interactions depending on annual growing conditions we used a similar approach to that used in Río, Schütze & Pretzsch (2014). We compared the annual productivity in mixed stands to the respective reference productivity. The latter reflects conditions where no mixing effect takes place, which is calculated as the sum of the productivities of the two species in monospecific stands times their proportion in the mixed stand ($\sum P_i \cdot m_i$) (Pretzsch *et al.* 2013; Río *et al.* 2016). When the annual basal area increment in the mixed stand is higher than the reference basal area increment, there is a positive species interaction or overyielding; whereas if one year it is lower this indicates that there is negative interaction or underyielding. In this section, as the aim is to study the temporal variation in species interaction but not the net effect or overyielding, 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 ($IBAI_{mixed}$ and $IBAI_{ref}$) to remove the net overyielding effect for the 15 year period (see Fig S1).

A year was considered to have favorable growing conditions when the IBAI was high and unfavorable when the IBAI was low. To test whether annual species interactions vary depending on growing conditions we fitted a linear model relating the two growth indices series ($IBAI_{mixed} = f(IBAI_{ref})$). If the slope is not different from one, the temporal variation in species interaction does not depend on annual growing conditions (i.e variation is similar in good and bad years), whereas if the slope is different from one it means that the interactions depend on annual growing conditions (see Fig S1). As the two variables are assumed to be measured with the same error and we were interested in the slope value and not in predicting new IBAI values, we used a major regression to estimate the slope per triplet and then explored if the slope values were related to TS.

## RESULTS

### Temporal stability at different levels: community, species and individual tree level

*Community level*

Temporal stability of annual stand basal area increment was lower in the monospecific stands than in the mixed stands ($P = 0.010$), the observed mean being TS=5.14 and 6.08 respectively. When the composition of monospecific stand was considered the TS in monospecific European beech plots was lower than the mixed plots ($P = 0.012$), whereas for Scots pine it was also lower although the difference was smaller ($P = 0.052$) (Table S4). We tested the possible influence of climatic variables but found no significant relationships. When analyzing the mean and the standard deviation 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 population levels. For pine, both the mean of annual basal area increments and the standard deviation were significantly lower in mixed than in monospecific stands, whereas for beech the mean and the standard deviation were significantly higher in mixed than in monospecific stands. Climatic variables did not explain TS variability for either of the two species.

*Individual tree level*

TS in annual tree basal area increment was significantly different between pure and mixed plots for pine ($P < 0.001$), being greater in monospecific stands. 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 in the mean were significant between monospecific and mixed stand whereas in the case of the standard deviation they were not. 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 standard deviation were significantly higher in the mixed compared to the monospecific stands.

*Overall effect*

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

**Overyielding**

The mean RPP of all triplets was 1.12 and it was statistically different from 1. This indicates that there was a general overyielding in stand basal area growth although the variability among triplets was large with some triplets showing underyielding (Fig S2). The RPP was not related to any of the site variables analyzed, nor to the TS in mixed stands. Accordingly, overyielding was not related to any of the mixing effects of TS at community level (ratio of TS in mixed stands to monospecific stands) (Fig. S2).

At population level we found overyielding in the case of beech (Relative productivity ($RP_{be} = 1.49$) and underyielding for pine ($RP_{pi} = 0.87$), both significantly different from one (note that there was no correlation between the $RP_i$ of the two species). $TS_{mixed}/TS_{mono}$ ratio at population level (i.e. mixing effect on stability) was negatively related to the relative productivity by species ($RP_i$). Thus, with increasing overyielding stability decreased in mixed stands (Fig 3). This suggests that at population level, under-yielding is linked to higher stability for pine, but it is important to highlight the absence of differences between mixed and monospecific stands in TS at this level.

**Species asynchrony**

The mean coefficient of correlation between basal area increment series of beech and pine in the mixed stand ($r_{mixed}$), or species synchrony at community level, was 0.37, but there was a high variability among triplets ranging from -0.62 to 0.89 (Fig. 4). The observed high negative values revealed the presence of a high species asynchrony at community level for some triplets. The respective mean correlation in monospecific stands ($r_{mono}$) was similarly 0.37 with a narrower range (-0.39 to 0.87), which indicates that in some triplets the two species use the annually available site resources differently whereas in other cases the response to the interannual fluctuations in environmental conditions is quite similar. However, it is important to highlight that the relationship between $r_{mixed}$ and $r_{mono}$ was not significant (Fig. S3), reflecting that the mixture changes the species-specific responses to annual environmental conditions. No effect of any site characteristic on correlation between species' basal area increments was found.

The temporal stability of community productivity in mixed stands was partially explained by the species asynchrony in mixed plots (Fig. 4), following a quadratic model ($R^2$ = 0.40; P<0.001). For coefficients of correlation higher than 0.6 the $TS_{mixed}$ decreases notably. 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 instead of in mixtures (Fig. S4). The mixing effect on stability at community level (ratio $TS_{mixed}/TS_{mono}$) 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. S5).

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

The relationship between overyielding (RPP) and species asynchrony in mixed stands at community level was significant ($R^2$ = 0.20; P=0.011), the overyielding increasing with the species asynchrony (Fig. 5). However, this relationship was not significant when relating RPP to the coefficient of correlation in monocultures. Therefore, the species asynchrony in mixed stands has an influence on the temporal variability and quantity of productivity at community level.

**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 in 10 out of the 31 triplets ($P$ < 0.05), 5 having a slope higher than one and 5 with a slope lower than one. The relationship between the temporal stability in mixed stands ($TS_{mix}$) and the slope values was negative ($R^2$ = 0.21; P=0.010). Hence, higher temporal stability seems to be linked to slopes lower than one and lower stability to higher slopes. As with other variables, site characteristics were not significant.

Accordingly the slopes were also negatively related to the mixing effect on stability ($TS_{mixed}/TS_{mono}$). In Fig. 6 it can be seen that lower slopes are linked to triplets where the TS is higher in mixed than in monospecific stands and this is particularly notable for pine ($R^2$ = 0.32; P=0.001 for beech; and $R^2$ = 0.53; P<0.001 for pine). Thus, the reduction in temporal variation of productivity in mixed stands compared to monocultures is linked to a temporal variation in species interaction, this interaction being more positive in years with low growth rates and more negative in years with high growth rates. In triplets where the stability is higher in monospecific stands, the slopes tend to be greater than one, which means more positive interactions in years with high growth and more negative interactions in years with low growth rates.

The slopes explained part of the variability in the coefficient of correlation between basal area increment series of beech and pine in the mixed stand ($r_{mixed}$) ($R^2$ = 0.16; P=0.027). The positive relationships between them suggest that part of the asynchrony observed in mixed stands is due to temporal changes in species interactions.

## DISCUSSION

Our findings show that species mixing can stabilize productivity at community level but not at population level. This stabilizing effect was mainly explained by species asynchrony in the mixed stands, which was influenced by the species interactions. This result along with the lack of any relationships between temporal stability and species asynchrony in monospecific stands suggests that the main driver in the stabilizing process was the temporal niche complementarity between species rather than differences in species-specific responses to environmental conditions. Overyielding was not linked to temporal stability but to species asynchrony in mixed stands, highlighting the important contribution of temporal niche complementarity to the level and stability of forest productivity.

### Drivers of temporal stability and the level of productivity

*Overyielding*

Overyielding was found to contribute to the stabilization of productivity in different types of communities (Hector *et al.* 2010; Isbell, Polley & Wilsey 2009, Jucker *et al.* 2014). Our analysis showed a significant overyielding at community level, but it was not linked to the temporal stability of productivity (Fig. S2). This result for our two species mixture is contrary to the findings of Jucker *et al.* (2014) for tree mixtures of 2-4 species. Based on long-term simulations, Morin *et al.* (2014) reported that temporal stability 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 in our case (Hector *et al.* 2010).

*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 confirm that asynchrony in species growth is an important driver of temporal stability (Fig. 4). Asynchrony of temporal responses to varying environmental conditions between species has also been identified as a stabilizing factor (Loreau & de Mazancourt 2013). However, it should be noted that in our case, species asynchrony in monospecific stands was not related to stability (Fig. S4), indicating 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 therefore changes the intrinsic species responses to yearly environmental variations at community level in comparison to monospecific stands, and temporal shifts in species interactions linked to temporal niche complementarity seem to play a key role in this change. 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 (Merlin *et al.* 2015; Grossiord *et al.* 2014). Nevertheless, those studies were either mainly based on tree level growth analyses or made no attempt to link the tree and community level analyses. Our results indicate that the changes in species asynchrony between mixed and monospecific stands were considerably lower at tree than at community level, but also that the asynchronies at the two levels were correlated, the latter suggesting that differences in species specific responses to variability in environmental conditions may also affect temporal stability. These results underline the need for further studies at community level and the importance of linking both levels.

The asynchrony-overyielding relationship identified in this study (Fig. 5) suggests that temporal niche complementarity is one of the most important mechanisms driving overyielding in this mixture. These results contradict the hypothesis stated by Jucker *et al*. (2014), who argued that asynchrony might not influence overyielding because it would require a rapid response in forest dynamics to environmental conditions. However, our study assumed no diversity effect on mortality, although significant effects of mixing on tree mortality, self-thinning lines and stand density indices have been reported previously (Binkley 1984, 2003; Condés & Río 2015; Pretzsch & Biber 2016; Woodall, Milles & Vissage 2005), and may influence overyielding as well as stability.

*Species interactions*

We found the higher temporal stability in mixed stands to be linked to shifts in species interactions that influenced the growth response of a given species to inter-annual environmental conditions. That is, the temporal variation in niche complementarity between species, which results in compensatory dynamics between species, is one of the main factors underlying the increase in temporal stability. These results provide an empirical corroboration of the simulation-based findings of Morin *et al*. (2014), which pointed to the greater importance of species interactions as opposed to species-specific differences in responses to environmental conditions. However, the temporal scale and the compensatory dynamics considered in the simulations are not directly comparable to our approach.

**Temporal stability and overyielding at different levels**

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

At population level, we found underyielding for pine and overyielding for beech when growing in the mixed stands. These changes in mean productivity in comparison to monospecific stands were also associated with comparable relative changes in the standard deviation, resulting in similar temporal stabilities. Nevertheless, mixing species resulted in a destabilizing effect on individual pines, mainly due to the lower mean productivity, 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 codominant trees were explored at tree level. Temporal variation in tree growth is generally lower as tree size increases, as indicated by the increasing stability of beech with tree size, even within the dominant and codominant trees included in this study. Similarly, tree responses to drought can vary among trees of different social status within a stand (Martín-Benito *et al*. 2008).

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

Our results clearly show that the behaviour of mixed species stands cannot be derived simply by assuming additive effects between the combined species (e.g., based on the traits or dynamics of the species in monocultures). Both the overyielding of mixed-species stands at community level and the differences in growth stability at the community, population, and individual tree levels point to a multiplicative character of mixing effects. Modelling approaches cannot derive mixed stand dynamics from the weighted mean of the respective monocultures and should be able to reproduce the spatial and temporal inter-specific 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 is higher at sites with lower mean water supply. 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 statistical effect of precipitation or de Martonne aridity index on the temporal stability of productivity. This finding may be due to the typical lack of *ceteris paribus* conditions in field experiments, such that many factors may change along the transect other than the water supply and humidity. These factors could modify the effect of water supply and confound any productivity-water relationship. Indeed, the high variability in species asynchrony observed in monospecific stands along the transect at both stand and mean tree levels (from negative values to almost one), suggests that different environmental factors might be influencing species-specific growth at the different sites. Similarly, species over- or under-yielding ($RPP_i$) 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. In the same plots as those used in this study, the RP for light absorption at stand level generally increased due to a combination of more stratified canopy structures, changes in diameter-crown allometric relationships and increases in mean tree size in the mixtures (Forrester *et al.* in prep). Water-related interactions may also play a role as a result of inter-specific differences in interception (Nihlgård 1970; Augusto *et al.* 2002; Gerrits, Pfister & Savenije. 2010; Staelens *et al.* 2006; Van Nevel 2015), the isohydric behavior of pine *vs.* the anisohydric behavior of beech (Hartman 2011) and contrasting vertical root distributions and litter layers (Bonnemann 1939; Heinsdorf 1999; Knapp 1991), which may influence the vertical profile of water availability and uptake. These differences could improve nutrient availability in the mixtures compared with the pine monocultures. 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; Sapijanskas *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 in these pine and beech mixtures.

**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 with monospecific stands. In our two-species mixture, species asynchrony in mixed stands improved the level and stability of productivity , while our results with regard to temporal shifts in species interactions highlight the role of temporal niche complementarity in the stabilizing process. This species assemblage may provide a model example for other widespread species combinations as regards 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 level and stability of productivity. We found the stability of productivity to be superior at most of the sites, regardless of the water supply and humidity, suggesting that the stabilization results from various complementarity effects together.

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## Data accessibility

Data available from the Dryad Digital Repository

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## Supporting Information

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

**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, standard deviation 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 stand level, species level and individual tree level for the prediction of temporal stability, mean and standard deviation of annual basal area increment.

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

**Figure S2.** Relationship between the mixing effect on stability and overyielding

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

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

**Figure S5.** Relationship between the mixing effect on temporal stability at community level and species asynchrony in mixed stands

## Figures

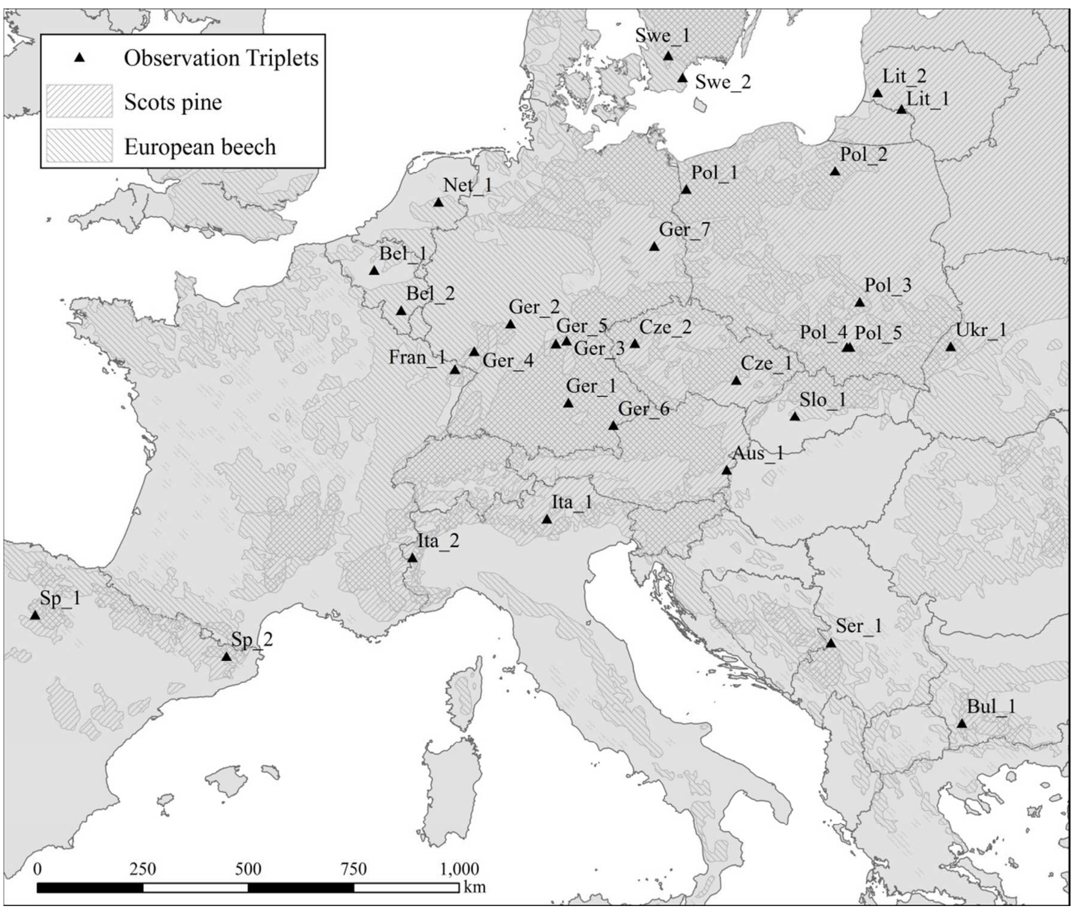


Fig 1. Location of the 31 triplets of monospecific and mixed stands of Scots pine and European beech over the distribution of *Pinus sylvestris* and *Fagus sylvatica* according to EUFORGEN (http://www.euforgen.org/distribution-maps/)

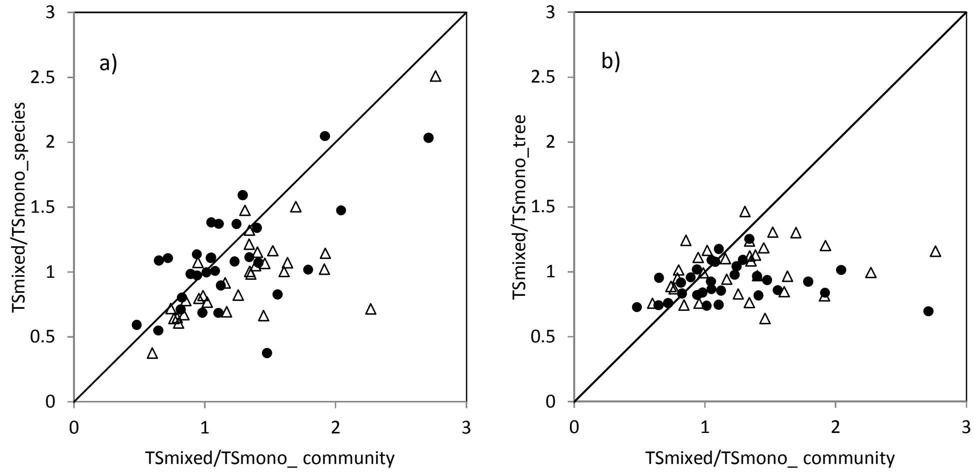


Fig 2. Relationship between mixing effects on temporal stability in basal area increment ($TS_{mixed}/TS_{mono}$) at different organizational levels for *F. sylvatica* (white triangles) and *P. sylvestris* (black circles); a) species vs. community levels; b) individual tree vs. community levels.

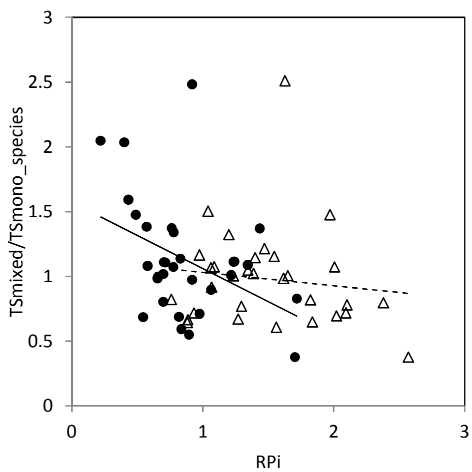


Fig. 3. Relationship between mixing effects on temporal stability in basal area increment at species level ($TS_{mixed}/TS_{mono}$) and relative productivity (RPi) for *F. sylvatica* (white triangles) and *P. sylvestris* (black circles). Straight lines are the linear trend lines, dashed for *F. sylvatica* (NS) and continue for *P. sylvestris* ($R^2$=0.17; P=0.023)

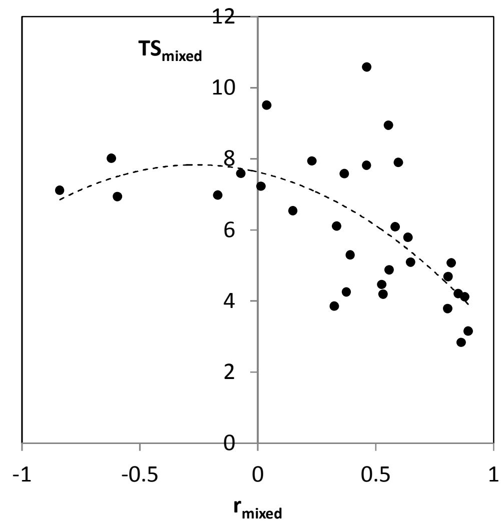


Fig 4. Temporal stability in stand basal area increment ($TS_{mixed}$) as a function of the coefficient of correlation between species increments in mixed stands ($r_{mixed}$) ($R^2$=0.40; P<0.001).

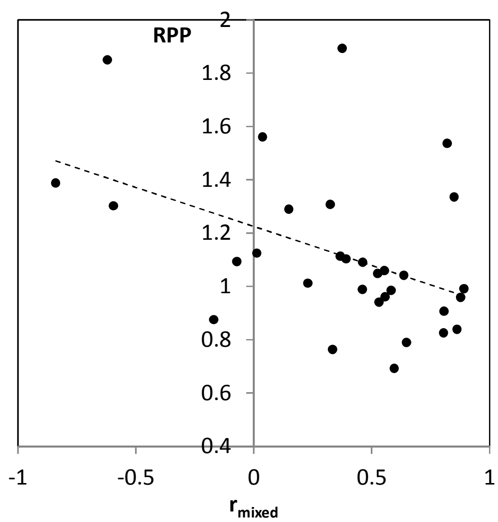


Fig 5. Relationship between overyielding (RPP) and the coefficient of correlation between species increments in mixed stands ($r_{mixed}$) ($R^2$=0.20; P=0.011).

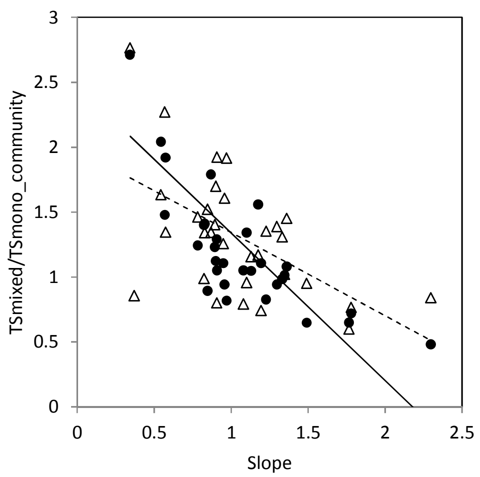


Fig. 6. Relationship between mixing effects on temporal stability in basal area increment ($TS_{mixed}/TS_{mono}$) at community level and slope of the major regression between observed and reference stand basal area growth indices in mixed stands ($IBAI_{mixed}=a+b\cdot IBAI_{reference}$; see text and Fig. S1 for additional information) for *F. sylvatica* (white triangles) and *P. sylvestris* (black circles). Straight lines are the linear trend lines, dashed for beech ($R^2$=0.32; P=0.001) and continue for pine ($R^2$=0.53; P<0.001).