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RESEARCH ARTICLE

Emerging stability of forest productivity by mixing two species buffers temperature destabilizing effect

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Abstract

1. The increasing disturbances in monocultures around the world are testimony to their instability under global change. Many studies have claimed that temporal stability of productivity increases with species richness, although the ecological

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fundamentals have mainly been investigated through diversity experiments. To adequately manage forest ecosystems, it is necessary to have a comprehensive understanding of the effect of mixing species on the temporal stability of productivity and the way in which it is influenced by climate conditions across large geographical areas.

2. Here, we used a unique dataset of 261 stands combining pure and two-species mixtures of four relevant tree species over a wide range of climate conditions in Europe to examine the effect of species mixing on the level and temporal stability of productivity. Structural equation modelling was employed to further explore the direct and indirect influence of climate, overyielding, species asynchrony and additive effect (i.e. temporal stability expected from the species growth in monospecific stands) on temporal stability in mixed forests.
3. We showed that by adding only one tree species to monocultures, the level (overyielding: +6%) and stability (temporal stability: +12%) of stand growth increased significantly. We identified the key effect of temperature on destabilizing stand growth, which may be mitigated by mixing species. We further confirmed asynchrony as the main driver of temporal stability in mixed stands, through both the additive effect and species interactions, which modify between-species asynchrony in mixtures in comparison to monocultures.
4. *Synthesis and applications*. This study highlights the emergent properties associated with mixing two species, which result in resource efficient and temporally stable production systems. We reveal the negative impact of mean temperature on temporal stability of forest productivity and how the stabilizing effect of mixing two species can counterbalance this impact. The overyielding and temporal stability of growth addressed in this paper are essential for ecosystem services closely linked with the level and rhythm of forest growth. Our results underline that mixing two species can be a realistic and effective nature-based climate solution, which could contribute towards meeting EU climate target policies.

KEYWORDS
additive effect, climate effect, forest ecosystems productivity, mixed forests, overyielding, species asynchrony, temporal stability

1 | INTRODUCTION

Forest ecosystems provide humankind with a wealth of ecosystem services. The necessary transition to a bioeconomy as a pathway towards the UN 2030 Sustainable Development Goals will require joint efforts in the near future to achieve a stable, sustainable flow of forest goods and services through nature-based solutions, the urgency of which is exacerbated by the pressure of accelerating climate change. In this context, the temporal stability of primary productivity is essential, not only for the current functioning of ecosystems (McCann, 2000) but also for securing the long-term provision of ecosystem services associated with productivity (Baeten et al., 2019).

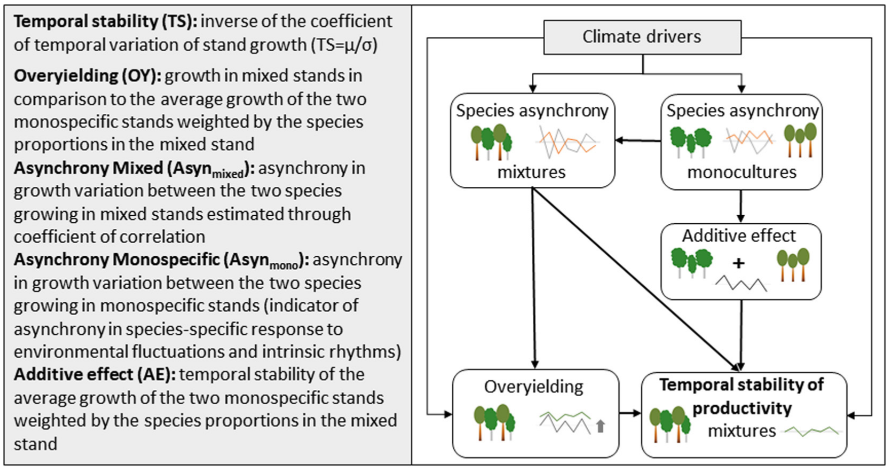
There is compelling evidence that tree species diversity may enhance forest primary productivity (Huang et al., 2018; Jactel et al., 2018; Liang et al., 2016) and its temporal stability (Jucker et al., 2014; Schnabel et al., 2019). The greater productivity is mainly due to tree species niche complementarity and facilitation which allow for a greater supply, capture or use of light, water and nutrient resources (Ammer, 2019). The stabilizing effect of species diversity can be explained by the insurance hypothesis, which states that species diversity insures against declines in functioning (i.e. greater stability) because some species will maintain functioning even if others fail (Yachi & Loreau, 1999). The temporal stability of productivity is usually estimated as the inverse of the coefficient of temporal variation ($TS = \mu/\sigma$). Thus, species diversity may enhance temporal stability by increasing the mean productivity (μ) *'performance-enhancing effect'* or by reducing the variance (σ) *'buffering effect'* over time (Hector et al., 2010; Tilman et al., 1998; Yachi & Loreau, 1999). Overyielding (Figure 1) has frequently been used to evaluate the effect of species diversity on community productivity in forest ecosystems (Pretzsch & Forrester, 2017), although its effect on the temporal stability of productivity (*performance enhancing effect*) is unclear, with previous research providing contrasting results (del Río et al., 2017; Jucker et al., 2014; Schnabel et al., 2019). However, there is consensus that the *buffering effect* emerges mainly from asynchrony fluctuations in productivity among species (Loreau et al., 2021). The existing analyses of forest ecosystems also point to a major role of species asynchrony (del Río et al., 2017; Dolezal et al., 2020; Jucker et al., 2014; Morin et al., 2014; Schnabel et al., 2021; Yuan et al., 2019), although the underlying mechanisms remain still unclear. Species asynchrony in mixtures may result from asynchronous species-specific responses to environmental fluctuations and intrinsic rhythms, although other factors such as species interactions or demographical stochasticity may also play a part (Loreau et al., 2021; Loreau & De Mazancourt, 2013). The two first mechanisms could theoretically be inferred from species-specific behaviours in monospecific stands, so between-species asynchrony in the respective monocultures may indirectly explain part of the species diversity stabilizing effect (Figure 1).

Beyond the underlying mechanisms, for forest management, it is important to infer to what extend mixing species can increase temporal stability of productivity. For this aim, it can be useful to estimate the average of species temporal stability in monocultures weighted by the species abundance in the mixture (Figure 1), referred to henceforth as *'additive effect'* (Forrester & Pretzsch, 2015; Jourdan et al., 2021), since it reflects the reduction in variance that can result from averaging out variations in species productivities when species are added and behave as they would do in monocultures.

Climate change can modify forest productivity (Pretzsch et al., 2014) and increase its variability due to the higher vulnerability to extreme climatic events (Anderegg et al., 2015; Choat et al., 2012). Several recent studies have revealed the impact of climate conditions on the temporal stability of ecosystem productivity and, more generally, on diversity–stability relationships (Garcia-Palacios et al., 2018; Hallett et al., 2014; Ma et al., 2017). Only a few studies have focused on this aspect for forest ecosystems (del Río et al., 2017; Jing et al., 2022; Jourdan et al., 2021; Ouyang et al., 2021), which still do not allow, a comprehensive understanding of climate as a driver of the temporal stability of forest productivity.

Although it is accepted that productivity increases with the number of species following an asymptotic pattern (Liang et al., 2016; Tilman et al., 1997), it is becoming increasingly patent that the underlying mechanisms start as soon as two species are mixed in forest ecosystems (Pretzsch & Forrester, 2017). To what extent this pattern can be extended to temporal stability of productivity is of great relevance to forest ecosystems management given that (i) there are already large areas of mixed forests composed of two species; (ii) from a management perspective, transition from monospecific to two-species mixed forests is often a more realistic option than direct conversion to multispecies forests.

In Europe, approximately 33% of the forested area is composed of monocultures (Van Brusselen et al., 2020). However, in relation to climate change, there are concerns about the ability of these forests to maintain their productivity over the long term. Recent observations suggest that monocultures are more vulnerable to biotic and abiotic hazards than mixed-species forests (Jactel et al., 2017; Knoke et al., 2008). In this study, we examine the temporal stability of stand growth (as an indicator of productivity) and its main drivers in monocultures and two-species mixtures along a climate gradient in Europe. We use a unique dataset of 261 plots including beech (*Fagus sylvatica* L.), oak (*Quercus robur* L. and *Q. petraea* [Matt.] Liebl.) or spruce (*Picea abies* [L.] H. Karst.) in combination with pine (*Pinus sylvestris* L.). All these tree species are native, productive and economically valuable for the European forestry sector, with the greatest values of growing stocks (Freudenschuss et al., 2020). In a previous study, we used 93 beech and pine plots to study temporal stability of productivity in mixed and monospecific stands at different organizational levels (tree, population, community; del Río et al., 2017). Here, we focus on the community level and specifically aim to: (i) assess the effect of two-species mixing on stand growth performance (overyielding) and temporal stability; (ii) evaluate direct and indirect effects of climate conditions on temporal stability; and



Temporal stability (TS): inverse of the coefficient of temporal variation of stand growth ($TS=\mu/\sigma$)

Overyielding (OY): growth in mixed stands in comparison to the average growth of the two monospecific stands weighted by the species proportions in the mixed stand

Asynchrony Mixed ($\text{Asyn}_{\text{mixed}}$): asynchrony in growth variation between the two species growing in mixed stands estimated through coefficient of correlation

Asynchrony Monospecific ($\text{Asyn}_{\text{mono}}$): asynchrony in growth variation between the two species growing in monospecific stands (indicator of asynchrony in species-specific response to environmental fluctuations and intrinsic rhythms)

Additive effect (AE): temporal stability of the average growth of the two monospecific stands weighted by the species proportions in the mixed stand

FIGURE 1 Definitions of temporal stability of stand growth in mixed stands and of its main drivers and hypotheses of mediated and causal effects among them.

(iii) determine which driver is the most relevant to explain temporal stability in mixtures. We hypothesize that: (H1) mixing two species results in overyielding and greater temporal stability of productivity; (H2) climate, overyielding and species asynchrony are the main direct drivers of temporal stability; (H3) the additive effect explains an important part of the temporal stability in two-species mixtures.

2 | MATERIALS AND METHODS

2.1 | Dataset

The data used come from 87 triplets distributed in three transects with different tree species compositions across Europe (Figure 2). Each triplet was composed of a two-species mixed plot and two related monospecific plots of their component species growing under similar site conditions (261 plots). The studied species compositions were beech–pine (32 triplets), oak–pine (35 triplets) and spruce–pine (20 triplets). The triplets covered a wide range of climatic conditions, with mean annual temperatures ranging from 3.2 to 11.1°C and mean annual total precipitation from 502 mm to 1336 mm (more details in Table S1 in Supporting Information). Plots were established in mature, mostly monolayered, fully stocked stands without signs of recent thinning interventions. Plot sizes ranged from 0.02 to 1.55 ha, where the diameter of all trees was measured, and two increment cores per tree were taken at a 1.3 m stem height in a sample of approximately 20 trees per species and plot. Annual ring widths were measured and cross-dated using standardized dendrochronological techniques. See Pretzsch et al. (2015, 2020) and Ruiz-Peinado et al. (2021) for more details on field measurements and main stand characteristic calculations (Table S2). Fieldwork permits were obtained from the respective forest owners when required. Ethical approval was not required.

The annual stand basal area increment (BAI, $m^2\ ha^{-1}\ year^{-1}$) was used as an indicator of community productivity (del Río et al., 2017; Dolezal et al., 2020), as this variable can be precisely estimated from field measurements and in forest stands is highly correlated with net above-ground productivity. The studied period was 2000–2013 for the beech–pine transect and 2004–2017 for the oak–pine and spruce–pine transects, the last year corresponding to triplet establishment. The series of annual stand basal area increments for the studied period (14 years) were estimated based on measured tree diameters and tree ring width series. Using data from cored trees, tree diameter increment–diameter models were fitted by year, species and plot to estimate annual diameter increments of noncored trees.

Annual climate data were obtained from meteorological weather stations located in the proximity of each triplet (50 triplets). When local station data were not available, national digital climatic atlas data (24 triplets) or more general gridded data (13 triplets) were used (see Table S1). For analyses, we considered the average mean annual temperature (T), total annual precipitation (P) and the Martonne aridity index ($M = P/[T+10]$) (Martonne, 1926) during the studied period, as they describe the large variability of climates in the study area (Figure 2), and are related to productivity variation at large scales in a simple way (Huang & Xia, 2019). In a preliminary analysis, we also explored the effects of the standard deviation and coefficient of variation of climate variables (Craven et al., 2018), but finally we discarded them due to their high correlations to the mean values (Figure S1).

2.2 | Overyielding

Overyielding (OY_j) was estimated for the 14-year study period by triplet j through the ratio of absolute productivity (Pretzsch & Forrester, 2017), which compares the observed productivity in the mixed stand (BAI_{mixed}) with the expected productivity if the two species would grow as in the monospecific stands (BAI_{exp}). The expected productivity was derived from the average productivity of the two species in neighbouring monospecific stands (BAI_{sp1_mono}, BAI_{sp2_mono}) weighted by species proportion in mixed stand (m_{sp1}, m_{sp2}) (see calculation of species proportion in Table S3).

$$OY_j = \frac{BAI_{mixed}}{BAI_{exp}} = \frac{BAI_{mixed}}{\left(BAI_{sp1\_mono} \cdot m_{sp1} + BAI_{sp2\_mono} \cdot m_{sp2}\right)}. \quad (1)$$

At the population level, we estimated the relative productivity by species (RP_{sp}) (Pretzsch & Forrester, 2017), that is, the ratio of the observed productivity of the species k in the mixture (BAI_{spk_mixed}) upscaled to the hectare to the observed productivity of species k in the monoculture (BAI_{spk_mono}) (see Table S3).

2.3 | Temporal stability

The temporal stability of productivity (TS) in each plot i was calculated as the inverse of the coefficient of temporal variation of BAI during the 14-year period, that is, the ratio of the mean to the standard deviation (s) (Equation 2).

$$TS_i = \frac{\overline{BAI}}{s_{BAI}}. \quad (2)$$

2.4 | Additive effect

We estimated the additive effect (AE) for each triplet as the expected temporal stability if the two species would grow like in the respective monocultures (Figure 1; Jourdan et al., 2021). First, we calculated the expected productivity for each year y,

$$BAI_{exp\_y} = BAI_{sp1\_mono\_y} \cdot m_{sp1\_y} + BAI_{sp2\_mono\_y} \cdot m_{sp2\_y}. \quad (3)$$

being all the variables like in equation 1. Then, we calculated the expected temporal stability as the inverse of the coefficient of variation of $BAI_{exp\text{-}y}$ during the 14 years (see Equation 2).

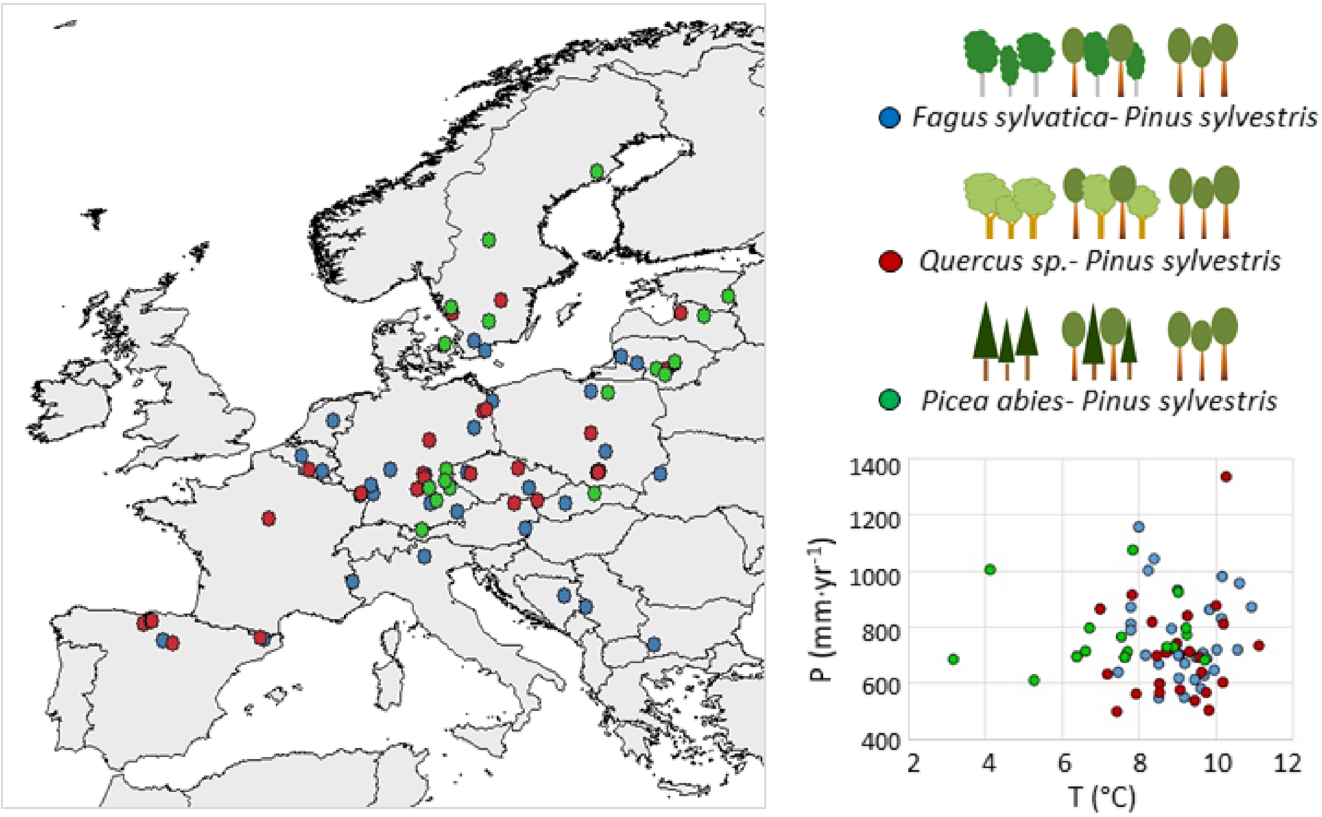


FIGURE 2 Location of the 87 triplets corresponding to the three transects: beech–pine, oak–pine (red), spruce–pine (green). Bottom-right panel shows the distribution of triplets by average site temperature (axis *x*) and precipitation (axis *y*).

2.5 | Between-species asynchrony

The asynchrony in a mixed plot ($\text{Asyn}_{\text{mixed}}$) was estimated following the synchrony metric proposed by Gross et al. (2014), that is, the average across species of correlation coefficients, which for two species mixtures results in the correlation coefficient between the two species growth series during the 14-year period, $\text{Asyn}_{\text{mixed}} = 1 - \text{corr}\ (\text{BAI}_{\text{sp1\_mixed}}, \text{BAI}_{\text{sp2\_mixed}})$. Additionally, we estimated in a similar way the asynchrony between the two species growing in monospecific stands (Figure 1) ($\text{Asyn}_{\text{mono}} = 1 - \text{corr}\ (\text{BAI}_{\text{sp1\_mono}}, \text{BAI}_{\text{sp2\_mono}})$). We also tested the metric community-wide asynchrony (Loreau & de Mazancourt, 2008), but the results were very similar as the two asynchrony metrics were highly correlated, $r = 0.93$.

2.6 | Statistical analysis

2.6.1 | Overyielding and temporal stability

To test whether OY was significantly greater than 1, we used a one-sided Student's t-tests. We tested mean OY of all triplets and by transect, as well as the relative productivity by species and by transect.

Whether TS was greater in mixed than in monospecific stands was evaluated by linear mixed models considering the type of composition (*Ty*: mixed vs. monospecific) as a fixed factor and the triplet as a random factor (Equation 4). TS was log-transformed to achieve normality of residuals.

$$\ln(\text{TS})_{ijk} = \mu + Ty_k + t_j + \varepsilon_{ijk}, \tag{4}$$

where TS_{ijk} is the temporal stability of productivity of plot *i*, in triplet *j*, of type of composition *k*; *Ty* is the type of composition; t_j is a random effect of the triplet; μ is the intercept of the model, and ε_{ijk}represents the independent and identically distributed residual error, both assumed to follow a normal distribution with mean zero and variance σ_j^2 and σ_e^2. A similar model was fitted by transect considering the identity of species composition (*Id*: mixed, monospecific species 1, monospecific species 2) as the fixed factor.

$$\ln(\text{TS})_{ijk} = \mu + Id_k + t_j + \varepsilon_{ijk}. \tag{5}$$

Differences between the three species mixtures (*Mix*: beech–pine, oak–pine, spruce–pine) were also explored using only data from mixed plots by a simple linear regression model.

$$\ln(\text{TS})_{jk} = \mu + \text{Mix}_k + \varepsilon_{jk}. \tag{6}$$

2.6.2 | Climate effects on TS

To analyse the influence of climate on TS, climate variables were added to Equation 4, including the interaction with the type of species composition.

$$\ln(\mathrm{TS})_{ijk} = \mu + Ty_k + Cli_j + Ty_k * Cli_j + t_j + \varepsilon_{ijk}, \tag{7}$$

where Cli_j represents the different climate variables tested (*T*, *P*, *M*, although *M* was not significant in the final models) in triplet *j*, and all other terms are defined analogously to those in Equation 4.

Then, we explored the overall climate effect on TS when considering the identity of species composition instead of the type of composition. We analysed all data together, including the seven levels of identity of species composition (*Id*: beech, oak, spruce, pine, beech–pine, oak–pine, spruce–pine).

$$\ln(\mathrm{TS})_{ijk} = \mu + Id_k + Cli_j + Id_k * Cli_j + t_j + \varepsilon_{ijk}. \tag{8}$$

To test whether the climate effect varied among the three mixtures, we included the climate in Equation 6 and fitted it using only mixed plots.

$$\ln(\mathrm{TS})_{jk} = \mu + \mathrm{Mix}_k + \mathrm{Mix}_k * Cli_j + \varepsilon_{jk}. \tag{9}$$

Selection of the best models was performed based on AIC and the *F*-test based on the extra sum of squares principle. The selected model was fitted by the restricted maximum likelihood procedure (REML). All models were fitted using the lme procedure from the NLME package in R (Pinheiro et al., 2021).

2.6.3 | Drivers of TS

The effect of drivers other than climate on TS in mixed stands ($\mathrm{TS}_{\mathrm{mixed}}$) was explored by simple linear regression using only data of mixtures. As potential drivers, we tested $\mathrm{Asyn}_{\mathrm{mixed}}$ and OY. We further explored the relationships between $\mathrm{TS}_{\mathrm{mixed}}$ and additive effect (AE).

To unravel the direct and indirect effects of climate and other drivers on $\mathrm{TS}_{\mathrm{mixed}}$, we applied structural equation modelling (SEM) (Shipley, 2016), using data of mixtures. As direct drivers of $\mathrm{TS}_{\mathrm{mixed}}$, we included climate variables, OY and $\mathrm{Asyn}_{\mathrm{mixed}}$ (Hector et al., 2010; Loreau & De Mazancourt, 2013; Figure 1). We also considered AE as direct factor, which may explain the effect of averaging species-specific variability. We included a path from $\mathrm{Asyn}_{\mathrm{mixed}}$ to OY, since a positive relationship has been previously reported (Allan et al., 2011), which could represent an indirect effect of $\mathrm{Asyn}_{\mathrm{mixed}}$ on TS. We also assumed that $\mathrm{Asyn}_{\mathrm{mono}}$ reflects the asynchrony in species-specific responses to environmental fluctuations and intrinsic rhythms in a given site, so it may explain a large part of $\mathrm{Asyn}_{\mathrm{mixed}}$ and AE. Accordingly, as $\mathrm{Asyn}_{\mathrm{mixed}}$ and the additive effect could covary, we included the covariance between them in the model. Moreover, we expected that climate could influence TS indirectly through changes in overyielding (Jactel et al., 2018) and in $\mathrm{Asyn}_{\mathrm{mixed}}$ (Ma et al., 2017). The preliminary analyses of the effect of different drivers on TS indicated that both temperature and precipitation modulated TS and that overyielding did not have any effect. Thus, overyielding was removed in the final fitted SEM to reduce paths due to the limited number of data from mixed stands ($n = 87$; Figure S2). All endogenous variables were log-transformed to achieve normality. We fitted the SEM based on a maximum likelihood method and used the χ^2 test, the comparative fit index (CFI) and standardized root mean square residual (SRMR) to evaluate the fit of the model. SEM fitting was performed using the R package LAVAAN (Rosseel, 2012).

3 | RESULTS

3.1 | Higher level and stability of stand growth in forest mixtures

We found that the overall mean overyielding across mixture types was 1.062 ($\ln(\mathrm{OY}) > 0$ *p*-value = 0.0446), that is, growth was 6.2% greater in mixtures than expected by the growth in monocultures. Overyielding (in %) was 9.5% ($\ln(\mathrm{OY}) > 0$ *p*-value = 0.0511) in the beech–pine mixture, 5.6% (OY >1 *p*-value = 0.0329) in the oak–pine mixture and 2% (OY >1 *p* value = 0.2195) in the spruce–pine mixture, with high variability within each mixture (Figure 3, Table S3, Figure S3). Beech, oak and spruce significantly benefited from the mixture by increasing their growth, while pine showed similar (beech–pine and oak–pine) or slightly lower (spruce-pine) growth than did the monocultures (Table S3).

The temporal stability of stand growth was 12.3% greater in mixed ($\mathrm{TS}_{\mathrm{mixed}} = 6.12$) than in monospecific ($\mathrm{TS}_{\mathrm{mono}} = 5.45$) stands (*p* value = 0.0016, Table S4a, Figure S4). There were no significant differences between the three species mixtures (Table S4e). TS was significantly improved for both beech and pine in the beech–pine mixture, for only pine in oak–pine mixtures and only spruce in spruce–pine mixtures (Figure 3, Table S4b–d).

3.2 | Climate effect on temporal stability of stand growth

Increasing the mean temperature had an overall negative effect on TS ($p < 0.0022$) in both monospecific and mixed stands, indicating a greater variability in stand growth at warmer sites (Figure 4a, Table S5a,b). In contrast, the effect of annual precipitation was only significant when the identity of species composition was considered in the analysis (Table S5b). The TS of beech–pine mixtures slightly increased with higher precipitation, whereas that of spruce–pine decreased (Figure 4). The stability of the oak–pine mixture growth was not affected by precipitation. The stabilizing effect of mixing species (i.e. difference between mixed and monospecific stands) was stronger under higher precipitation for the beech–pine mixture (Figure 4b) and weaker for spruce–pine (Figure 4d). When comparing the three mixtures, there were only slight differences among the precipitation effect

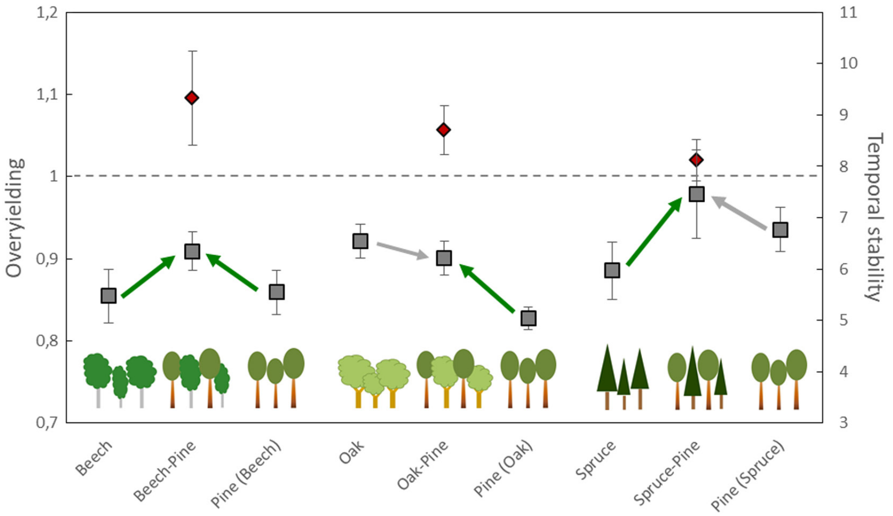


FIGURE 3 Overyielding (red diamonds) and temporal stability of stand growth (grey quadrats) for the three types of mixtures: beech–pine, oak–pine, spruce–pine (mean and standard error). Temporal stability is given for monospecific and mixed stands. Green arrows indicate significant stabilizing effects by mixing species, and grey arrows indicate nonsignificant effects (Table S4).

on their TS (Table S5c; Figure S5). The effect of climate variables on overyielding was also tested, but we did not find any significant effect.

3.3 | Drivers of temporal stability of stand growth in mixed forest stands

Simple linear regressions (Table S6) indicated that among the different drivers tested, the additive effect had the strongest relationship (positive) with $\mathrm{TS}_{\mathrm{mixed}}$ ($R^2 = 0.34$, $p < 0.0001$). $\mathrm{Asyn}_{\mathrm{mixed}}$ was also positively correlated with $\mathrm{TS}_{\mathrm{mixed}}$ ($R^2 = 0.21$, $p < 0.0001$), while overyielding did not show any relation. Interestingly, $\mathrm{Asyn}_{\mathrm{mixed}}$ had a significant effect on overyielding.

The results of the SEM confirmed the direct negative effect of temperature (−0.21) and reflected the relevance of species asynchrony on $\mathrm{TS}_{\mathrm{mixed}}$ (Figure 5; Table S7). Precipitation had an indirect weak influence ($0.06 = 0.25 \times 0.24$) on $\mathrm{TS}_{\mathrm{mixed}}$ through its positive effect (0.25) on $\mathrm{Asyn}_{\mathrm{mixed}}$. $\mathrm{Asyn}_{\mathrm{mono}}$ indirectly explained $\mathrm{TS}_{\mathrm{mixed}}$ by the effect on $\mathrm{Asyn}_{\mathrm{mixed}}$ and by AE (Figure 5, Table S7). It is noteworthy that $\mathrm{Asyn}_{\mathrm{mixed}}$ increased $\mathrm{TS}_{\mathrm{mixed}}$ beyond the AE. This reflects the effect of species interactions, which may modify the species fluctuations in mixed stands in comparison to monospecific stands, emerging in more stable forest stands. However, the AE effect was greater (0.50) than the direct effect of $\mathrm{Asyn}_{\mathrm{mixed}}$ (0.24).

4 | DISCUSSION

Based on observational data of three relevant mixtures with Scots pine and another tree species across Europe, we demonstrate that adding one species to monocultures yields important benefits in terms of the level and stability of community productivity. We further reveal the negative effect of temperature on TS and the relative importance of different factors acting on the stability gain.

The significant mean OY and greater stability in mixtures confirm results from previous overarching analysis that include two-species forest mixtures (Jactel et al., 2018; Jucker et al., 2014; Pretzsch & Forrester, 2017), as well as a previous analysis on beech–pine transect (del Río et al., 2017). It highlights general complementarity and buffering effects in mixtures in terms of stand growth. However, the magnitude of mixtures' benefits can vary with species composition (Figure 3), which suggests the importance of species traits on diversity effects (Baeten et al., 2019; Craven et al., 2018; Schnabel et al., 2021) and the need to assess specific species compositions.

Previous results from experimental studies point to a high relevance of climate conditions for TS (Craven et al., 2018; Schnabel et al., 2021), but their results cannot be easily generalized to other sites. Our observational approach allowed us to address for the first time the effect of climate on TS for specific forest mixtures along their main distribution range. We identify the destabilizing effect of temperature on stand productivity for all the studied forest types, as found for other plant communities (Ma et al., 2017; Valencia et al., 2020). Greater temperatures may be linked to sites where the species show greater climate sensitivity, which might increase growth variability. Nonetheless, the large variability observed (Figure 4a) points to the need for a deeper analysis considering monthly climate variables and local growing seasons to clarify the reasons for the observed temperature effect. Although the temperature destabilizing effect was common for monocultures and mixtures, the positive effect of mixing species on TS may counterbalance the negative effect of temperature. The greater TS in mixed stands was, on average, equivalent to the TS of corresponding monocultures under ≈2°C lower temperature (Figure S6), although uncertainty is large.

In accordance with other studies (Ouyang et al., 2021; Valencia et al., 2020), TS was also modulated by annual precipitation, but we found distinct effects depending on species identities in monospecific and mixed stands (Figure 4) (Jourdan et al., 2021). We did not find any climate influence on OY, as found in previous analyses of beech–pine and spruce–pine transects for a shorter period (Pretzsch et al., 2015; Ruiz-Peinado et al., 2021), but against those of the oak–pine transect (Pretzsch et al., 2020). Nevertheless, precipitation may have an indirect positive influence on OY, as found by Jactel et al. (2018), through its effect on $\mathrm{Asyn}_{\mathrm{mixed}}$ (Table S6).

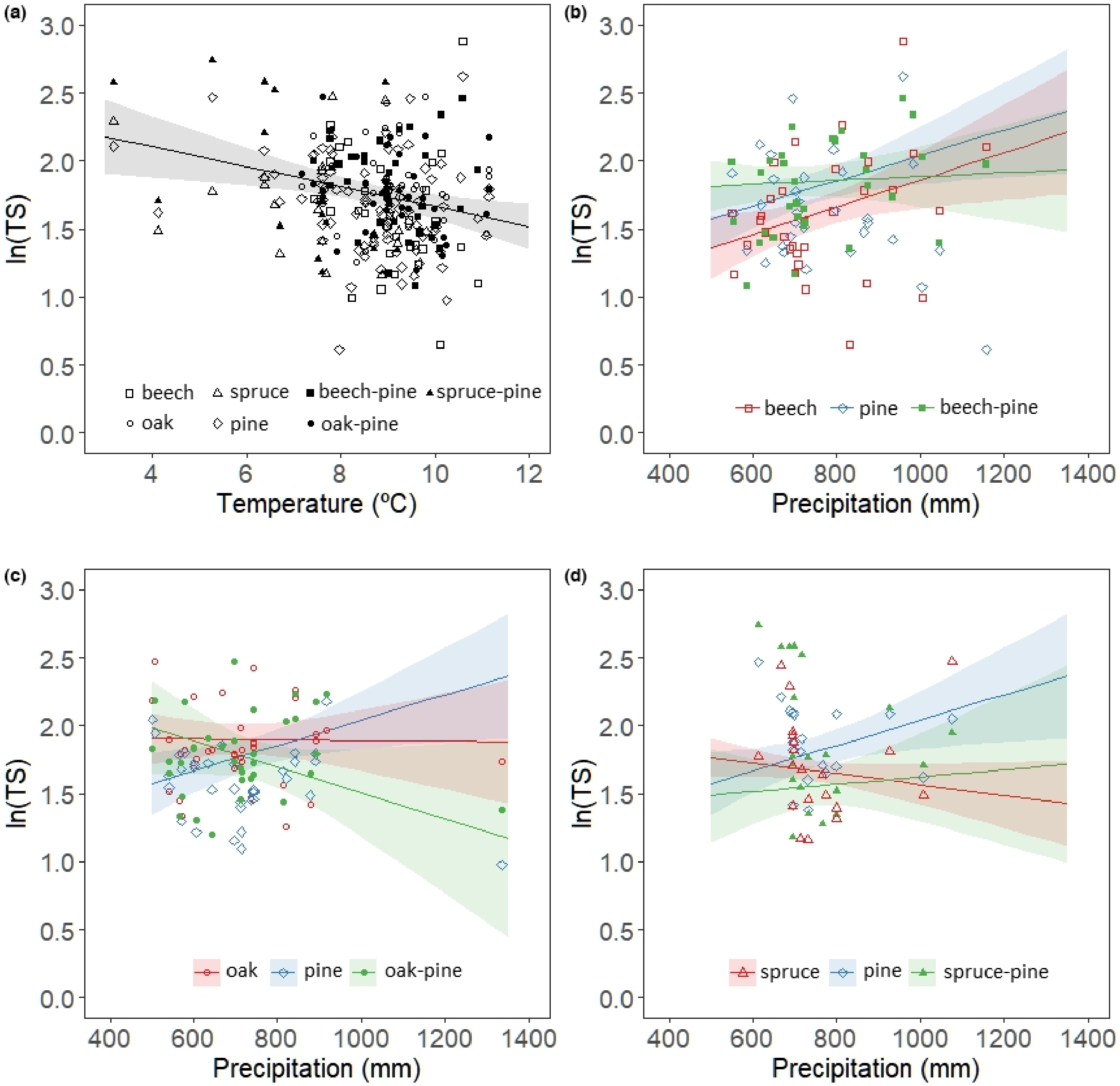


FIGURE 4 Climate effects on temporal stability of stand growth (in logarithm, ln(TS)), according to the model 'equation 8' presented in Table S5b (marginal effects): general effect of mean annual temperature (a); effect of annual precipitation on monospecific and mixed stands of beech–pine (b), oak–pine (c) and spruce–pine (d) transects. Shaded areas represent 95% confidence intervals (fixed effects).

Asynchrony in species productivities is often reported as the main driver of the greater TS with increasing species diversity (Blüthgen et al., 2016; Schnabel et al., 2021; Yuan et al., 2019). By exploring Asyn$_{mixed}$ and Asyn$_{mono}$, we demonstrated the relevant effect of asynchrony through two complementary mechanisms (Figure 5), that is, the difference between intrinsic species-specific fluctuations (responses to climatic variations and intrinsic rhythms) and species interactions, which results in the stabilizing effect of mixing species as predicted by the insurance hypothesis (Yachi & Loreau, 1999). Accordingly, our results reveal the substantial influence of AE on TS (Jourdan et al., 2021), which suggests the potential stabilizing effect by mixing any tree species (van der Plas, 2019), even when mixed by patches (i.e. spatial stability, (Loreau et al., 2021)). Asyn$_{mixed}$ also had a positive effect on OY, which indicates the presence of temporal niche complementarity and points asynchrony in species growth as a key driver of forest ecosystem functioning (van der Plas, 2019). The lack of influence of OY on TS reveals that TS increased by the variance buffering effect (Schnabel et al., 2021) and that OY and TS were independent effects (Cardinale et al., 2013; Jing et al., 2022). However, caution is needed for causal interpretation of our SEM results given the observational, not experimental, approach.

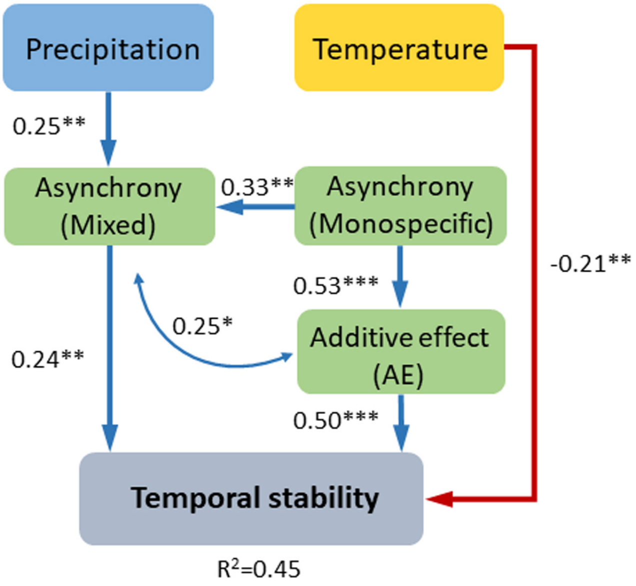


FIGURE 5 Structural equation model illustrating the direct and indirect drivers of the temporal stability of stand growth in mixed-species forests ($n = 87$). Arrows indicate significant pathways with the adjacent number indicating the standardized path coefficients, and $^*p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$; blue and red colours indicate positive and negative effects, respectively; the double arrow reflects covariance terms. R^2 indicates the proportion of variance explained (see Table S7).

We found that on average, in two-species stands, growth was 6% higher than expected and that temporal stability was 12% higher than in monospecific stands. Although the level and stability of productivity may increase with the number of species (Liang et al., 2016; Schnabel et al., 2021; Vilà et al., 2013), we demonstrate that adding one additional species to monocultures has already a strong effect. Monocultures of conifers, such as pine and spruce stands, are efficient systems for timber supply because of their high growth rates and simplified management. However, admixing just one species in these stands could stabilize the provision of wood and other ecosystem services linked with the level and stability of growth, such as nutrient and water cycling, carbon sequestration and storage or protective functions (Knoke et al., 2008), beyond the reduction and distribution of risks under higher climate uncertainty (Jactel et al., 2017). These findings underline that promoting two-species mixtures can be a realistic and effective nature-based climate solution, supporting the sustainability of forest productivity and contributing further to climate change mitigation (Mori et al., 2021).

AUTHOR CONTRIBUTIONS

Miren del Río, Hans Pretzsch and Andrés Bravo-Oviedo conceived the ideas and designed methodology; Hans Pretzsch, Ricardo Ruiz-Peinado, Magnus Löf, Jorge Aldea, Mathias Steckel and Michael Heym compiled and elaborated the data; Miren del Río, Ricardo Ruiz-Peinado and Charlotte Poeydebat performed the analyses; Miren del Río led the writing with inputs from Hans Pretzsch, Ricardo Ruiz-Peinado, Hervé Jactel, Luís Coll, Magnus Löf, Sonia Condés, Andrés Bravo-Oviedo; Miren del Río, Hans Pretzsch, Ricardo Ruiz-Peinado, Lluís Coll, Magnus Löf, Jorge Aldea, Christian Ammer, Admir Avdagić, Ignacio Barbeito, Kamil Bielak, Felipe Bravo, Gediminas Brazaitis, Jakub Cerný, Catherine Collet, Lars Drössler, Marek Fabrika, Michael Heym, Stig-Olof Holm, Gro Hylen, Aris Jansons, Viktor Kurylyak, Fabio Lombardi, Bratislav Matović, Marek Metslaid, Renzo Motta, Thomas Nord-Larsen, Arne Nothdurft, Jan den Ouden, Maciej Pach, Marta Pardos, Quentin Ponette, Tomas Pérot, Ditlev Otto Juel Reventlow, Roman Sitko, Vit Sramek, Mathias Steckel, Miroslav Svoboda, Kris Verheyen, Sonja Vospernik, Barbara Wolff, Tzvetan Zlatanov contributed data. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICTS OF INTERESTS

The authors declare no conflicts of interests.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.0rxwdbs3r (del Río et al., 2022).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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