100 YEARS Journal of Ecology British Ecological Society

Journal of Ecology 2015, **103**, 502–512 doi: 10.1111/1365-2745.12353

Overyielding in mixed forests decreases with site productivity

Maude Toïgo[1], Patrick Vallet[1]*, Thomas Perot[1], Jean-Daniel Bontemps[2,3], Christian Piedallu[2,3] and Benoit Courbaud[4]

[1]*IRSTEA, UR EFNO Ecosystèmes Forestiers, F-45290 Nogent-sur-Vernisson, France;* [2]*AgroParisTech Centre de Nancy UMR 1092 INRA/AgroParisTech LERFoB (Laboratoire d'Étude des Ressources Forêt-Bois), F-54000 Nancy, France;* [3]*INRA Centre de Nancy-Lorraine UMR 1092 INRA/AgroParisTech LERFoB (Laboratoire d'Etude des Ressources Forêt-Bois), F-54280 Champenoux, France; and* [4]*IRSTEA UR EMGR Ecosystèmes Montagnards Centre de Grenoble, F-38402 St Martin d'Hères, France*

Summary

1. There is a rising interest in the role of species diversity in ecosystem functioning and services, including productivity. Yet, how the diversity–productivity relationship depends on species identity and abiotic conditions remains a challenging issue.

2. We analysed mixture effects on species productivity along site productivity gradients, calculated from a set of abiotic factors, in two biogeographic contexts (highlands and lowlands). We compared the productivity of 5 two-species mixtures (i.e. 10 cases of mixed species) with that of monocultures of the same species. Five main European tree species were considered: sessile oak (*Quercus petraea* Liebl.), Scots pine (*Pinus sylvestris* L.), European beech (*Fagus sylvatica* L.), silver fir (*Abies alba* Mill.) and Norway spruce (*Picea abies* (L.) H. Karst).

3. Our data set was compiled from the 2006 to 2010 French National Forest Inventory data base and covers 2361 plots including pure and mixed stands.

4. Overall productivity of mixtures in highlands, that is European beech–Norway spruce, European beech–silver fir and to a lesser extent, silver fir–Norway spruce, was found to be higher than expected from the productivity of corresponding monospecific stands. Overyielding was mainly due to European beech for the first two mixtures and to silver fir for the third one.

5. No effect of mixture was found for sessile oak–Scots pine and sessile oak–European beech stands in lowlands. Overyielding of sessile oak mixed with Scots pine was not strong enough to significantly increase overall stand productivity. Overyielding of European beech was balanced by an underyielding of sessile oak.

6. The mixture effect changed along site productivity gradients for six cases out of the 10 studied, with a stronger and positive effect on sites with low productivity. The magnitude of this change along site productivity gradients varied up to 89% depending on the tree species.

7. *Synthesis.* The nature of species interaction in mixtures with regard to productivity changes with species assemblage and abiotic conditions. Overyielding is strongest when species grow in highlands on less productive sites. A negative link between mixture effect and site productivity was found, in line with the stress-gradient hypothesis.

Key-words: abiotic gradient, basal area increment, diversity, National Forest Inventory, plant–plant interactions, site productivity index, tree

Introduction

There is a rising interest in the role species diversity plays in ecosystem services and in ecosystem functioning (Cardinale *et al.* 2012; Hooper *et al.* 2012; Gamfeldt *et al.* 2013). Particular emphasis has been placed on the effect of vegetation diversity on ecosystem productivity, the so-called diversity–productivity relationship (Rajaniemi 2003). This relationship has been studied both in herbaceous communities (Hector *et al.* 1999) and in forests (Zhang, Chen & Reich 2012) with contrasting results ranging from positive to negative (Mittelbach *et al.* 2001). How abiotic conditions shape these

*Correspondence author: E-mail: patrick.vallet@irstea.fr

relationships in ecosystem productivity is a crucial question. Species interactions are dependent on the abiotic conditions, but little is known about how the sign and the magnitude of the outcome of interactions change along abiotic gradients (Chamberlain, Bronstein & Rudgers 2014).

Sampling effects and complementarity are the two classic mechanisms proposed to explain the positive effect of diversity on productivity (Loreau & Hector 2001). Sampling effects stem from the fact that, within a limited regional species pool, the probability that a community will include a highly productive dominant species increases with species richness (Tilman, Lehman & Thomson 1997) and this may blur the processes influencing productivity in highly diverse communities. Complementarity encompasses facilitation and resource partitioning. Facilitation is defined as the improvement of a given species' habitat by its neighbouring species (Vandermeer 1989; e.g. when nurse species such as shrubs protect seedlings from solar radiation; Callaway 1992), or the increase in a limiting resource thanks to another species (e.g. N_2-fixing species can increase available nitrogen; Forrester *et al.* 2006). Resource partitioning refers to how species with dissimilar ecological niches share resources in a way that leads to a higher total consumption of resources per surface unit than in monocultures (Jolliffe 1997). Resource partitioning can also occur due to differences in resource use efficiency (Nijs & Impens 2000), differences in annual growth rhythms leading to a spatial or temporal complementarity in resource use (Pretzsch 2005), plasticity in soil or light resource acquisition (Jumpponen *et al.* 2002; Ishii, Azuma & Nabeshima 2013) or stand vertical structure (Morin *et al.* 2011) leading to canopy stratification (Ishii & Asano 2010).

Most studies on the effects of diversity on productivity have been conducted in limited abiotic contexts and do not explicitly take into account possible variations related to changing abiotic conditions. Yet, the environmental-context dependency of the complementarity effect has been found for facilitation as well as resource partitioning. The stress-gradient hypothesis (Bertness & Callaway 1994) posits a transition from competition in favourable environments to facilitation in harsh environments, also suggested by Grime's (1977) triangle of plant strategies. The stress gradient may be defined by comparing species productivity across biomes with contrasted abiotic conditions (e.g. arid environment versus temperate). However, the species pools differ between these biomes. Because species are more or less adapted to particular abiotic conditions, how the abiotic context is actually growth limiting for the species considered is difficult to state. A stronger positive effect of diversity has been found in boreal forest compared to temperate forest (Paquette & Messier 2011), and despite the more harsh conditions in the boreal biome, the question of the environmental determinism of this result remains (Zhang, Chen & Reich 2012; Ruiz-Benito *et al.* 2014). Identifying the abiotic factors limiting species growth and quantifying the change in species productivity with the variation of those factors at a local scale is needed for an appropriate definition of site productivity gradients. Fridley (2003) found that soil fertility promotes resource partitioning for light by enhancing canopy stratification, and Forrester *et al.* (2013) hypothesized that the effect of root stratification might be stronger at low fertility sites where competition for resources is higher. These studies underscore the influence of the abiotic conditions on the diversity effect and stress the importance of defining site productivity gradients relative to the abiotic factors limiting species growth.

Studying the diversity–productivity relationship in forests ecosystems is particularly difficult. First, the long life span of tree species and the size of mature trees make it difficult to carry out experiments in controlled conditions with homogeneous soils and climates, especially for mature forests. Only a few long-term experiments exist and they include a limited number of species (Brown 1992; Pretzsch 2005; Boyden *et al.* 2009). Secondly, forest growth models need to take into account more factors than those in herbaceous communities, in particular ageing effects (or effects related to developmental stage) and effects associated with silvicultural practices that control the level of growing stock. Examples of overyielding have been detected in the few long-term experiments which compare pure versus two-species tree mixtures (Brown 1992; Pretzsch *et al.* 2013) and in studies using large-scale data bases such as national forest inventories (del Rio & Sterba 2009; Vallet & Pérot 2011).

In our work, we studied whether a given tree species is more productive when grown in a mixture than in a monoculture and whether this mixture effect on species productivity depends on site productivity indices made up of explicit abiotic factors limiting species growth. We also compared the overall productivity of a mixed stand to the cumulative productivity in corresponding monospecific stands. Studying communities with low levels of diversity (i.e. two-species mixtures) allowed us to reduce the sampling effects (Fridley 2001). Because the outcome of interactions depends on species assemblage, we hypothesized that the mixture effect on species productivity would depend on species identity in the mixture. Based on the stress-gradient hypothesis and Forrester *et al.* (2013), we hypothesized that the species overyielding due to complementarity would be stronger on low productivity sites. The explicit consideration of abiotic factors limiting species growth in the site productivity index enabled us to identify the possible drivers of the mixture effect.

Materials and methods

We used the French National Forest Inventory (NFI) data base (IFN 2011) to investigate mixture effect on species productivity in two-species mixtures at a national scale. The data set covered broad abiotic conditions in temperate forests, from oceanic to semi-continental climatic conditions and from lowlands to highlands. Annual mean temperatures ranged from 4.1 to 12.4 °C and annual precipitation from 600 to 2400 mm; site altitudes were from 6 to 1848 m. We compared productivity (basal area increment per hectare over 5 years) of species in sessile oak (*Quercus petraea* Liebl.)–European beech (*Fagus sylvatica* L.), sessile oak (*Quercus petraea* Liebl.)–Scots pine (*Pinus sylvestris* L.), European beech (*Fagus sylvatica* L.)–Norway spruce (*Picea abies* (L.) H. Karst.), European beech (*Fagus sylvatica* L.)–silver fir (*Abies alba* Mill.) and Norway spruce (*Picea abies* (L.) H. Karst.)–silver fir (*Abies alba* Mill.) mixtures with their corresponding monospecific stands. We chose species with contrasting characteristics (deciduous/coniferous, lowland/highland) among the most widespread in Europe.

NFI SAMPLING DESIGN

We used the 2006 to 2010 French annual NFI data sets. The NFI sampling is systematic and representative of the national forest resource. Each year, 6000–7000 temporary plots equally dispersed on a 1 km-by-1 km grid over the territory are measured (one-tenth of the grid is measured every year). Tree variables, such as circumference at conventional breast height (1.30 m), radial increment over 5 years and total height, are collected in three concentric subplots of 6, 9 and 15 m in diameter where, respectively, trees with a diameter at breast height (dbh) of dbh $\geq$ 7.5 cm, dbh $\geq$ 22.5 cm and dbh $\geq$ 37.5 cm are measured. Stand-scale variables (including vertical structure of the stand, topography, soil variables, harvesting during the last 5 years) and a floristic inventory complete the data.

PLOT SELECTION

In order to compare species productivity in pure stands and mixtures, we selected pure stands among NFI plots where the corresponding species represented 100% of the basal area. We retained plots for the two-species mixtures if the two studied species represented at least 80% of the total basal area and if the basal area of the other species present was less than that of each species studied (see Fig. S1 in Supporting Information for a description of the species proportions per plot). To avoid confounding effects from different abiotic growing conditions, mixed plots and their corresponding pure plots were selected in the same geographic area with similar abiotic conditions according to the GRECO ('Large Ecological Regions') variables as defined by the French NFI. To avoid confounding effects from silvicultural practices, plots were selected in stands dominated by one upper tree layer where no major cutting of the overstory had occurred in the past 5 years. We thus obtained a selection of 2361 plots (Fig. 1). In lowland forests, two broadleaved species (sessile oak and European beech) and one coniferous species (Scots pine) resulted in two possible mixtures: sessile oak–European beech and sessile oak–Scots pine. In highland forests, one broadleaved species (European beech) and two coniferous species (silver fir and Norway spruce) resulted in three possible two-species combinations. Because European beech had a broader altitudinal distribution in monospecific stands than in mixtures, we split the beech data set into lowlands (LL) and highlands (HL) before comparing productivity in monospecific stands and mixtures (Table 1).

ABIOTIC FACTORS

To characterize the set of abiotic factors limiting species growth in site productivity indices, we used plot variables provided by the NFI data base or extracted from geographic information system layers. The highest slope of the plot, in percentage, gave information on plot topography. Soil properties were given by the percentage of rocky outcrops, the major bedrock type (siliceous or limestone) and humus form: mull (eumul; mesomull; oligomull; dysmull), moder (moder; hemimoder; dysmoder) and mor (Brêthes *et al.* 1995). We used an index of soil water holding capacity (SWHC in millimetres) derived from soil texture, depth (in centimetres), percentage of stone content and rocky outcrops (Piedallu *et al.* 2011). A set of indicator values was derived from the floristic inventory: soil moisture (SM; Ellenberg 1992), soil acidity (pH), organic carbon to total nitrogen ratio as a measure of mineralization of organic matter (C : N) and base saturation (S : T) of the first soil layer (Gégout *et al.* 2005). The 30-year climatic normals for the 1961–1990 period came from the AURELHY Météo France spatial layer, we used mean, minimum and maximum monthly temperatures (*t* in Celsius degree) and precipitation (ppt in millimetres) averages at a 1-km resolution (Bénichou & le Breton 1987). Monthly potential evapotranspiration from June to August (PET in millimetres) was derived from climatic variables (Piedallu & Gégout 2007; Piedallu *et al.* 2013).

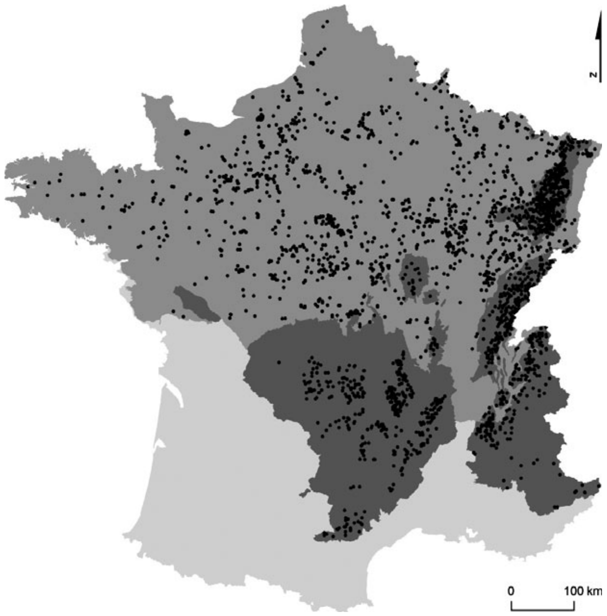

Fig. 1. Distribution of the study plots from the French NFI (black dots). We distinguished plots with European beech, sessile oak and Scots pine in lowlands (light grey) and plots with European beech, Norway spruce and silver fir in highlands (dark grey; IFN 2011).

MODELLING FRAMEWORK

To compare species productivity in pure stands and mixtures, we used the generic modelling framework developed by Vallet & Pérot (2011). The first step of the analysis consisted in modelling the productivity in pure stands, taking into account site productivity, growing stock and species developmental stage effects. In the second step, we computed the relative differences between the observed productivity of the species in mixed stands and the expected productivity given by the growth model in mixtures. As the models developed in pure stands take into account site productivity, growing stock, and species developmental stage effects, those relative differences represent the mixture effects. The third step consisted in analysing the influence of the site productivity on these mixture effects. We defined the site productivity index as a linear function of non-resource and resource factors represented by a set of abiotic factors that impact the productivity of a species in pure stands (Charru *et al.* 2010; Bontemps & Bouriaud 2014).

Since species-specific mixture effects in a given two-species forest may be of opposite signs and, at least partially, cancel out at the stand scale, we investigated mixture effects for both individual species and the overall stand. Because the abiotic determinants of the site productivity index may be different for the two species, we studied the dependency of the mixture effect in the site productivity index only for individual species.

We used NFI data to calculate stand attributes, such as basal area increment ($m^2\ ha^{-1}$ per 5 years), quadratic mean diameter (cm) and stand density index (see Appendix S1). The stand density index is the

Table 1. Means and standard deviations (SD) of the main dendrometric and climatic stand characteristics. For beech, we distinguished plots in lowlands (LL) and in highlands (HL). Average climatic conditions from the 1961 to 1990 period are considered

Species	Biogeographic contexts	Number of plots	Mean Elevation (m)	Mean annual temperature (°C)	Mean annual precipitation (mm)	Quadratic mean diameter (cm)	Mean basal area (m^2 ha^{-1})	Mean basal area increment (m^2 ha^{-1} per 5 years)
Pure stands								
Sessile oak	LL	334	184 (86)	10.4 (0.6)	752 (104)	33.0 (16.7)	20.1 (9.5)	2.5 (1.9)
Scots pine	LL	100	189 (117)	10.2 (0.7)	777 (119)	23.1 (10.1)	19.4 (10.7)	3.7 (2.8)
European beech	LL	129	242 (121)	9.5 (0.5)	881 (125)	35.2 (19.5)	19.5 (11.7)	3.0 (2.3)
European beech	HL	138	753 (364)	8.3 (1.2)	1274 (314)	31.9 (12.1)	27.5 (13.4)	2.5 (1.4)
Silver fir	HL	172	827 (274)	8.0 (1.1)	1210 (229)	30.7 (10.7)	35.9 (17.0)	4.5 (2.7)
Norway spruce	HL	257	910 (328)	7.6 (1.2)	1368 (296)	27.0 (9.8)	39.2 (18.7)	6.6 (3.5)
Mixed stands								
S. oak	LL	107	198 (104)	10.2 (0.6)	776 (132)	26.9 (12.8)	13.8 (8.9)	1.4 (0.9)
S. pine						36.7 (11.5)	13.8 (10.2)	1.2 (1.3)
S. oak	LL	469	270 (104)	9.8 (0.6)	882 (131)	44.1 (15.8)	14.3 (8.9)	1.1 (0.9)
E. beech						32.5 (15.3)	10.1 (7.0)	1.2 (1.0)
E. beech	HL	246	861 (281)	7.9 (1.0)	1417 (358)	28.3 (12.0)	13.1 (11.1)	1.4 (1.3)
S. fir						33.3 (13.5)	22.5 (14.7)	2.6 (2.1)
E. beech	HL	117	990 (276)	7.2 (1.5)	1521 (328)	26.0 (8.8)	17.3 (11.8)	1.5 (1.1)
N. spruce						36.1 (13.4)	18.7 (12.5)	1.8 (1.8)
N. spruce	HL	292	926 (302)	7.6 (1.1)	1439 (305)	33.7 (14.1)	17.9 (14.3)	2.3 (2.3)
S. fir						32.2 (12.9)	20.4 (15.4)	2.4 (1.9)

ratio between the number of stems in the stand and the maximum number of stems according to the self-thinning rule (Reineke 1933).

Model of species productivity in a pure stand

We used the calculated 5-year basal area increment as a response variable to model species productivity in pure stands (eqn 1):

$$\mathrm{BAI}_i = f_1(X_m) \times f_2(\mathrm{DI}) \times f_3(\mathrm{Dg}_i) + \varepsilon_i \qquad \text{eqn 1}$$

where BAI_i (m^2 ha^{-1} per 5 years) is the basal area increment of species i in a plot over 5 years; f_1 is a function of m abiotic variables (X_m) defining the abiotic factors limiting species growth; f_2 is a function of the growing stock represented by the stand density index (DI); and f_3 is a function of the developmental stage of species i represented by the quadratic mean diameter (Dg_i); ε_i are the model residuals assumed to be normally distributed and independent. In f_1 function, we discarded highly correlated abiotic variables and those retained were selected according to the Akaike information criterion (AIC; Akaike 1974). We selected the best model (i.e. model with the lowest AIC). The best and the second best models were presented in Table S1. The f_2 and f_3 functions were chosen according to scatter plot analysis (see Appendix S1) and the existing literature (Dhôte, Hatsch & Rittie 2000) in order to obtain robust and parsimonious forms. The detailed function is (eqn 2):

$$\mathrm{BAI}_i = \left(a_0 + \sum_{m=1}^{n}(a_{m,i} \times X_m)\right) \times \left(\frac{(1+b_i) \times \mathrm{DI}}{b_i + \mathrm{DI}}\right) \times \left(\frac{e^{\left(d_{1,i} \times (\mathrm{Dg}_i - 7.5)\right)}}{1 + d_{2,i}}\right) + \varepsilon_i \qquad \text{eqn 2}$$

where BAI_i (m^2 ha^{-1} per 5 years) is the basal area increment of species i in a plot over 5 years; X_m is a vector of abiotic factors; DI is the stand density index; Dg_i (cm) is the mean quadratic diameter of species i; a_0, $a_{m,i}$, b_i, $d_{1,i}$, $d_{2,i}$, are the estimated parameters. As both functions f_2 and f_3 are bounded by 0 and 1, the site productivity index f_1 corresponds to the maximum productivity of the stand for the species, that is when DI = 1 and Dg = 7.5 cm.

Mixture effect on the productivity of each species

In a second step, we compared the observed productivity of the species in a mixture to their expected productivity, all things being equal (i.e. abiotic factors limiting species growth, growing stock and species developmental stage; see Fig. S2) as suggested by Loreau (1998). We calculated the proportion of a given species i in a mixture as the ratio between the basal area of species i and the total basal area of the plot.

If x_i is the proportion of species i in the mixture, the expected productivity of species i in the mixture based on its productivity in pure stands is (Loreau 1998)

$$E_i = x_i \times \widehat{\mathrm{BAI}}_i \qquad \text{eqn 3}$$

where $\widehat{\mathrm{BAI}}_i$ is the productivity of species i in mixed stands predicted from the monospecific growth model (eqn 2).

If no mixture effect occurs, the observed productivity of species i in a mixture is equal to its expected productivity. If a mixture effect occurs, the observed productivity of species i in a mixture deviates from the expected productivity of species i. The 'mixture effect' is defined as the relative deviation from the expected productivity of species i in a pure stand (Loreau 1998). We calculated the mixture effect as follows (eqn 4):

$$u_{i,j} = \frac{\mathrm{BAI}_{i,j} - E_i}{E_i} \qquad \text{eqn 4}$$

where $u_{i,j}$ is the mixture effect on the basal area increment of species i in the mixture with species j, and $\mathrm{BAI}_{i,j}$ is the observed basal area increment of species i in a mixture with species j over 5 years. E_i is the expected basal area increment of species i in a mixture.

Exploratory analyses revealed that $u_{i,j}$ is a linear function of the proportion of other species in the mixture (see Fig. S3). We modelled $u_{i,j}$ calculated as follows (eqn 5):

$$u_{i,j}(x_i) = a_{0,i,j} \times (1 - x_i) + \varepsilon_i \qquad \text{eqn 5}$$

where $a_{0,i,j}$ is the estimated parameter giving the effect of species j on the basal area increment of species i. This form allowed us to set $u_{i,j}$

to zero when x_i was equal to 1 (pure stand). If $a_{0,i,j} > 0$, species i overyields; if $a_{0,i,j} < 0$, species i underyields.

To study whether the mixture effect is dependent on site productivity, we calculated the species i site productivity index (SPI_i) for every plot in mixtures from the estimated parameters of the f_1 function (eqn 2) and the corresponding abiotic factors X_m in mixtures:

$$\text{SPI}_i = \left(a_0 + \sum_{m=1}^{n} (a_{m,i} \times X_m) \right) \qquad \text{eqn 6}$$

We added the site productivity index to the 'mixture effect' model as an explanatory variable. We fitted the following model (eqn 7):

$$u_{i,j}(x_i, \text{SPI}_i) = (s_{0,i,j} + s_{1,i,j} \times \text{SPI}_i) \times (1 - x_i) + \varepsilon_i \qquad \text{eqn 7}$$

where $s_{0,i,j}$ and $s_{1,i,j}$ are the estimated parameters of the model. If $s_{1,i,j} > 0$, then the mixture effect on species productivity increases with the site productivity index, and if $s_{1,i,j} < 0$, then the mixture effect on species productivity decreases with the site productivity index. The nature of the mixture effect (overyielding or underyielding) is given by the sign of the mixture effect predicted by eqn 7.

Mixture effect on the overall productivity

To evaluate the mixture effect on overall stand productivity, we used the weighted average proportional deviation from the expected yield in a mixture as proposed by Loreau (1998):

$$\bar{u} = \frac{x_i}{x_i + x_j} \times u_{i,j} + \frac{x_j}{x_i + x_j} \times u_{j,i} \qquad \text{eqn 8}$$

Rearranging eqn 8 with eqns 3 and 4 leads to:

$$\bar{u} = \left(\frac{\text{BAI}_{i,j}}{\widehat{\text{BAI}}_i} + \frac{\text{BAI}_{j,i}}{\widehat{\text{BAI}}_j} \right) \times \left(\frac{1}{x_i + x_j} \right) - 1 \qquad \text{eqn 9}$$

We fitted the following form (eqn 10):

$$\bar{u} = a_0 \times x_i \times x_j + \varepsilon \qquad \text{eqn 10}$$

where $\bar{u}$ is the calculated mixture effect on overall stand productivity; $\text{BAI}_{i,j}/\widehat{\text{BAI}}_i$ and $\text{BAI}_{j,i}/\widehat{\text{BAI}}_j$ are the relative productivities of species i and j in the mixture; x_i and x_j are species i and species j proportions; the a_0 parameter, estimated with the model, directly gives the sign of the mixture effect on stand productivity.

Data were analysed with the R software v. 2.10 (R Development Core Team 2013). Models were fitted with weighted nonlinear regressions from the gnls function in the NLME package (Pinheiro *et al.* 2010), following power variance models (Pinheiro & Bates 2000).

$$Var = \sigma^2 |v|^{2\delta} \qquad \text{eqn 11}$$

where σ is the residual standard error, v the covariate and δ the power parameter to be fitted with the gnls procedure. To account for heteroscedasticity in the pure growth model (eqn 2), the weight was a power of the basal area increment value fitted with the gnls procedure. For mixture effect models (eqns 5 and 7), the weight was a power of species proportion. We used the significance threshold of 0.05 for all the estimated parameters; we also considered P-values comprised between 0.1 and 0.05 to be marginally significant. For models of species productivity in pure stands, we provided the normalized root mean square error (NRMSE) calculated as the ratio between RMSE and the mean of observed species productivity values. NRMSE is a relative value expressed in percentage. Low values of NRMSE indicated a high predictive power of the model.

Results

SPECIES PRODUCTIVITY IN PURE STANDS

In pure stands, stand basal area increment increased with growing stock and decreased with species development stage for all the studied species (Table 2). The NRMSE was the lowest for the Norway spruce BAI model and represented 5% of the mean BAI observed. The NRMSE was the highest for the European beech models and represented 15% of the mean BAI observed.

MIXTURE EFFECT ON OVERALL STAND PRODUCTIVITY AND SPECIES PRODUCTIVITY

Considering overall stand productivity, the three mixtures studied in highlands overyielded (Table 3): European beech–Norway spruce ($P < 0.001$), European beech–silver fir ($P < 0.001$) and silver fir–Norway spruce ($P = 0.088$; in decreasing order), mainly due to European beech and silver fir (Table 4). The mixture effect was non-significant for overall productivity of sessile oak–Scots pine ($P = 0.478$) and European beech–sessile oak ($P = 0.956$) mixtures in lowlands. For a mixture proportion of 50%, the observed productivity of the European beech–Norway spruce stand was 26% higher than expected (Fig. 2a).

When considering the mixture effect on the productivity of each species in mixtures (i.e. difference in productivity between one species in the mixture and the productivity of that species in a pure stand), five out of the 10 species studied overyielded, the mixture effect was not significant in four cases, and one species underyielded (Table 4). For a mixture proportion of 50%, observed European beech productivity in a mixture with Norway spruce was 51% higher than expected in pure stands (Fig. 2b).

VARIATIONS IN MIXTURE EFFECT ON SPECIES PRODUCTIVITY ALONG SITE PRODUCTIVITY GRADIENTS

Depending on the species, the SPI was made of two to four abiotic variables (see Appendix S2). As expected abiotic variables retained were species-specific, and ranged from climatic and soil chemistry to topographic variables (Table 2). The mixture effect on species productivity varied significantly according to the SPI for the species in highlands which corresponds to six out of the 10 cases studied (Table 5). The mixture effect increased from 10% to 99% for European beech mixed with Norway spruce from sites with high SPI to sites with low SPI (Fig. 3). Mixture increased species productivity more when SPI was low than when it was high (see Fig. S3). European beech always overyielded, whereas Norway spruce and silver fir shifted from overyielding to underyielding when SPI increased (Fig. 3). The mixture effect was not significantly influenced by SPI in the four cases in lowlands: sessile oak with Scots pine, Scots pine with sessile oak, sessile oak with European beech and European beech with sessile oak.

Table 2. Coefficients (Est.), *P*-values (*P*) and standard deviations (SD) of the six basal area increment models in pure stands (eqns 1 and 2) according to abiotic factors (f_1), growing stock (f_2) and developmental stage (f_3). We distinguished species in lowlands (LL) and in highlands (HL)

		Sessile oak (LL)				European beech (LL)				European beech (HL)				Scots pine (LL)				Norway spruce (HL)				Silver fir (HL)			
Function	Factors	Detail	Est.	SD	*P*	Detail	Est.	SD	*P*	Detail	Est.	SD	*P*	Detail	Est.	SD	*P*	Detail	Est.	SD	*P*	Detail	Est.	SD	*P*
f_1 (X_m)	Intercept		36.194	*5.390*	$<10^{-3}$		38.583	*7.075*	$<10^{-3}$		7.404	*3.094*	0.018		14.476	*2.067*	$<10^{-3}$		27.063	*3.458*	$<10^{-3}$		23.931	*5.698*	$<10^{-3}$
	t									December min.	0.809	*0.319*	0.013					January min.	1.020	*0.303*	$<10^{-3}$	March max.	1.002	*0.477*	0.037
	PET	July	−0.198	*0.043*	$<10^{-3}$	July	−0.245	*0.059*	$<10^{-3}$																
	Humus					Moder	−2.562	*0.821*	0.002	Moder	−1.787	*0.858*	0.039					Mull	4.330	*1.013*	$<10^{-3}$	Dysmoder	−5.498	*1.758*	0.002
	C : N		−0.171	*0.045*	$<10^{-3}$																				
	SWHC		0.035	*0.007*	$<10^{-3}$		0.031	*0.012*	0.012																
	SM										1.213	*0.544*	0.027												
	Rocky outcrops										−0.377	*0.147*	0.012		−1.251	*0.329*	$<10^{-3}$		−0.853	*0.232*	$<10^{-3}$				
	Bedrock	Limestone	−3.989	*0.821*	$<10^{-3}$									Limestone	−4.135	*1.084*	$<10^{-3}$								
	Slope																		−0.104	*0.028*	$<10^{-3}$		−0.215	*0.054*	$<10^{-3}$
f_2 (DI)	DI		1.002	*0.154*	$<10^{-3}$		0.812	*0.212*	$<10^{-3}$		0.743	*0.236*	0.002		0.471	*0.125*	$<10^{-3}$		0.816	*0.151*	$<10^{-3}$		0.623	*0.173*	$<10^{-3}$
f_3 (Dg_i)	Dg_i (d1)		−0.090	*0.007*	$<10^{-3}$		−0.050	*0.010*	$<10^{-3}$		−0.126	*0.036*	$<10^{-3}$		−0.071	*0.018*	$<10^{-3}$		−0.087	*0.014*	$<10^{-3}$		−0.096	*0.016*	$<10^{-3}$
	Dg_i (d2)		0.182	*0.013*	$<10^{-3}$		0.274	*0.049*	$<10^{-3}$		0.408	*0.110*	$<10^{-3}$		0.117	*0.063*	0.069		0.303	*0.036*	$<10^{-3}$		0.205	*0.037*	$<10^{-3}$
	δ	0.99				0.68				1.00				0.96				1.00				0.67			
	RMSE (NRMSE)	0.31 (12%)				0.45 (15%)				0.38 (15%)				0.38 (10%)				0.31 (5%)				0.63 (14%)			

Standard deviations are in italics. All the abiotic factors tested are included in the table. We specified only the estimated parameters including the power of variance function (δ), the root mean square error (RMSE) and the normalized root mean square error (NRMSE) of the selected best model. *t*, temperatures; PET, potential evapotranspiration; C : N, organic carbon to total nitrogen ratio; SWHC, soil water holding capacity; SM, soil moisture; DI, density index; Dg_i, quadratic mean diameter.

Discussion

Our results show that the nature of the mixture effect changes with species assemblage and abiotic conditions. Overyielding is strongest in highlands and on sites of weaker productivity corresponding to more growth-limiting abiotic conditions.

We used BAI as a measure of productivity, since it is the only growth variable actually measured by the NFI and does not require using allometric equations that would be needed to assess volume growth. Using these equations would bring additional uncertainty that could blur the effects we studied. Species interactions may cause a change in growth allocation from radial growth to height growth (Pinto *et al.* 2008), thus influencing tree morphology. Allometric relationships are usually calibrated in pure stands. Then, using them to estimate volumes or biomass in mixed stands would suffer from a possible modification of these relationships by the mixture. Our results on BAI would gain from being extended to volume in order to have a complete overview of how diversity–productivity relationships are modified by abiotic factors, but addressing this issue is not trivial on the NFI data.

THE NATURE OF THE MIXTURE EFFECT CHANGES WITH SPECIES ASSEMBLAGE

We found that depending on the mixture of species, species overyielded, underyielded or had equal productivity compared to monocultures (Fig. 2b). This result is consistent with findings in grasslands where species identity and species evenness have been put forward to explain the relationship between productivity and diversity (Wilsey & Potvin 2000; Assaf, Beyschlag & Isselstein 2011). On average, the three mixed stands in highlands, European beech–Norway spruce, European beech–silver fir and to a lesser extent, silver fir–Norway spruce mixtures overyielded (Fig. 2a) possibly due to a release of intraspecific competition in mixtures (Forrester *et al.* 2013). Overyielding was mainly due to European beech for the first two mixtures, the release of the strong beech intraspecific competition (Bolte, Kampf & Hilbrig 2013) in mixture held regardless of abiotic conditions (Fig. 3). For silver fir and Norway spruce, the nature of the mixture effect was dependent on abiotic conditions (Fig. 3), leading to a null mixture effect when averaged across the abiotic conditions studied. On the other hand, there is no mixture effect on the overall productivity of the two stands in lowlands, European beech–sessile oak and sessile oak–Scots pine stands. The null mixture effect for sessile oak–European beech stands hides an overyielding of European beech counter balanced by an underyielding of sessile oak. Based on the examination of the abiotic factors included in the site productivity index for the two species, both species were limited by resource proxies. Humus form and C : N ratio are both related to soil fertility, while the effects of SWHC and July PET are strongly linked to water availability. Sessile oak and European beech were competing for the same limiting resources, and the European beech overyielding indicates the competitive advantage of European beech over sessile oak and explains the observed

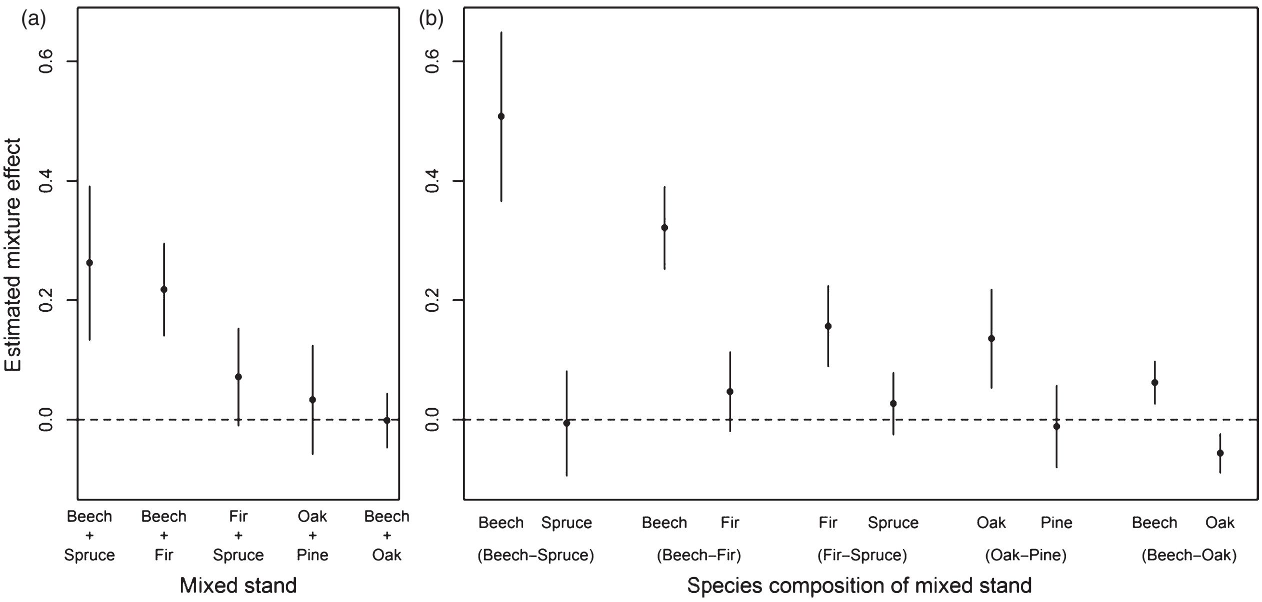

Fig. 2. Estimates and 95% confidence intervals of (a) the mixture effect on total stand productivity for the five mixtures (eqn 10), (b) the mixture effect on the productivity of each species in mixture (eqn 5). A proportion of 50% has been used for each species in the mixture. Beech with spruce refers to the mixture effect on the productivity of beech mixed with spruce.

Table 3. Coefficients (Est.), *P*-values (*P*) and standard deviations (SD) of mixture effect models (eqn 10) for the five mixtures in lowlands (LL) and highlands (HL): beech–spruce, beech–fir, fir–spruce, oak–pine, beech–oak

	Beech–Spruce (HL)		Beech–Fir (HL)		Fir–Spruce (HL)		Oak–Pine (LL)		Beech–Oak (LL)	
Mixtures	Est.	*P*	Est.	*P*	Est.	*P*	Est.	*P*	Est.	*P*
a_0	1.049	$<10^{-3}$	0.872	$<10^{-3}$	0.286	0.088	0.132	0.478	−0.005	0.956
SD	*0.263*		*0.158*		*0.167*		*0.186*		*0.093*	

Standard deviations are in italics.

null stand mixture effect. These results are in accordance with previous findings that have shown the high below-ground and above-ground competitiveness of beech (Rewald & Leuschner 2009; Longuetaud *et al.* 2013). Sessile oak overyielded when mixed with Scots pine (Fig. 2b), whereas it was not strong enough to increase the overall productivity of the stands (Fig. 2a). Scots pine is less resource-limited than sessile oak in the range of the studied abiotic conditions (Table 2) and the sessile oak overyielding we observed would imply that Scots pine is less competitive than sessile oak allowing a release of intraspecific competition for sessile oak in a mixture with Scots pine. A stronger mixture effect for sessile oak than for Scots pine was also observed by Pérot & Picard (2012); however, they found overyielding in sessile oak-Scots pine stands, which was not the case in our study. This difference could be explained by the fact that Pérot & Picard (2012) studied only one site, whereas we considered sessile oak-Scots pine stands in different ecological contexts throughout the country.

OVERYIELDING IS STRONGER ON UNPRODUCTIVE SITES AND IN HIGHLAND CONDITIONS

Abiotic factors as well as stand density (Forrester *et al.* 2013) and species developmental stage (Cavard *et al.* 2011) shape the diversity–productivity relationship. Our results show that mixture effect varied with site productivity for European beech, silver fir and Norway spruce. In five out of 10 forest types, species underyielded (negative mixture effect) on highly productive sites, and in eight out of 10 forest types, species overyielded (positive mixture effects) on sites with the lowest productivity (Fig. 3). This result is in accordance with the stress-gradient hypothesis. Variations of the mixture effect with site productivity indices revealed that overyielding is stronger for highland species on low productivity sites (Fig. 3), which are often located at higher altitudes. Pretzsch *et al.* (2010) studied the productivity of a European beech–Norway spruce lowland mixture along a site productivity gradient and found a greater positive effect on productive sites

Table 4. Coefficients (Est.), *P*-values (*P*) and standard deviations (SD) of mixture effect models (eqn 5) for each species in lowlands (LL) and highlands (HL): beech–spruce, beech–fir, fir–spruce, oak–pine and beech–oak mixtures were considered

Mixtures	Beech–Spruce (HL)				Beech–Fir (HL)				Fir–Spruce (HL)				Oak–Pine (LL)				Beech–Oak (LL)			
	Beech		Spruce		Beech		Fir		Fir		Spruce		Oak		Pine		Beech		Oak	
Species	Est.	*P*	Est.	*P*	Est.	*P*	Est.	*P*	Est.	*P*	Est.	*P*	Est.	*P*	Est.	*P*	Est.	*P*	Est.	*P*
$a_{0,i,j}$	1.015	$<10^{-3}$	−0.012	0.889	0.643	$<10^{-3}$	0.094	0.168	0.313	$<10^{-3}$	0.054	0.310	0.271	0.002	−0.023	0.746	0.124	$<10^{-3}$	−0.113	$<10^{-3}$
SD	*0.145*		*0.089*		*0.070*		*0.068*		*0.069*		*0.053*		*0.084*		*0.070*		*0.037*		*0.033*	

Standard deviations are in italics.

Table 5. Coefficients (Est.), *P*-values (*P*) and standard deviations (SD) of mixture effect variation with site productivity models (eqn 7) for the five mixtures in lowlands (LL) and highlands (HL): beech–spruce, beech–fir, fir–spruce, oak–pine, beech–oak

Mixtures	Beech–Spruce (HL)				Beech–Fir (HL)				Fir–Spruce (HL)				Oak–Pine (LL)				Beech–Oak (LL)			
	Beech		Spruce		Beech		Fir		Fir		Spruce		Oak		Pine		Beech		Oak	
Species	Est.	*P*	Est.	*P*	Est.	*P*	Est.	*P*	Est.	*P*	Est.	*P*	Est.	*P*	Est.	*P*	Est.	*P*	Est.	*P*
$s_{0,i,j}$	3.014	$<10^{-3}$	1.425	$<10^{-3}$	1.646	$<10^{-3}$	1.556	$<10^{-3}$	2.370	$<10^{-3}$	0.875	$<10^{-3}$	−0.042	0.918	0.711	0.300	0.299	0.182	0.073	0.623
SD	*0.554*		*0.287*		*0.453*		*0.315*		*0.315*		*0.255*		*0.413*		*0.683*		*0.224*		*0.148*	
$s_{1,i,j}$	−0.230	$<10^{-3}$	−0.080	$<10^{-3}$	−0.098	0.026	−0.064	$<10^{-3}$	−0.085	$<10^{-3}$	−0.041	$<10^{-3}$	0.031	0.440	−0.053	0.283	−0.016	0.428	−0.016	0.200
SD	*0.062*		*0.015*		*0.044*		*0.014*		*0.013*		*0.012*		*0.039*		*0.049*		*0.020*		*0.013*	

Standard deviations are in italics.

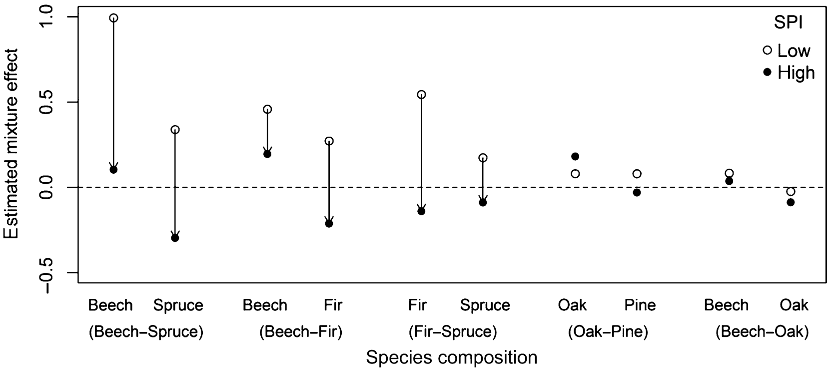

Fig. 3. Variation in the mixture effect on individual species with site productivity index (SPI) (eqn 7), for a species proportion of 50%. Species overyield when the mixture effect is positive and underyield when it is negative. Arrows indicate an increase in SPI [from the 5th percentile (i.e. low SPI) to the 95th percentile (i.e. high SPI)]. Significant effects are indicated by black lines; non-significant effects are indicated by grey lines.

for beech. This result was discussed in terms of the high competitiveness of European beech, which we also found for European beech mixed with sessile oak, indicating that either the intensity or the nature of the mechanisms involved is different in lowlands and highlands. The greater sensitivity of the mixture effect to site productivity for highland species in our study may be related to the fact that the site productivity range for Norway spruce and silver fir was broader than for sessile oak and Scots pine in lowlands (see Appendix S2). Nevertheless, we found no evidence of a change in mixture effect with site productivity for lowland European beech with sessile oak, whereas we did for highland European beech, even though the site productivity range was similar. The stress-gradient hypothesis states that facilitative interactions are more frequent in sites with severe abiotic stress. Facilitation has been found to be more common in herbaceous communities at high altitudes and near the tree line; neighbours bring about a reduction in abiotic stress, which is more limiting for growth than resource availability at high altitudes (Callaway *et al.* 2002). In our study, the abiotic conditions were not so extreme. Our results show that even in less severe abiotic conditions, complementarity between species is frequent. Species for which the mixture effect varies with site productivity are all growth-limited by non-resource factors such as slope, rocky outcrops or temperature. In contrast, in the abiotic conditions studied here, lowland species were not limited by such non-resource abiotic factors indicating that non-resource abiotic factors can be important drivers of the diversity–productivity relationship (Maestre *et al.* 2009).

Conclusions

Over the set of species and abiotic conditions we studied, we found that overyielding was stronger for highland species on sites with low productivity. We used a site productivity index made up of explicit abiotic factors to identify growth-limiting abiotic conditions. Our results show that mixture effect depends on site productivity index only for highland species for which productivity index was driven by non-resource factors. These results suggest a stronger effect of non-resource factors than resource factors on the mixture effects. Complementary approaches such as experimental design, process-based models and trait-based approaches offer promising tools to disentangle the mechanisms underlying the complementarity effects (Morin *et al.* 2011; Roscher *et al.* 2012; Tobner *et al.* 2014).

Acknowledgements

This work was funded by the French National Forest Office. The authors thank J.C. Gégout for providing bio-indicator values for NFI sites, editors and referees for their constructive comments, as well as Vicki Moore for correcting the English.

Data accessibility

The 2006 to 2010 annual French NFI data sets used in this paper are available online at inventaire-forestier.ign.fr.

References

Akaike, H. (1974) A new look at the statistical model identification. *Automatic Control, IEEE Transactions on*, **19**, 716–723.

Assaf, T.A., Beyschlag, W. & Isselstein, J. (2011) The relationship between plant diversity and productivity in natural and in managed grasslands. *Applied Ecology and Environmental Research*, **9**, 157–166.

Bénichou, P. & le Breton, O. (1987) Prise en compte de la topographie pour la cartographie de champs pluviométriques statistiques: la méthode Aurelhy. *Colloques de l'INRA*, **39**, 51–69.

Bertness, M.D. & Callaway, R. (1994) Positive interactions in communities. *Trends in Ecology & Evolution*, **9**, 191–193.

Bolte, A., Kampf, F. & Hilbrig, L. (2013) Space sequestration below ground in old-growth spruce-beech forests – signs for facilitation? *Frontiers in Plant Science*, **4**, 1–11.

Bontemps, J.D. & Bouriaud, O. (2014) Predictive approaches to forest site productivity: recent trends, challenges and future perspectives. *Forestry*, **87**, 109–128.

Boyden, S.B., Reich, P.B., Puettmann, K.J. & Baker, T.R. (2009) Effects of density and ontogeny on size and growth ranks of three competing tree species. *Journal of Ecology*, **97**, 277–288.

Brêthes, A., Brun, J.J., Jabiol, B., Ponge, J.F. & Toutain, F. (1995) Classification of forest humus form: a French proposal. *Annales des Sciences Forestieres*, **52**, 535–546.

Brown, A.H.F. (1992) Functioning of mixed-species stands at Gisburn, NW England. *The Ecology of Mixed-Species Stands of Trees* (ed. M.G.R. Cannell), pp. 125–150. Blackwell Scientific; British Ecological Society Special Publication Series, 11.

Callaway, R.M. (1992) Effect of shrubs on recruitment of *Quercus douglasii* and *Quercus lobata* in California. *Ecology*, **73**, 2118–2128.

Callaway, R.M., Brooker, R.W., Choler, P., Kikvidze, Z., Lortie, C.J., Michalet, R. *et al.* (2002) Positive interactions among alpine plants increase with stress. *Nature*, **417**, 844–848.

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P. *et al.* (2012) Biodiversity loss and its impact on humanity. *Nature*, **486**, 59–67.

Cavard, X., Bergeron, Y., Chen, H.Y.H., Paré, D., Laganière, J. & Brassard, B. (2011) Competition and facilitation between tree species change with stand development. *Oikos*, **120**, 1683–1695.

Chamberlain, S.A., Bronstein, J.L. & Rudgers, J.A. (2014) How context dependent are species interactions? *Ecology Letters*, **17**, 881–890.

Charru, M., Seynave, I., Morneau, F. & Bontemps, J.D. (2010) Recent changes in forest productivity: an analysis of national forest inventory data for common beech (*Fagus sylvatica* L.) in north-eastern France. *Forest Ecology and Management*, **260**, 864–874.

Dhôte, J.F., Hatsch, E. & Rittie, D. (2000) Stem taper curves, volume tables and volume yield compartments in Sessile Oak. *Annals of Forest Science*, **57**, 121–142.

Ellenberg, H. (1992) Zeigerwerte der Gefäßpflanzen (ohne *Rubus*). *Scripta Geobotanica*, **18**, 9–166.

Forrester, D.I., Bauhus, J., Cowie, A.L. & Vanclay, J.K. (2006) Mixed-species plantations of Eucalyptus with nitrogen-fixing trees: a review. *Forest Ecology and Management*, **233**, 211–230.

Forrester, D.I., Kohnle, U., Albrecht, A.T. & Bauhus, J. (2013) Complementarity in mixed-species stands of *Abies alba* and *Picea abies* varies with climate, site quality and stand density. *Forest Ecology and Management*, **304**, 233–242.

Fridley, J.D. (2001) The influence of species diversity on ecosystem productivity: how, where, and why? *Oikos*, **93**, 514–526.

Fridley, J.D. (2003) Diversity effects on production in different light and fertility environments: an experiment with communities of annual plants. *Journal of Ecology*, **91**, 396–406.

Gamfeldt, L., Snall, T., Bagchi, R., Jonsson, M., Gustafsson, L., Kjellander, P. *et al.* (2013) Higher levels of multiple ecosystem services are found in forests with more tree species. *Nature Communications*, **4**, 1340.

Gégout, J.C., Coudun, C., Bailly, G. & Jabiol, B. (2005) EcoPlant: A forest site database linking floristic data with soil and climate variables. *Journal of Vegetation Science*, **16**, 257–260.

Grime, J.P. (1977) evidence for existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *The American Naturalist*, **111**, 1169–1194.

Hector, A., Schmid, B., Beierkuhnlein, C., Caldeira, M.C., Diemer, M., Dimitrakopoulos, P.G. *et al.* (1999) Plant diversity and productivity experiments in European grasslands. *Science*, **286**, 1123–1127.

Hooper, D.U., Adair, E.C., Cardinale, B.J., Byrnes, J.E.K., Hungate, B.A., Matulich, K.L., Gonzalez, A., Duffy, J.E., Gamfeldt, L. & O'Connor, M.I. (2012) A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature*, **486**, 105–108.

IFN (2011) *Les Résultats Issus des Campagnes d'Inventaire 2006, 2007, 2008, 2009 et 2010*. Inventaire Forestier National, Nogent-sur-Vernisson, FR.

Ishii, H. & Asano, S. (2010) The role of crown architecture, leaf phenology and photosynthetic activity in promoting complementary use of light among coexisting species in temperate forests. *Ecological Research*, **25**, 715–722.

Ishii, H., Azuma, W. & Nabeshima, E. (2013) The need for a canopy perspective to understand the importance of phenotypic plasticity for promoting species coexistence and light-use complementarity in forest ecosystems. *Ecological Research*, **28**, 191–198.

Jolliffe, P.A. (1997) Are mixed populations of plant species more productive than pure stands? *Oikos*, **80**, 595–602.

Jumpponen, A., Högberg, P., Huss-Danell, K. & Mulder, C.P.H. (2002) Interspecific and spatial differences in nitrogen uptake in monocultures and two-species mixtures in north European grasslands. *Functional Ecology*, **16**, 454–461.

Longuetaud, F., Piboule, A., Wernsdörfer, H. & Collet, C. (2013) Crown plasticity reduces inter-tree competition in a mixed broadleaved forest. *European Journal of Forest Research*, **132**, 621–634.

Loreau, M. (1998) Separating sampling and other effects in biodiversity experiments. *Oikos*, **82**, 600–602.

Loreau, M. & Hector, A. (2001) Partitioning selection and complementarity in biodiversity experiments. *Nature*, **412**, 72–76.

Maestre, F.T., Callaway, R.M., Valladares, F. & Lortie, C.J. (2009) Refining the stress-gradient hypothesis for competition and facilitation in plant communities. *Journal of Ecology*, **97**, 199–205.

Mittelbach, G.G., Steiner, C.F., Scheiner, S.M., Gross, K.L., Reynolds, H.L., Waide, R.B., Willig, M.R., Dodson, S.I. & Gough, L. (2001) What is the observed relationship between species richness and productivity? *Ecology*, **82**, 2381–2396.

Morin, X., Fahse, L., Scherer-Lorenzen, M. & Bugmann, H. (2011) Tree species richness promotes productivity in temperate forests through strong complementarity between species. *Ecology Letters*, **14**, 1211–1219.

Nijs, I. & Impens, I. (2000) Underlying effects of resource use efficiency in diversity–productivity relationships. *Oikos*, **91**, 204–208.

Paquette, A. & Messier, C. (2011) The effect of biodiversity on tree productivity: from temperate to boreal forests. *Global Ecology and Biogeography*, **20**, 170–180.

Pérot, T. & Picard, N. (2012) Mixture enhances productivity in a two-species forest: evidence from a modeling approach. *Ecological Research*, **27**, 83–94.

Piedallu, C. & Gégout, J.C. (2007) Multiscale computation of solar radiation for predictive vegetation modelling. *Annals of Forest Science*, **64**, 899–909.

Piedallu, C., Gégout, J.C., Bruand, A. & Seynave, I. (2011) Mapping soil water holding capacity over large areas to predict potential production of forest stands. *Geoderma*, **160**, 355–366.

Piedallu, C., Gégout, J.C., Perez, V. & Lebourgeois, F. (2013) Soil water balance performs better than climatic water variables in tree species distribution modelling. *Global Ecology and Biogeography*, **22**, 470–482.

Pinheiro, J.C. & Bates, D.M. (2000) *Mixed-Effects Models in S and S-PLUS*. Springer, New York.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & Team, R.D.C. (2010) NLME: Linear and Nonlinear Mixed Effects Models. R package version 3.1-111.

Pinto, P.E., Gégout, J.C., Hervé, J.C. & Dhôte, J.F. (2008) Respective importance of ecological conditions and stand composition on *Abies alba* Mill. dominant height growth. *Forest Ecology and Management*, **255**, 619–629.

Pretzsch, H. (2005) Diversity and productivity in forests: evidence from long-term experimental plots. *Forest Diversity and Function* (eds M. Scherer-Lorenzen, C. Körner & E.-D. Schulze), pp. 41–64. Springer, Berlin, Heidelberg.

Pretzsch, H., Block, J., Dieler, J., Dong, P.H., Kohnle, U., Nagel, J., Spellmann, H. & Zingg, A. (2010) Comparison between the productivity of pure and mixed stands of Norway spruce and European beech along an ecological gradient. *Annals of Forest Science*, **67**, 712.

Pretzsch, H., Bielak, K., Block, J., Bruchwald, A., Dieler, J., Ehrhart, H.P., Kohnle, U., Nagel, J., Spellmann, H., Zasada, M. & Zingg, A. (2013) Productivity of mixed versus pure stands of oak (*Quercus petraea* (Matt.) Liebl. and *Quercus robur* L.) and European beech (*Fagus sylvatica* L.) along an ecological gradient. *European Journal of Forest Research*, **132**, 263–280.

R Development Core Team (2013) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. Avaliable at http://www.R-project.org/.

Rajaniemi, T.K. (2003) Explaining productivity–diversity relationships in plants. *Oikos*, **101**, 449–457.

Reineke, L.H. (1933) Perfecting a stand-density index for even-aged forests. *Journal of Agricultural Research, Washington*, **46**, 627–638.

Rewald, B. & Leuschner, C. (2009) Belowground competition in a broad-leaved temperate mixed forest: pattern analysis and experiments in a four-species stand. *European Journal of Forest Research*, **128**, 387–398.

del Rio, M. & Sterba, H. (2009) Comparing volume growth in pure and mixed stands of *Pinus sylvestris* and *Quercus pyrenaica*. *Annals of Forest Science*, **66**, 502.

Roscher, C., Schumacher, J., Gubsch, M., Lipowsky, A., Weigelt, A., Buchmann, N., Schmid, B. & Schulze, E.D. (2012) Using plant functional traits to explain diversity–productivity relationships. *PLoS One*, **7**, e36760.

Ruiz-Benito, P., Gomez-Aparicio, L., Paquette, A., Messier, C., Kattge, J. & Zavala, M.A. (2014) Diversity increases carbon storage and tree productivity in Spanish forests. *Global Ecology and Biogeography*, **23**, 311–322.

Tilman, D., Lehman, C.L. & Thomson, K.T. (1997) Plant diversity and ecosystem productivity: theoretical considerations. *Proceedings of the National Academy of Sciences of the United States of America*, **94**, 1857–1861.

Tobner, C.M., Paquette, A., Reich, P.B., Gravel, D. & Messier, C. (2014) Advancing biodiversity-ecosystem functioning science using high-density tree-based experiments over functional diversity gradients. *Oecologia*, **174**, 609–621.

Vallet, P. & Pérot, T. (2011) Silver fir stand productivity is enhanced when mixed with Norway spruce: evidence based on large-scale inventory data and a generic modelling approach. *Journal of Vegetation Science*, **22**, 932–942.

Vandermeer, J.H. (1989) *The Ecology of Intercropping*. Cambridge University Press, Cambridge, UK.

Wilsey, B.J. & Potvin, C. (2000) Biodiversity and ecosystem functioning: importance of species evenness in an old field. *Ecology*, **81**, 887–892.

Zhang, Y., Chen, H.Y.H. & Reich, P.B. (2012) Forest productivity increases with evenness, species richness and trait variation: a global meta-analysis. *Journal of Ecology*, **100**, 742–749.

Received 2 July 2014; accepted 20 November 2014
Handling Editor: Charles Canham

Supporting Information

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

Appendix S1. Calculation and scatter plots of basal area increment (BAI_i), mean quadratic diameter (Dg_i) and density index (DI).

Appendix S2. Description and calculation of the site productivity indices (SPI_i).

Figure S1. Species basal area proportion per plots in mixtures.

Figure S2. Densities of site productivity indices (SPI_i), mean quadratic diameters (Dg_i) and density indices (DI) for each species in pure plots and mixtures.

Figure S3. Scatter plots of the variation in the mixture effect on species i with species j proportion for three levels of site productivity index (SPI_i).

Table S1. Delta AIC of the best and the second best model of basal area increment.