

Competition for light and water play contrasting roles in driving diversity–productivity relationships in Iberian forests

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Summary

1. Mixed-species forests generally sequester and store more carbon in above-ground woody biomass compared to species-poor systems. However, the mechanisms driving the positive relationship between diversity and above-ground wood production (AWP) remain unclear.
2. We investigate the role of competition for light and water as possible sources of complementarity among Iberian pine and oak species. Using tree core data from permanent plots, we test the hypotheses that (i) contrasting abilities of pines and oaks to tolerate shade will promote AWP in mixtures, while (ii) drought stress results in less room for complementarity.
3. We found that pine species receive more light, develop larger crowns and grow 138–155% faster when in mixture with oaks. However, this positive effect of species mixing on growth was severely reduced under drought conditions due to increased competition for water with neighbouring oaks. In contrast to pines, oak trees were less responsive to mixing, primarily as a result of their ability to tolerate shade and water shortage.
4. Mixed pine-oak forests produce an average 48% more above-ground woody biomass compared to monocultures each year. However, the magnitude of the diversity effect on AWP fluctuates with time, decreasing noticeably in strength during drought years.
5. *Synthesis.* Complementary light use strategies among neighbouring trees are critical in explaining why above-ground wood production (AWP) increases in mixed-species stands. In contrast, drought causes trees in mixture to compete more fiercely for below-ground resources, leaving less room for complementarity and causing positive diversity effects to lessen in strength. Together, these two mechanisms provide much needed context for AWP–diversity relationships in Mediterranean forests. Whether or not managing for mixed pine-oak forests proves to be beneficial for AWP is likely to depend on how climate changes in the Iberian Peninsula.

Key-words: biodiversity and ecosystem function, biomass growth, drought tolerance, FunDivEUROPE, *Pinus*, plant–plant interactions, *Quercus*, shade tolerance, species richness

Introduction

Motivated by the threat of a global biodiversity crisis, ecologists have been trying to understand how biodiversity loss will affect the way in which ecosystems function (Schulze & Mooney 1993; Naeem *et al.* 1994; Loreau *et al.* 2001; Hooper *et al.* 2005, 2012; Tilman, Reich & Isbell 2012). Recent syntheses suggest that across a variety of systems, and for a number of ecological processes, diverse communities generally outperform ones which are species poor (Cardinale *et al.* 2012). Forest ecosystems are no exception, and mixed-species stands have been shown to harbour greater numbers of

associated taxa (Castagneyrol & Jactel 2012), exhibit fewer pest and pathogen outbreaks (Pautasso, Holdenrieder & Stenlid 2005; Jactel & Brockerhoff 2007), store more carbon below-ground (Brassard *et al.* 2011; Lei, Scherer-Lorenzen & Bauhus 2012; Gamfeldt *et al.* 2013), and cycle nutrients more efficiently (Rothe & Binkley 2001; Hättenschwiler 2005). Importantly, diverse forests also sequester and store a greater amount of carbon in above-ground woody biomass compared to monocultures (Vilà *et al.* 2007, 2013; Paquette & Messier 2011; Morin *et al.* 2011). This beneficial effect of admixing is substantial, amounting to an average 25% increase in productivity across forest types (Zhang, Chen & Reich 2012). Maintaining forest diversity is therefore not only a conservation priority, but has important implications for forest management practises and efforts to mitigate climate change.

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Consequently, understanding why above-ground wood production (AWP, in $\text{MgC ha}^{-1} \text{ year}^{-1}$) is greater in diverse forests is critical.

Here, we adopt a novel comparative approach based on controlled field observations made in permanent forest plots with different combinations of Iberian pines and oaks (Baeten *et al.* 2013). We ask whether mixing species with contrasting ecological strategies – light and water demanding pines vs. shade and drought tolerant oaks (Poorter *et al.* 2012) – results in the complementary use of resources in mixed-species stands, and explore the role of competition for light and water as possible candidate mechanisms behind positive AWP–diversity relationships in Mediterranean forests (Vilà *et al.* 2007; Ruiz-Benito *et al.* 2014).

Of the mechanisms which have been proposed to explain why diversity increases productivity (Hooper *et al.* 2005), complementarity effects offer an intuitive explanation as to why mixing tree species with contrasting life history traits can promote AWP. Complementarity effects influence ecosystem processes in two ways: by favourably shaping species interactions and by increasing resource use efficiency as a result of niche partitioning (Loreau & Hector 2001). Mixing tree species with contrasting ecological strategies can therefore increase AWP by alleviating competitive inhibition among neighbouring trees (Potvin & Gotelli 2008; Pretzsch & Schütze 2009; Gómez-Aparicio *et al.* 2011), and by allowing diverse forests patches to access a greater portion of available resources and growing space (Morin *et al.* 2011; Vilà *et al.* 2013; Brassard *et al.* 2013; Tobner *et al.* 2014). However, the fact that species compete for multiple resources complicates matters, as they might exhibit complementary use of one resource but not another (Scherer-Lorenzen *et al.* 2007; Forrester 2014). In Mediterranean forests, light and water are arguably the two primary resources for which trees compete (Valladares & Niinemets 2008; Poorter *et al.* 2012; Carnicer *et al.* 2013). The question therefore becomes whether pines and oaks can partition these resources in a way that is advantageous to both.

Competition for light is a major determinant of forest structure and growth (Coomes, Lines & Allen 2011). At the stand level, mixing species with complementary crown architectures, leaf economics and phenological strategies results in vertically structured canopies that intercept a greater portion of incoming solar radiation (Morin *et al.* 2011; Seidel *et al.* 2013). Indeed, contrasting abilities of species to tolerate shade is thought to be one of the primary mechanisms through which diversity can promote AWP (Zhang, Chen & Reich 2012). Changes in the way light is distributed through the canopy can also directly benefit the growth of individual trees by alleviating competition among neighbours in mixtures (e.g. Pretzsch & Schütze 2009). This is likely to be especially true for light demanding species, which tend to exhibit suppressed growth as a result of competition for light when in monoculture (Gómez-Aparicio *et al.* 2011). Furthermore, trees which experience reduced competition for light from neighbours have been shown to invest a greater portion of their resources in expanding their crowns, thereby reinforcing the beneficial

effects of diversity on growth (Pretzsch & Schütze 2005; Kim *et al.* 2011; Dieler & Pretzsch 2013).

Below-ground competition for water is also an important driver of tree growth (Coomes & Grubb 2000; Craine & Dyzinski 2013; Brzostek *et al.* 2014). During drought events, competition for water among neighbouring trees increases, leading to decreased growth (Gómez-Aparicio *et al.* 2011). However, it remains unclear whether mixed-species stands are more or less susceptible to drought compared to monocultures. While some studies have reported decreased sensitivity to drought of species in mixtures (e.g. Lebourgeois *et al.* 2013), others suggest that drought triggers a proportionally greater increase in competition for water in mixed-species stands (Grossiord *et al.* 2014). Recent theoretical work by Craine & Dyzinski (2013) reconciles these seemingly contrasting results by suggesting that competition for water occurs primarily through availability reduction, favouring species that are best able to deal with high soil water deficits. Assuming this is the case, drought tolerant species might be expected to benefit from mixing in dry years, while water demanding species are likely to suffer in mixtures under these conditions.

To better understand how AWP relates to diversity in Mediterranean forests, we tested the following hypotheses:

H1: Species mixing changes the distribution of light among trees. Pines have access to more light in mixtures, resulting in faster growth and a greater investment in crown development. In contrast, the ability of oaks to tolerate shade results in a less pronounced response to mixing.

H2: Because below-ground competition for water favours drought tolerant species, pines benefit considerably less from mixing during dry years, while oaks respond similarly in wet and dry years.

H3: At the stand level, mixing species with contrasting crown architectures and light requirements increases resource use efficiency and leads to greater AWP. However, the positive effect of diversity on AWP will decrease in strength during drought years.

Materials and methods

FIELD SITE AND STUDY DESIGN

The study was conducted in Mediterranean mixed forests of the Alto Tajo Natural Park, located in the Guadalajara province of central Spain (40.9°N, 1.9°W). The reserve extends along the Sistema Ibérico mountain range and is characterized by rugged topography (960 to 1400 m.a.s.l.), calcic cambisol soils (FAO classification) and Mediterranean climate [mean annual temperature (MAT) = 10.2 °C; mean annual precipitation (MAP) = 499 mm year⁻¹]. Forested areas are primarily dominated by two species of pine, *Pinus sylvestris* and *P. nigra*, and two species of oak, *Quercus ilex* and *Q. faginea*, which were selected as target species for this study.

In 2011, 36 forest plots (30 × 30 m in size) with different combinations of the four target species were established in the Alto Tajo

region as part of a European-wide project (<http://www.fundiveurope.eu/>). The study is based on a similar design to that typically found in biodiversity-ecosystem functioning experiments (Baeten *et al.* 2013), in which species richness and species composition are manipulated independently so that the effects of the two treatments can be teased apart (Hector *et al.* 2011). Plots range in species richness from monoculture to 2, 3 and 4-species mixtures. Each target species is represented in all diversity levels and each combination of species (i.e. species composition) was replicated at least twice. To allow meaningful comparisons among diversity levels, selected plots were chosen from a wider pool of candidate plots following a screening procedure which aimed to minimize differences in topography, soil properties and management history among stands. Particular care was also taken to ensure that the relative abundance of target species was as balanced as possible in all mixtures, thereby maximizing evenness (see Baeten *et al.* 2013 for further details on how plots were selected).

ALLOMETRIC DATA

Across all 36 plots, stems >7.5 cm in diameter were identified to species and permanently marked (2647 stems in total). For each stem, we recorded diameter (to the nearest 0.1 cm, using diameter tape), height, crown width and crown depth (to the nearest 0.1 m, using a vertex hypsometer, Haglöf AB, Sweden). In addition, we used the crown illumination index (*CI*) to characterize crown dominance (Clark & Clark 1992). Each tree was scored on a scale of 1 to 5 based on exposure to direct sunlight: suppressed crowns with no direct access to light received a score of 1, trees exposed only to lateral light were assigned to class 2, trees experiencing overhead light on a portion of their crown were scored as 3, crowns with complete access to overhead light belong to class 4, while fully exposed dominant crowns were assigned to class 5 (Clark & Clark 1992). *CI* scores have been shown to effectively capture the degree to which tree crowns are exposed to light, and offer a simple way of assessing the effect of shading on tree growth (e.g. Jennings, Brown & Sheil 1999).

Diameter and height measurements were used to estimate the above-ground biomass (*AGB*, in kgC) of each tree based on species-specific allometric functions obtained by weighing stems and branches of felled trees across the Spanish National Forest Inventory network (Ruiz-Peinado, del Rio & Montero 2011; Ruiz-Peinado, Montero & del Rio 2012). *AGB* was expressed in units of carbon by applying the standard conversion of 0.5 gC per gram of biomass. In addition to this, we combined crown width and depth measurements to calculate the crown volume (in m³) of each tree (see Appendix S1 in Supporting Information for details on biomass and crown volume equations).

WOOD CORES

To determine individual tree growth rates and estimate wood production at the plot level, in March 2012 we collected bark to pith increment cores (using a 5.15 mm diameter increment borer, Haglöf AB, Sweden) for a subset of trees in each plot. We extracted 12 cores per plot in monoculture stands and 6 cores per species in each of the mixtures, resulting in a total of 488 cored trees. Trees were randomly selected for coring based on a size-stratified sampling approach: in a given plot, trees were first assigned to one of six diameter classes, following which one (in mixtures) or two (in monocultures) trees were randomly selected from each class. This ensured that the size distribution of each plot was adequately represented by the subsample. Wood cores were stored in polycarbonate sheeting and allowed

to air dry, before being mounted on wooden boards and sanded with progressively finer grit sizes. A high resolution flatbed scanner (2400 dpi optical resolution) was then used to image the cores.

We measured yearly radial growth increments (mm year⁻¹) for each cored tree from the scanned images. Most trees developed clearly distinguishable yearly ring boundaries (see Appendix S2 for examples of scanned wood cores). Nevertheless, missing or false rings can bias growth estimates derived from wood cores and can be particularly hard to identify in non-ring-porous hardwood trees such as *Q. ilex* (Cherubini *et al.* 2003). To minimize measurement errors associated with incorrectly placed ring boundaries, we therefore cross-dated each sample against a reference curve obtained by averaging all ring-width chronologies of a given species. Both radial growth measurements and cross-dating were performed using the CDendro software suite (Cybis Elektronik & Data, Saltsjöbaden, Sweden).

ANALYTICAL FRAMEWORK

The following sections (a–e) describe the approach we have taken to test the hypotheses outlined in the introduction. Briefly, (a) we used field data to model changes in crown dominance related to species mixing and develop above-ground allometries for each species; (b) we used wood cores, together with biomass functions and height-diameter allometries, to reconstruct the biomass growth of individual trees; (c) we fitted statistical models to characterize the biomass growth rate of each species; (d) we used the models to explore species growth responses to mixing; (e) we scaled-up patterns of individual tree growth to wood production at the plot level. All analyses were performed in R (3.0.1; R Development Core Team 2013), relying primarily on packages *lme4* (Bates *et al.* 2013), *MuMIn* (Barton 2013), *ordinal* (Christensen 2012) and *smatr* (Warton *et al.* 2012).

(a) Modelling changes in crown dominance and fitting above-ground allometries

To determine whether species mixing affects the distribution of light among trees (**H1**), we used the inventory data collected for all 2647 stems to test whether trees in monoculture and mixture have different distributions of *CI* scores. Because *CI* is an ordered categorical response variable, we used ordinal logistic regression to model the effects of species mixing on crown dominance (e.g. Sheil *et al.* 2006). For each species, we used the *clm* function (R library *ordinal*) to estimate the probability that a tree belongs to a given *CI* class based on its size (*D*) and on the species composition of the plot it is growing in (treated as a factor in the model). This allowed us to compare the crown dominance of same-sized trees found in different mixture treatments.

In addition to this, we used the inventory data to develop height-diameter (H–D) and crown volume-diameter (CV–D) allometric functions for each species. Allometries were fitted using standardized major axis regression (*sma* routine in R), which is preferable to ordinary least squares regression when two variables are not tied by a clear causal relationship and the objective is simply to estimate the slope of the bivariate line (Smith 2009). Allometric relationships were linearized by log-transforming diameter, height and crown volume measurements, which assumes that above-ground allometries follow a power law function on the original axes (Warton *et al.* 2006). To test whether crown architecture is influenced by species mixing and neighbour identity (**H1**), we allowed the shape of the H–D and CV–D regressions (i.e. slope and intercept parameters) to vary according to plot species composition (treated as a factor in the model).

(b) Estimating biomass growth rates from wood cores

We combined radial increments and allometric functions to express the growth rate of individual trees in terms of biomass growth (G , in kgC year^{-1}). For each cored tree, G was calculated as the average yearly increase in biomass:

$$G = \frac{AGB_{t2} - AGB_{t1}}{\Delta t} \quad \text{eqn 1}$$

where AGB_{t2} is a tree's current biomass (end of 2011), AGB_{t1} is the biomass at the end of 2001 and Δt is the time interval (10 years). AGB_{t1} was estimated by replacing present-day diameter and height measures used to fit the previously described biomass functions with estimated values at $t1$. Past diameters were reconstructed directly from wood core samples by simply doubling the observed radial increments over the last 10 years and subtracting them from current diameter values. Height growth was estimated using the H–D function developed in section (a) to predict the past height of a tree based on its diameter at $t1$ (see Appendix S2).

We focus on biomass growth as it provides a direct measure of above-ground carbon sequestration and storage (Babst *et al.* 2013). Other measures of tree growth, such as diameter or basal area increment, ignore the importance of tree architecture and wood density in determining the rate at which trees remove carbon from the atmosphere, while biomass growth integrates both (Stephenson *et al.* 2014). However, estimating growth in units of biomass comes at a price, since both biomass equations and height-diameter allometries are potential sources of error (Molto, Rossi & Blanc 2013). To minimize the uncertainty in the biomass estimates, we selected species-specific biomass functions that were developed in the same region as our study site.

(c) Modelling individual tree growth

For each species, we used the *lmer* function in R to fit hierarchical models of tree growth in which G is expressed as a function of tree size, competition for light and two non-nested random effects, one which accounts for the effect of diversity on growth, the other a random plot effect (Gelman & Hill 2007):

$$\log(G_i) = \alpha_{j[i],k[i]} + \beta_{k[i]} \times \log(D_i) + \gamma \times CI_i + \varepsilon_i \quad \text{eqn 2}$$

where G_i , D_i and CI_i are, respectively, the biomass growth, stem diameter and crown illumination index of tree i growing in plot j with species composition k ; α_{jk} is a species' intrinsic growth rate for a tree growing in plot j with a species composition k ; β_k defines the growth response to size for a tree growing in a plot with species composition k ; γ is a species' growth response to light; and ε_i is the residual error.

In eqn 2, biomass growth is expressed as a power function of D (log-log relationship; Rüger *et al.* 2012), while competitive inhibition by taller neighbours is assumed to be an exponential function of CI (log-linear scale; Caspersen *et al.* 2011). Although CI is a categorical variable, the fact that it is ordinal and that it comprises multiple levels means it can be treated as a continuous predictor (Torra *et al.* 2006). To account for the effects of diversity on tree growth, we allowed parameters α and β to vary according to the species composition of the plot in which tree i is found. Species composition is treated as a factor in the model, and can be considered analogous to a treatment level in an experiment (*sensu* Hector *et al.* 2011). We focus on species composition as a measure of diversity because (i) it allows us to compare how each species responds to all possible neighbour combinations and (ii) species composition is directly relatable to other,

more commonly used measures of diversity (Fig. S2). Finally, to account for the tendency of species' baseline growth rates (α) to vary systematically among stands, we fitted a random intercept term for each of the j plots (Caspersen *et al.* 2011). Because errors (ε_i) were log-normally distributed (Appendix S4), we log-transformed G and D instead of implementing non-linear regression (Xiao *et al.* 2011).

Model robustness was assessed through visual diagnostic tests (Q-Q plots and predicted vs. observed plots; see Appendix S5). In addition to this, we used AIC to compare the fit of increasingly complex models, ranging from an "intercept-only" null model to the one presented in eqn 2 (see Appendix S5 for a full list of models that were compared). For each model, we calculated conditional R^2 values, which account for the explanatory power of both fixed and random effects (Nakagawa & Schielzeth 2013), as a measure of goodness-of-fit.

(d) Testing whether individual species respond to mixing and drought

To test the hypothesis that pines and oaks differ in their response to mixing (**H1**), for each species we predicted the biomass growth of a tree of a given size in mixtures of increasing functional diversity. Growth predictions were generated using the *predict.lmer* function. For each growth estimate we calculated 95% confidence intervals using parametric bootstrapping (1000 replicates). To illustrate this using an example (Fig. S2), we compared the growth rate of a 20 cm diameter *P. nigra* tree in monoculture, mixed with *P. sylvestris*, growing in combination with a member of the contrasting functional group (i.e. one or both of the two oak species), and in full functional mixture (i.e. with *P. sylvestris*, *Q. faginea* and/or *Q. ilex*). We repeated the analysis for a range of size classes (from 10 to 40 cm for pines, and 10–30 cm for oaks, in 5 cm intervals), which also allowed us to test whether species responses to mixing vary depending on tree size. For this purpose, we calculated the proportional difference in growth (ΔG) between trees in monoculture and trees in mixture (≥ 2 species) for each of the diameter classes. ΔG values greater than 1 indicate a positive diversity effect, while anything below 1 suggests that growth is greater in monoculture. By comparing ΔG values among size classes, we can determine whether small and large trees respond differently to mixing.

To test whether drought influences how species respond to mixing (**H2**), we used FetchClimate (<http://fetchclimate.cloudapp.net>) to obtain yearly MAP records for the study site and identify the driest (2005; 181 mm) and wettest year (2008; 544 mm) of the last decade (Fig. S6). We used the approach presented in eqn 1 to calculate the biomass growth of each cored tree in both 2005 and 2008, and then modelled growth using eqn 2 for the 2 years separately. The fitted models were used to predict the growth of a tree of standard size (20 cm in diameter, the median diameter of inventoried trees) in monoculture vs. mixture (≥ 2 species) under conditions of both high and low rainfall.

(e) Quantifying stand-level AWP

Having characterized how individual species respond to mixing, we then tested whether AWP increases with diversity and whether this relationship is affected by drought (**H3**). To quantify AWP, we used eqn 2 to estimate the biomass growth of all trees for which we did not collect wood cores. For each plot, we then summed the biomass growth of all standing trees to obtain an estimate of AWP averaged over 10 years. Lastly, we repeated the analysis focusing exclusively

on growth data for 2005 and 2008 in order to estimate AWP under conditions of drought (AWP_d) and abundant rainfall (AWP_w).

Having quantified AWP, we used multiple regression to tease apart the effects of diversity (species richness) on AWP from those of stand structure (basal area, $m^2 ha^{-1}$), soil quality (mean soil depth, cm) and microclimate (aspect and elevation, m) (see Table S1 for plot summary statistics). All regression predictors were weakly correlated with one another (Pearson correlation coefficients < 0.5). Separate regressions were fitted for AWP, AWP_d and AWP_w so that the contribution of species richness to productivity could be compared among the three. Because errors were log-normally distributed, we fitted models on a log-log scale. We adopted a multi-model inference approach to model selection (Burnham & Anderson 2002), which consists in fitting a series of competing models that include all possible combinations of the five explanatory variables (32 candidate models), and then using AIC to select between them. To assess the relative importance of each predictor, we summed the Akaike weights (Σw_i) of all models in which a given variable i occurs. Σw_i values range between 0 (variable i is not retained in any of the models) to 1 (variable i is present in all models).

Results

GENERAL PATTERNS OF INDIVIDUAL TREE GROWTH

For each species, the full growth model presented in eqn 2 was best supported, outperforming simpler models which lacked random effect terms (Table S2). The best fitting models explained a high proportion of the variance in individual tree biomass growth ($\log G$), with conditional R^2 values ranging from 0.78 for *Q. ilex* to 0.94 for *P. nigra* (see Appendix S5). While the relationship between G and stem diameter (D)

was similar across all four species, crown illumination index (CI) had a much more pronounced influence on the growth of pines, highlighting the greater ability of oaks to tolerate shade (Fig. S5). The inclusion of species composition as a random effect substantially improved model fit in all four species, demonstrating that species mixing plays an important role in shaping species' growth rates (see following sections). Lastly, random plot effects indicate that species growth rates tend to vary systematically among plots, but do so more for some species (*P. nigra*, $\Delta AIC = 28$ when comparing models with and without a random plot effect) than for others (*P. sylvestris*, $\Delta AIC = 1$).

H1: Changes in crown dominance and above-ground allometries related to species mixing

Species mixing had contrasting effects on the crown dominance of pine and oak trees. Ordinal logistic regressions revealed that for a tree of a given size, pines had significantly higher CI values when growing in mixed-species stands (*P. sylvestris*: $z = 6.2$, $P < 0.001$; *P. nigra*: $z = 3.9$, $P < 0.001$; Fig. 1, top panels). In contrast, oaks growing in mixture with pines had significantly lower CI values than trees growing either in monoculture or oak mixtures (*Q. faginea*: $z = -5.9$, $P < 0.001$; *Q. ilex*: $z = -3.3$, $P = 0.001$; Fig. 1, bottom panels).

Above-ground allometries also shifted predictably in response to species mixing (Fig. 2). For a given stem diameter, both pine species tended to be significantly shorter and have considerably larger crown volumes in mixed stands, especially when growing with oaks (Fig. 2a–b and e–f). This pattern is

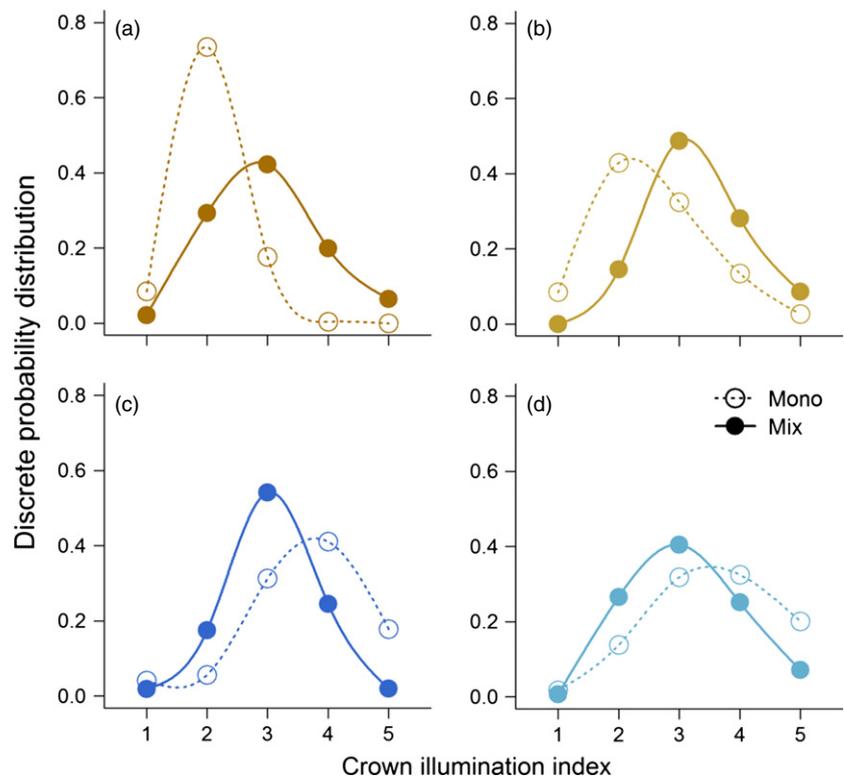


Fig. 1. Probability of a tree of standard size (20 cm diameter) belonging to each of the five crown illumination index classes in (a) *Pinus sylvestris*, (b) *Pinus nigra*, (c) *Quercus faginea* and (d) *Quercus ilex*. Empty circles correspond to trees growing in monoculture, while full circles indicate trees in mixtures. To aid visual comparison, interpolation splines were used to fit smooth curves through the data (dotted lines for monocultures and continuous lines for mixtures).

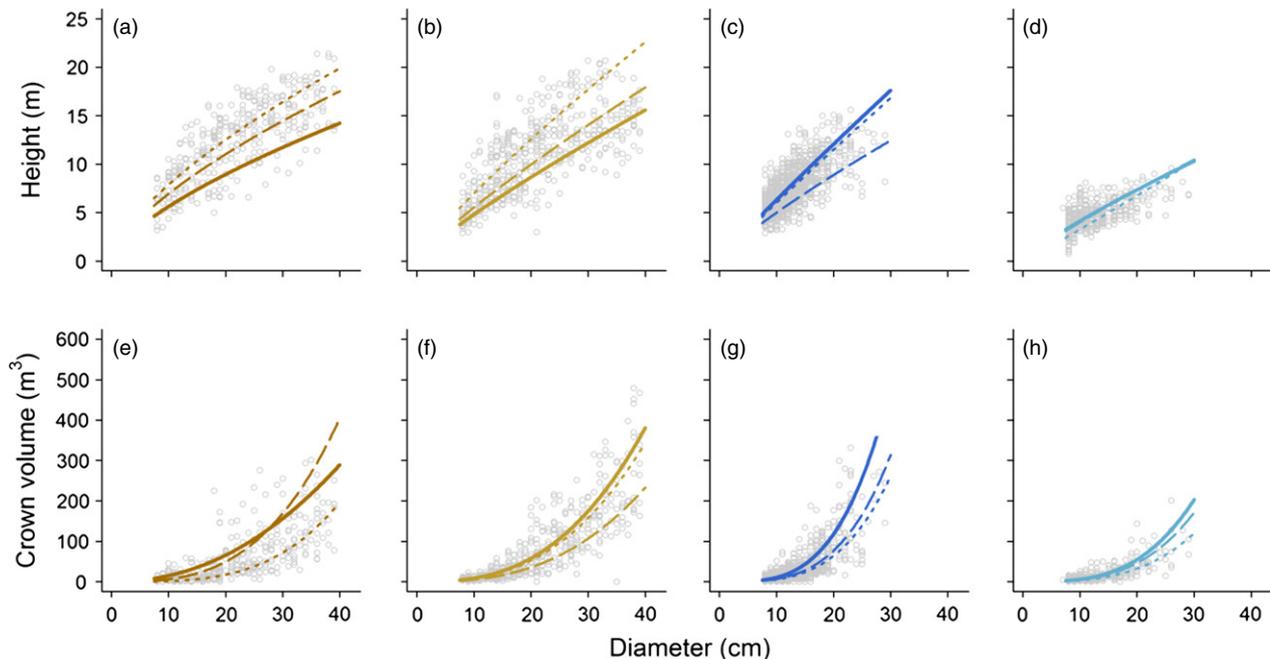


Fig. 2. Height-diameter (top panels) and crown volume-diameter (bottom panels) functions for (a, e) *Pinus sylvestris*, (b, f) *Pinus nigra*, (c, g) *Quercus faginea* and (d, h) *Quercus ilex*. Dotted lines indicate trees in monoculture, dashed lines are trees growing in mixture with the species belong to their same genus (e.g. *P. nigra* with *P. sylvestris*) and continuous lines are trees growing in mixture with species of the contrasting functional group (e.g. *P. nigra* with *Q. faginea* and/or *Q. ilex*).

consistent with pine crowns receiving more light when in mixture, and therefore experiencing less competition for light. Crown architecture was less variable in oaks (Fig. 2c–d and g–h). However, *Q. faginea* grew significantly shorter when mixed with *Q. ilex*, and both oaks had lower crown volumes when growing in monoculture.

H1: The influence of diversity on species growth rates

Species growth rates depended on the identity of neighbouring trees (Fig. 3). *P. sylvestris* trees in monoculture grew more slowly than those in mixed stands (Fig. 3a). For a 20 cm diameter tree, a 155% increase in growth was seen when going from monoculture ($0.53 \pm 0.06 \text{ kgC year}^{-1}$) to full mixture ($1.35 \pm 0.18 \text{ kgC year}^{-1}$). *P. nigra* showed much the same response to mixing (Fig. 3b). Relative to monocultures ($0.73 \pm 0.05 \text{ kgC year}^{-1}$), *P. nigra* grew significantly faster in all mixtures, the effect being greatest for trees in full mixture ($1.74 \pm 0.20 \text{ kgC year}^{-1}$). In contrast to pines, both *Q. faginea* and *Q. ilex* did not respond strongly to mixing except when growing with each other (Fig. 3c–d). In *Q. faginea* – *Q. ilex* mixtures, both species of oak experienced a more than 50% increase in growth when compared to monoculture.

For pines, the effect of mixing on growth was not the same across size classes and small trees tended to benefit significantly more from growing in mixture than large individuals (Fig. 4, top panels). Small *P. sylvestris* trees ($D = 10 \text{ cm}$) in mixed-species stands grew almost three times faster than those in monoculture ($\Delta G = 2.82 \pm 0.50$). In contrast, ΔG for relatively large *P. sylvestris* trees ($D > 40 \text{ cm}$) was much less pronounced (1.59 ± 0.30), although still considerably

greater than one. This pattern emerged even more clearly for *P. nigra*, where 10 cm diameter trees grew almost 300% faster when in mixture ($\Delta G = 3.97 \pm 0.42$), while ΔG was not significantly different from one for individuals larger than 40 cm. In contrast, oaks showed little or no size-dependent variation in their growth response to mixing (Fig. 4, bottom panels).

H2: The effects of drought on growth–diversity relationships

All species showed reduced biomass growth in the dry year we selected, but pines were more strongly affected by drought than oaks (Fig. 5 and S7). Drought also reduced the magnitude of the diversity effect in all but one species (*Q. ilex*). This pattern was particularly evident in pines, where the positive effect of mixing on growth was significantly reduced in the dry year (Fig. 5, top panels). Generally, the benefit of being in mixture in dry years depended on a species ability to tolerate drought (Fig. 6). *P. nigra*, the most drought sensitive of the four species (based on its decrease in growth between dry and wet years), experienced the greatest decline in diversity effect in the dry year. In contrast, the drought tolerant *Q. ilex* showed essentially the same response to mixing in both dry and wet years.

H3: The effect of diversity on plot-level AWP

AWP estimates for the 36 plots ranged between 0.22–1.25 $\text{MgC ha}^{-1} \text{ year}^{-1}$. Averaged across plots, AWP was significantly lower under the dry conditions of 2005 ($\text{AWP}_d = 0.42 \pm 0.06 \text{ MgC ha}^{-1}$) compared to the relatively wet year of 2008 ($\text{AWP}_w = 0.73 \pm 0.09 \text{ MgC ha}^{-1}$). Multiple regression analysis revealed that of the five covariates we

Fig. 3. Biomass growth of a 20 cm diameter tree as a function of functional group diversity for (a) *Pinus sylvestris*, (b) *Pinus nigra*, (c) *Quercus faginea* and (d) *Quercus ilex*. From left to right, species composition refers to trees growing in monoculture (MONO), in mixture with the functionally similar species, mixed with a member of the contrasting functional group and in full mixture. Error bars represent 95% confidence intervals based on 1000 bootstrap replicates. PISY = *P. sylvestris*; PINI = *P. nigra*; QUFA = *Q. faginea*; QUIL = *Q. ilex*.

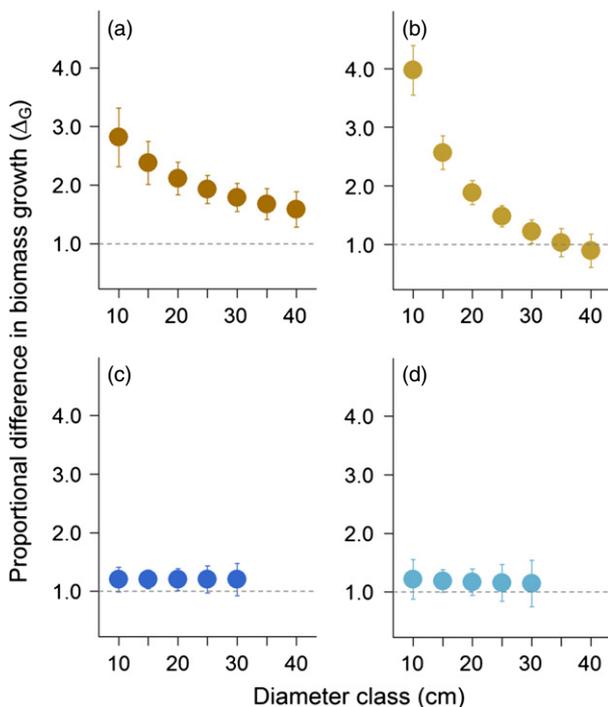
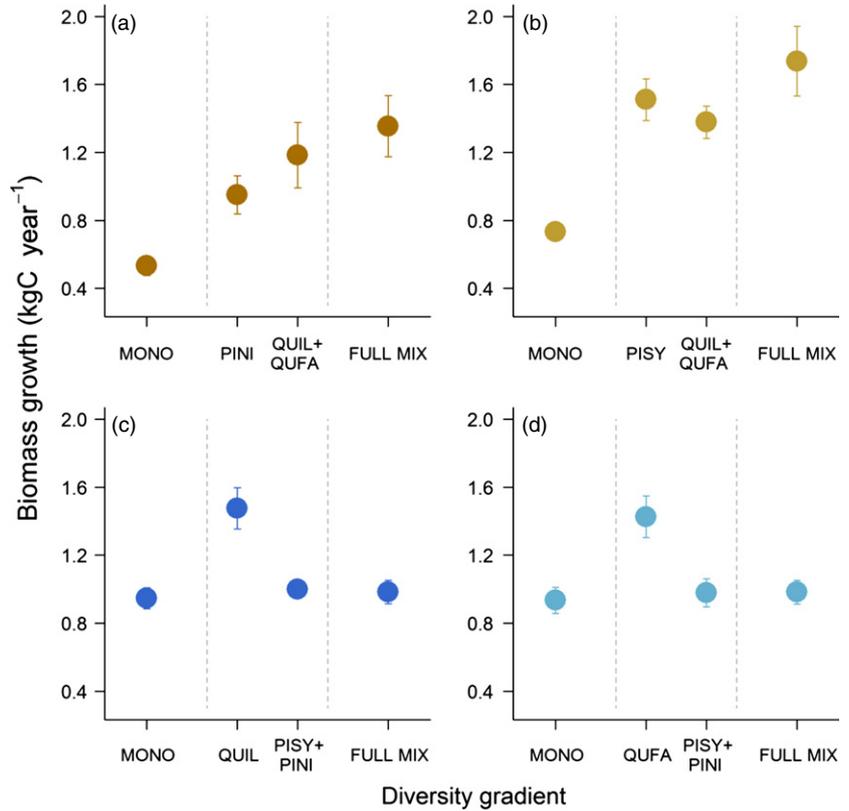


Fig. 4. Proportional difference in biomass growth (ΔG ; growth in mixture divided by growth in monoculture) for trees of increasing diameter in (a) *Pinus sylvestris*, (b) *Pinus nigra*, (c) *Quercus faginea* and (d) *Quercus ilex* (mean \pm 95% confidence intervals). Dashed lines indicate equivalent growth rates in monoculture and mixture.

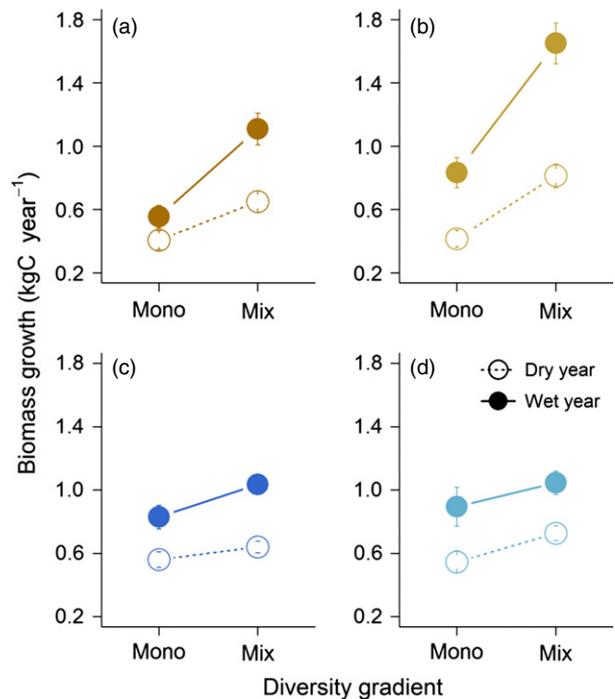


Fig. 5. Biomass growth of a 20 cm diameter tree in monoculture and mixture in the dry year of 2005 (empty circles) and the wet year of 2008 (full circles) for (a) *Pinus sylvestris*, (b) *Pinus nigra*, (c) *Quercus faginea* and (d) *Quercus ilex*. Slopes indicate the effect of diversity of growth in the dry (dashed line) and wet year (continuous line). Error bars represent 95% confidence intervals.

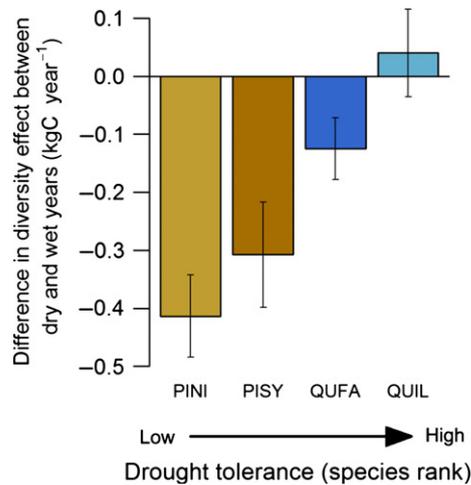


Fig. 6. Difference in diversity effect (growth in mixture – growth in monoculture) between dry and wet years (2005 vs. 2008) as a function of species ability to tolerate drought (rank order). Error bars represent 95% confidence intervals. PISY = *Pinus sylvestris*; PINI = *Pinus nigra*; QUFA = *Quercus faginea*; QUIL = *Quercus ilex*.

accounted for in the model, only basal area and species richness emerged as significant predictors of AWP (Table 1). Both were positively related to AWP and together explained 46% of the variation in AWP among stands. All other environmental covariates were dropped during model simplification, suggesting that the plot selection phase of the project was successful in selecting sites that differ in diversity but not in underlying environmental factor. When we focused on AWP in the wet year, species richness and basal area were again found to exert a positive influence on AWP (Fig. 7, dotted line). In contrast, under drought conditions we found no evidence of a significant diversity effect on AWP (Fig. 7, dashed line), and the best sup-

ported model accounted solely for the effect of basal area on AWP.

Discussion

Over the past decade, mixed pine-oak stands in the Alto Tajo region have produced an average 0.27 MgC ha⁻¹ more woody biomass each year than monocultures, corresponding to a 48% increase in AWP (Fig. 7). We show that complementary light-use strategies of Iberian pine and oak species are critical in shaping this positive association between AWP and diversity. In contrast, increased competition for water under conditions of drought substantially weakened complementarity effects between pines and oaks, all but cancelling out the beneficial effects of diversity on AWP. Together, our results elucidate several of the key mechanisms behind diversity–productivity relationships in Mediterranean mixed forests, and help put previous findings relating to these systems into context (Vilà *et al.* 2007; Ruiz-Benito *et al.* 2014).

LIGHT AS A KEY DRIVER OF DIVERSITY–PRODUCTIVITY RELATIONSHIPS

We found that species mixing changes the way light is distributed among trees (Figs 1 and 2), and that this had a profound effect on tree growth, especially in the case of light demanding species such as pines (Figs 3 and 4). A number of other studies have also suggested that competition for light plays a critical role in driving positive diversity–productivity relationships in forests, primarily through a more efficient use of space achieved when mixing species with contrasting abilities to tolerate shade (for a review see Zhang, Chen & Reich 2012). For instance, Morin *et al.* (2011) used a forest succession model to show that mixing species with different light requirements leads to vertically structured canopies that

Table 1. Outputs from the models of AWP (averaged over 10 years; 2002–11), AWP_w (wet year, 2008) and AWP_d (dry year, 2005). Σw_i column gives the sum of the Akaike weights (w_i) for each predictor; Coef column reports the parameter estimate (\pm SE); P column refers to statistical significance, with $P > 0.05$ reported as n.s. (non-significant). Model summary statistics include R^2 and Akaike weights (w_i)

| Predictor | AWP (2002–11) | | | AWP _w (2008) | | | AWP _d (2005) | | |
|------------------|---------------|------------------|--------|-------------------------|------------------|--------|-------------------------|------------------|-------|
| | Σw_i | Coef (\pm SE) | P | Σw_i | Coef (\pm SE) | P | Σw_i | Coef (\pm SE) | P |
| Diversity | | | | | | | | | |
| Species richness | 0.82 | 0.28 (0.12) | 0.025 | 0.84 | 0.32 (0.13) | 0.019 | 0.34 | 0.15 (0.18) | n.s. |
| Stand structure | | | | | | | | | |
| Stand basal area | 0.99 | 0.54 (0.11) | <0.001 | 0.99 | 0.61 (0.12) | <0.001 | 0.97 | 0.44 (0.12) | 0.001 |
| Soil quality | | | | | | | | | |
| Soil depth | 0.18 | 0.10 (0.16) | n.s. | 0.22 | 0.08 (0.17) | n.s. | 0.23 | 0.01 (0.18) | n.s. |
| Microclimate | | | | | | | | | |
| Elevation | 0.24 | –0.49 (0.80) | n.s. | 0.24 | –0.29 (0.96) | n.s. | 0.23 | 0.49 (1.01) | n.s. |
| Aspect | 0.02 | | n.s. | 0.02 | | n.s. | 0.05 | | n.s. |
| N | | –0.06 (0.23) | | | 0.01 (0.25) | | | –0.15 (0.26) | |
| S | | –0.10 (0.24) | | | –0.05 (0.26) | | | –0.29 (0.27) | |
| W | | –0.06 (0.37) | | | 0.11 (0.38) | | | –0.03 (0.40) | |
| Model summary | | | | | | | | | |
| R^2 | | 0.46 | | | 0.48 | | | 0.27 | |
| w_i | | 0.51 | | | 0.50 | | | 0.35 | |

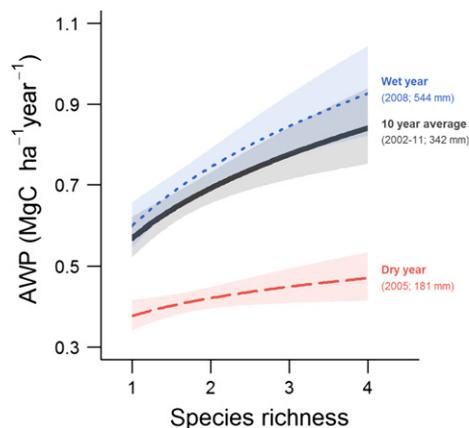


Fig. 7. Relationship between species richness and above-ground wood production (AWP) averaged over the past decade (continuous line), in the wet year of 2008 (dotted line) and in the drought year of 2005 (dashed line). Fitted regression lines are plotted with shaded 95% confidence intervals.

intercept more light. Our analysis revealed that species mixing can also increase AWP by alleviating competition for light among neighbouring trees, thereby enhancing species growth rates.

Iberian pines and oaks differ in a number of key physiological and structural traits which affect their ability to tolerate shade (Valladares & Niinemets 2008; Poorter *et al.* 2012; Carnicer *et al.* 2013). Pines are characterized by strong apical dominance, meaning they invest heavily in height growth and less in branching (Fig. 2). Combined with low leaf area ratios (i.e. total leaf area per total plant mass), this makes pines particularly susceptible to competition for light with neighbouring trees. We found that competitive inhibition was strongest for trees growing in monoculture, while pines in mixed-species stands received considerably more light and had significantly faster growth rates (Fig. 3, top panels). This effect was particularly pronounced in mixed conifer-broadleaf plots, where the contrasting crown architectures of oaks and pines complemented each other best. Small understorey trees, which are most affected by competition with neighbours (Gómez-Aparicio *et al.* 2011), were able to capitalize best on the increased light availability in mixtures (Fig. 4, top panels) and showed a distinct shift in their crown dominance status (Fig. 1, top panels). In contrast, large canopy-dominant pines showed less of an effect of diversity on growth, as their access to light was less affected by species mixing (Fig. 4, top panels).

The effects of changes in light environment were not limited to those on tree growth. Differently from herbaceous species which rebuild most of their above-ground biomass each year, trees invest a considerable portion of their photosynthate into stems and branches, meaning that competition for light can have long-lasting effects on crown architecture (Scherer-Lorenzen *et al.* 2007; Lines *et al.* 2012). We found that pines growing next to conspecific neighbours invested heavily in height growth in order to escape shading, while those in mixture tended to be shorter and have larger crown volumes

(Fig. 2). Dieler & Pretzsch (2013) reported similar results for European beech when mixed with pine, oak or spruce. Beech trees in mixture had larger crown cross-sectional areas compared to trees in monoculture, primarily as a result of decreased competition for light in mixtures. Our results suggest that these shifts in crown structure play an important role in reinforcing the positive effects of species mixing on growth by enhancing the ability of pines to intercept light.

Oaks are shorter than pines of similar stem diameter, but have larger crown volumes (Fig. 2), lower leaf mass per area and higher leaf area ratios, allowing them to maximise light interception and use (Valladares & Niinemets 2008; Poorter *et al.* 2012; Carnicer *et al.* 2013). Although oaks tended to receive less light when mixed with pines (Fig. 1, bottom panels), their ability to tolerate shade meant their growth rates remained relatively consistent regardless of the identity of their neighbours (Fig. 3, bottom panels). However, mixtures of the two oaks were different, with both oak species growing decidedly faster than in all other species combinations. This pattern seems to result from the fact that *Q. faginea* and *Q. ilex* are able to partition access to light both spatially and temporally (Fridley 2012). *Q. faginea*, which is the least shade tolerant of the two oaks (Gómez-Aparicio *et al.* 2011), achieves significantly greater maximum heights compared to *Q. ilex* and is therefore able to dominate the canopy (Fig. 2). *Q. ilex*, on the other hand, is better equipped to deal with shade (as is typically the case with evergreen oaks; Valladares & Niinemets 2008), and benefits from the fact that *Q. faginea* is deciduous, as this allows understorey trees access to direct sunlight during spring and autumn months.

DROUGHT STRESS AND ITS INFLUENCE ON COMPETITIVE INTERACTIONS

We found that in years with low rainfall species tended to benefit less from mixing, especially if they were unable to tolerate drought (Figs 5 and 6). This suggests that drought decreases room for complementarity between Iberian pine and oak species, and explains why at the stand level the AWP–diversity relationship weakened in the dry year of 2005 (Fig. 7, dashed line). Recently, a number of studies have raised the question of whether abiotic conditions play a role in shaping biodiversity–ecosystem functioning relationships by modifying the way in which species interact (Maestre *et al.* 2009; Gessner & Hines 2012). Attempts to address this question have yet to yield a definitive answer, with studies having reported both stronger (Paquette & Messier 2011; Steudel *et al.* 2011; Jucker & Coomes 2012; Wang *et al.* 2013) and weaker diversity effects (Steudel *et al.* 2012; Grossiord *et al.* 2014) under conditions of heightened environmental stress. Part of the reason for the lack of consensus is that up until now studies have focused on different aspects of environmental stress (e.g. drought, salinity, nutrient availability, physical damage), and have failed to make the distinction between the response of different communities along environmental gradients (e.g. Paquette & Messier 2011; Jucker & Coomes 2012) from those of the same community

subjected to fluctuating conditions over time (e.g. Grossiord *et al.* 2014). A clearer framework within which to evaluate the outcome of individual studies is therefore needed (Gessner & Hines 2012). This raises the question of how our results, which show that mixed pine-oak stands are more vulnerable to drought compared to monocultures, can be interpreted in light of what is currently known about competition for water among trees.

Iberian pines and oaks differ significantly in their ability to tolerate drought (Ferrio *et al.* 2003; Gómez-Aparicio *et al.* 2011; Poorter *et al.* 2012; Granda *et al.* 2013). While oaks have extensive and deep root systems which enable them to maintain an adequate supply of water to their leaves even during dry summer months (Quero *et al.* 2011; Poorter *et al.* 2012), recent studies show that as Spanish forests have become warmer and drier, growth, survival and recruitment have declined in pines (Coll *et al.* 2013; Carnicer *et al.* 2014). In 2008, when annual rainfall was above average, pines growing in mixture strongly outperformed those in monoculture, suggesting they were able to access enough water to meet their photosynthetic demands (Fig. 5, top panels). In contrast, as we hypothesized in the introduction, during the drought of 2005 pines benefitted significantly less from being in mixture (Fig. 6). Presumably, this is because as soil water potential declined, the greater ability of oaks to compete for below-ground resources meant that pines in mixture had less access to water than those in monoculture. This would have been further exacerbated by the fact that pines in mixture develop larger crowns than those in monoculture, meaning they require more water to meet their evapotranspiration demands (Vertessy *et al.* 1995; Dawson 1996). These results are consistent with Craine & Dybzinski's (2013) idea that competition for water works by availability reduction and explains why diversity effects in oaks were less sensitive to drought, especially in the case of *Q. ilex* (Fig. 6). A recent study by Grossiord *et al.* (2014) found the same pattern in a mixed conifer-broadleaf boreal forest, where water use efficiency (which reflects below-ground competition for water) increased decidedly more in mixed species stands compared to monocultures during a drought year. This suggests that when environmental conditions become stressful there may be less room for complementarity. Whether similar patterns also apply to other forest types and species combinations, or whether responses are inherently context dependent remains to be seen. Future work extending the approach we adopt here to other study sites across the FunDivEUROPE plot network may well help answer this question.

Conclusion

Numerous studies have reported positive effects of diversity on AWP in forests (Piotto 2008; Paquette & Messier 2011; Gamfeldt *et al.* 2013; Vilà *et al.* 2013), including in Mediterranean systems (Vilà *et al.* 2007; Ruiz-Benito *et al.* 2014). Together, this work has helped pave the way towards a consensus regarding the importance of preserving forest biodiversity in order to maintain ecosystem functioning (Zhang,

Chen & Reich 2012; Cardinale *et al.* 2012). However, largely as a result of the scale at which most of these studies have been conducted, deriving a more mechanistic understanding of diversity–productivity relationships in forests has proved challenging. Using data collected at the tree level to deconstruct AWP into individual species growth patterns, we were able to take a step closer towards linking patterns with processes. We found that mixing species with complementary light-use strategies can have a sizable impact on productivity in Iberian pine-oak forests. However, this degree of complementarity hinges on the assumption that trees have access to enough water to maintain high photosynthetic rates. When conditions become too dry, declining carbon fixation rates and increased competition for water reduce the strength of the complementarity effect. In particular, our analysis suggests that if annual rainfall continues to decline in the Alto Tajo region, the potential benefits of mixing pines and oaks for timber production and carbon sequestration will be lost.

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Data Accessibility

AWP data: FunDivEUROPE online data portal (<http://fundiv.befdata.biow.uni-leipzig.de/>).

Individual tree growth data: FunDivEUROPE online data portal (<http://fundiv.befdata.biow.uni-leipzig.de/>).

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Supporting Information

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

Appendix S1. List of biomass and crown volume equations used in the study.

Appendix S2. Using tree cores to estimate biomass growth.

Appendix S3. Description of the Alto Tajo permanent plot network.

Appendix S4. Comparing nonlinear regression and log-transformation for characterizing the relationship between biomass growth and stem diameter.

Appendix S5. Evaluation of individual tree growth models.

Appendix S6. Rainfall trends and their influence on tree biomass growth.

Table S1. Summary statistics for each study plot.

Table S2. Comparison of individual tree growth models.

Figure S1. Examples of scanned wood cores for each of the four study species.

Figure S2. Schematic diagram illustrating the design of the FunDiv-EUROPE plot network.

Figure S3. Diagnostic plots characterizing the error structure of the biomass growth data.

Figure S4. Predicted vs. observed and Q-Q plots of the tree growth models for each of the four study species.

Figure S5. Species biomass growth response to size and light availability.

Figure S6. Rainfall trends between 1960 and 2009 in the Alto Tajo Natural Park.

Figure S7. Scatterplot relating biomass growth in 2008 (wet year) to growth in 2005 (dry year).