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LETTER

Competitive interactions between forest trees are driven by species' trait hierarchy, not phylogenetic or functional similarity: implications for forest community assembly

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Abstract

The relative importance of competition vs. environmental filtering in the assembly of communities is commonly inferred from their functional and phylogenetic structure, on the grounds that similar species compete most strongly for resources and are therefore less likely to coexist locally. This approach ignores the possibility that competitive effects can be determined by relative positions of species on a hierarchy of competitive ability. Using growth data, we estimated 275 interaction coefficients between tree species in the French mountains. We show that interaction strengths are mainly driven by trait hierarchy and not by functional or phylogenetic similarity. On the basis of this result, we thus propose that functional and phylogenetic convergence in local tree community might be due to competition-sorting species with different competitive abilities and not only environmental filtering as commonly assumed. We then show a functional and phylogenetic convergence of forest structure with increasing plot age, which supports this view.

Keywords

Community assembly, competition, environmental filtering, functional similarity, niche similarity, phylogenetic relatedness, plant interaction, traits hierarchy.

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INTRODUCTION

Understanding the processes that structure natural communities is one of the most enduring quests in ecological research (Diamond 1975). Community assembly may be driven by a number of processes including environmental filtering, stochasticity and biotic filtering (Kraft & Ackerly 2010). Among biotic filtering processes, competition is probably the most studied and deemed the most important (Keddy 1989). Numerous studies have sought evidence for competitive effects in the phylogenetic or functional structure of natural communities, (Webb *et al.* 2002; Cavender-Bares *et al.* 2004; Kraft & Ackerly 2010); these studies are all based on the common assumption that ecologically similar species tend to compete more intensely for resources than dissimilar species and therefore are less likely to coexist locally (i.e. the competition-niche similarity hypothesis, MacArthur & Levins 1967). Recent work has shown that ecological similarity between species can be quantified by using functional traits – such as leaf, seed and wood characteristics – on the basis that these traits capture key ecological strategies related to competitive interactions such as rapid resource acquisition, regeneration ability or shade tolerance (Goldberg 1996; Westoby *et al.* 2002; Chave *et al.* 2009). This leads to the competition-trait similarity hypothesis, which predicts that competitive interaction strengths between species will increase with decreasing niche distance, measured as their absolute traits distance $|t_A - t_B|$, where t_A and t_B are the functional trait values of species A and B. If traits responsible for ecological similarity are conserved in a phylogeny, then this will translate into more intense competition for resources between closely related than between more distantly related species: this is the competition-relatedness hypothesis (Cahill *et al.* 2008).

A recent review by Mayfield & Levine (2010) challenges the view that trait- and phylogenetic similarity are the predominant drivers of community structure, on the grounds that processes other than trait similarity may be important drivers of competition among species. Specifically, they suggest that competition may be driven by hierarchical differences in species' competitive abilities, leading to competitive exclusion of inferior competitors in the absence of niche segregation (Chesson 2000). A species' position in a competitive ability hierarchy may be related to its functional trait values compared with other species in the community because of the link between traits and ability to acquire limiting resources (Westoby *et al.* 2002). In summary, both competitive ability and niche difference determine the outcome of competition (Chesson 2000; Adler *et al.* 2007; Mayfield & Levine 2010). The competitive-ability hierarchy hypothesis leads to very opposite predictions to the ones arising from the competition-trait similarity and competition-relatedness hypotheses (Mayfield & Levine 2010): the competitive effect of species A on species B will be related to the hierarchical distance of functional traits (i.e. if the trait t is positively related to competitive ability, then competitive effect of species A on species B will increase with increasing $t_A - t_B$). We call this the competition-trait hierarchy hypothesis.

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The way in which competition affects community assembly depends greatly upon whether the strength of interactions is controlled by trait similarity, phylogenetic relatedness or by trait hierarchy. If a link between interaction strengths and relatedness is assumed, then biotic processes (competition, facilitation or natural enemies) lead to an overdispersion of functional or phylogenetic community structure (i.e. more dissimilar than expected by chance). In contrast, environmental filtering (tolerance of the abiotic conditions) leads to a clustered community structure (i.e. more related than expected by chance; Kraft & Ackerly 2010). In the context of forest succession, it has been reasoned that communities will become increasingly overdispersed over time under these mechanisms, because competitive effects are cumulative (Letcher 2010; Uriarte *et al.* 2010; Letcher *et al.* 2012; Norden *et al.* 2012). In contrast, competition is predicted to result in functional clustering within natural communities if competition is driven by the hierarchical distance of species' functional traits, because more competitive species will be favoured under a given environment (Mayfield & Levine 2010), and the degree of clustering would increase over the course of succession, accompanying a shift in forest composition towards species with traits conferring strong competitive ability. We would expect functional clustering to translate into phylogenetic clustering, provided that closely related species share similar functional traits. To our knowledge, no study tested the competition-trait hierarchy hypothesis vs. the competition-trait similarity and the competition-relatedness using field measurements of plant interactions. In addition, there has been no attempt to correlate these contrasting community assembly rules with both measured interaction strengths among species and data on changes in community structure along succession.

In this study, we evaluated support for the competition-trait similarity, competition-relatedness, and competition-trait hierarchy hypotheses using data from 14 000 forest inventory plots in the French Alps. We evaluated these hypotheses using two approaches: (1) by quantifying interaction strengths between species pairs from the tree growth data and (2) by testing whether changes in community structure along successional sequences correspond most strongly with one theory over another. We used Bayesian neighbourhood models of tree radial growth to estimate interactions coefficients between tree species in mountain forests. Using these coefficient estimates, together with a species-resolved phylogeny and data on four key functional traits, we asked the following questions: (1) are interaction coefficients between tree species related to their functional trait similarity or phylogenetic distance? Alternatively, (2) are interaction coefficients between tree species related to the hierarchical distance of their functional traits? (3) Do changes in average functional composition and dispersion along forest successional sequences support the competition-trait similarity or the competition-trait hierarchy hypothesis? Finally (4), are changes in phylogenetic structure with forest succession explained by the change in functional structure, due to phylogenetic signal in functional traits?

METHODS

Forestry Inventory Dataset

In the French Alps, the French National Forest Inventory (NFI) comprises a network of about 17 000 temporary small plots (circular plots of radius 15 m, see Kunstler *et al.* 2011 for data description). For each tree measured in these plots, stem diameter, species, status (dead or alive) and radial growth over 5 years (based on short cores taken at breast height) were recorded. In addition, a long core was taken from the three largest trees in the plot to estimate their ages; these were averaged to provide an estimate of forest age for each plot. Soil properties were analysed using a soil pit of up to 1 m depth located in the centre of the plot and used to estimate the maximum soil water content using the texture method (Baize & Jabiol 1995). We focused on a 66 000 km² study area that extends from the Jura Mountains to the south of the Alps (see Fig. S1 of the Supporting Information). We selected 22 common tree species for analysis of their growth response to environment and neighbourhood competition (Table 1). We excluded plots if any evidence of a recent (< 5 years) logging operation or disturbance was recorded during the inventory.

Environmental variables

The NFI plots spanned a large range of environmental conditions with climate of the lowlands varying from Mediterranean through oceanic to continental types, and a wide range of soil types. Time of plot sampling varied over a 10-year period. To account for this spatio-temporal heterogeneity, we used two variables that are known to have strong impacts on tree growth: the sum of degree-days over the growing season (*DD*) and water availability over the growing season (*WB*). Water availability was computed using a 'bucket approach' taking into account the maximum soil water content, and therefore it reflects the combination of local soil type and climate (see Appendix S1). These variables were computed from a set of climatic grids (100 × 100 m) of monthly temperature and precipitation for each year of measurement. The variables were generated by downscaling the AURHELY (Benichou & Le Breton 1987) and CRU TS 1.2 (Mitchell *et al.* 2003) datasets – see Kunstler *et al.* (2011) for details.

Functional traits and phylogeny

We focused on four key functional traits to represent species' niche similarity and competitive ability hierarchy: leaf mass per unit area (LMA), wood density (WD), seed mass (SM) and tree maximum height (H_{max}; Westoby *et al.* 2002; Chave *et al.* 2009). These traits are frequently used in analyses of the functional structure of forest communities (e.g. Kraft & Ackerly 2010), so it is crucial to test their link with direct measurements of tree interactions. LMA is one component of the leaf economic spectrum, contrasting fast-growing species with cheap leaf construction costs against slow-growing and stress-tolerant species with expensive leaf construction costs (Wright *et al.* 2004). LMA is also negatively related to plant shade tolerance and its ability to harvest light (Valladares & Niinemets 2008; Niinemets 2010). WD underpins an axis contrasting fast-growing species with low wood density against slow-growing but stress-tolerant – i.e. high-survival – species with high wood density (Chave *et al.* 2009). SM discriminates species with high seed production and low establishment rate vs. species with low seed production but high establishment rate (Westoby *et al.* 2002). Finally, H_{max} is a key determinant of light competition (Westoby *et al.* 2002). Most trait data values were taken from the TRY database (Kattge *et al.* 2011; Chave *et al.* 2009; Wright *et al.* 2004; see Appendix S2 for details).

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Table 1 List of target tree species (or group of species) and their acronyms

Target species acronym	Species or group of species	No. plots	No. trees	No. competitor species	Models DIC			R^2_D
					$M_{neighbour\ null}$	$M_{neighbour}$	$M_{neighbour\ species}$	$M_{neighbour\ species}$
ABIALB	*Abies alba*	2110	12885	19	25843.1	25743.4	**25640.7**	0.29
ACEg	*Acer pseudoplatanus & A. platanoides*	993	2501	13	4278.7	4231.2	**4145.1**	0.40
ACEs	*Acer campestre, A. opalus* and *A. monspessulanum*	1462	3799	16	6232.7	6195.1	**6116.1**	0.38
ALNb	*Alnus glutinosa, A. incana* and *A. cordata*	249	1627	7	2611.8	2593.1	**2553.6**	0.37
BETPUB	*Betula pubescens*	423	1030	6	1944.2	1916.7	**1873.5**	0.34
CARBET	*Carpinus betulus*	1403	7811	21	12834.2	12791.7	**12670.2**	0.35
CASSAT	*Castanea sativa*	474	3633	12	6225.8	6200.0	**6133.8**	0.35
CORAVE	*Corylus avellana*	261	809	5	1428.3	1421.2	**1410.6**	0.25
FAGSYL	*Fagus sylvatica*	3275	21291	25	37145.2	37069.1	**36828.1**	0.35
FRAs	*Fraxinus excelsior, F. oxyphylla* and *F. ornus*	1536	5104	21	9456.4	9361.3	**9216.7**	0.35
LARDEC	*Larix decidua*	1000	6557	9	11144.0	11124.6	**11091.9**	0.32
OSTCAR	*Ostrya carpinifolia*	105	629	4	524.4	522.9	**522.0**	0.59
PICABI	*Picea abies*	2710	19651	23	34833.1	34770.6	**34548.3**	0.34
PINCEM	*Pinus cembra*	85	271	3	530.0	**515.9**	517.2	0.25
PINNIG	*Pinus nigra*	864	6944	8	9129.4	9078.7	**9032.2**	0.51
PINSYL	*Pinus sylvestris*	3186	21962	21	39231.8	38967.2	**38878.5**	0.28
PINUNC	*Pinus uncinata*	325	2230	6	4009.6	3995.4	**3987.9**	0.28
POPTRE	*Populus tremula*	460	1610	13	2518.0	2478.3	**2440.8**	0.42
QUEILE	*Quercus ilex*	1298	9699	9	6001.3	5997.3	**5982.7**	0.73
QUEPET	*Quercus petraea*	1441	7325	19	12655.0	12576.8	**12443.8**	0.35
QUEPUB	*Quercus pubescens*	3268	22023	16	28994.0	28889.2	**28802.7**	0.39
QUEROB	*Quercus robur*	669	2235	12	4246.4	4203.5	**4126.1**	0.28

Listed for each species are the number of individuals, plots and competitor species analysed. For each species, the model selection statistics (Deviance Information Criteria, DIC) for the three candidate models of tree radial growth are given. The best-fitting model is highlighted in bold. Model $M_{neighbour\ null}$ includes no competition effects of neighbouring trees, model $M_{neighbour}$ includes competition effects of neighbouring trees proportional to their basal area, but with the same effect for all competitor species, and model $M_{neighbour\ species}$ includes a competition effect different for each competitor species. The percentage of deviance explained (R^2_D) by the model $M_{neighbour\ species}$ is given for all target species.

The exception was H_{max}, which was estimated for each species from the NFI data by computing the 99% quantile of the height measurements across all plots.

We developed a species-resolved phylogeny for all tree species occurring in NFI plots by combining published phylogenetic trees and sequence data. As no gene sequence data were systematically available for all study species, we had to first build a genus-level phylogeny and then resolve each genus with published phylogenetic information (see Appendix S3 for details of methods). On the basis of resulting phylogenetic tree, we computed evolutionary distances between all pairs of species as a measure of their evolutionary relatedness.

Hierarchical Bayesian neighbourhood models of tree growth

We estimated tree interaction coefficients using a hierarchical Bayesian model of individual trees radial growth based on a non-linear function of tree diameter (D), bioclimatic variables (DD and WB) and local interactions with neighbouring trees based on a crowding index (CI).

The crowding index (CI) assumes that the effect of a neighbouring tree on the growth of a target tree is a function of its size and species identity. For tree i of target species k in plot p, CI_i was computed as $\sum_{s=1}^{S_p} \lambda_{ks} BA_{ps}$, where S_p is the number of species present in plot p, λ_{ks} is a parameter to be estimated representing the interaction coefficient effect of species s on k and BA_{ps} is the basal area (m² ha^{-1}) of trees neighbouring species s in plot p. We estimated the interaction coefficients λ_{ks} only for pairs of species co-occurring in more than 200 plots (see Appendix S4 for list of competitor species per target species). The remaining competitive species were grouped and represented by λ_{kr}, the interaction coefficient of rare species (the interaction coefficient of pooled rare species was, however, not used in the subsequent analysis on traits and phylogeny effects). Despite the large environmental gradients present in the data, we estimated a single interaction coefficient representing average competition effects because a previous study has shown that the intensity of plant interaction was largely stable over these gradients (Kunstler *et al.* 2011).

Separate growth models were fitted for the 22 selected species. As in Kunstler *et al.* (2011), for each target species k, radial growth of individual i in plot p was modelled as:

$$G_{pi} = \frac{\alpha_p \times D^{\beta 1} \times DD^{\beta 2} \times WB^{\beta 3}}{1 + CI_i}, \quad (1)$$

where α_p, β_1, β_2, β_3 and λ_{ks} are parameters to be estimated and α_p is modelled as a plot-random effect using a log-normal distribution. This main growth model ($M_{neighbour\ species}$) was compared with a model assuming equivalent interaction coefficients for all species ($M_{neighbour}$) and a model assuming no competition ($M_{neighbour\ null}$). Models were fitted within a hierarchical Bayesian framework; the likelihood function for model $M_{neighbour\ species}$, as well as a detailed description of our priors and MCMC simulation and diagnostic, is

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given in Appendix S5. All models were compared using the Deviance Information Criterion (DIC; Spiegelhalter *et al.* 2002). We evaluated the goodness of fit of model $M_{\text{neighbour species}}$ by computing the proportion of deviance explained $R^2_D = 1 -$ residual deviance of the model/deviance of the null model.

Regression between interaction coefficients and trait distances, phylogenetic relatedness and hierarchical trait distances

We tested whether interaction coefficients (λ_{ks}) within our neighbourhood model were related to absolute trait distances, hierarchical trait distance and/or phylogenetic distance by including these predictors (hereafter referred to as $pred_{ks}$) as terms in a regression. Absolute trait distance was calculated as $|t_k - t_s|$, where t_k and t_s are the functional trait values of species k and s respectively, whilst hierarchical trait distance was calculated as $t_k - t_s$. As species' niche similarity may be better measured by a multi-trait than by a single-trait approach, we also computed species' absolute distance in a multidimensional space defined by the four (centred and standardised) functional trait axes. All predictor variables were centred and standardised to facilitate comparison. The model (with non-informative priors) assumed a linear relationship between the interaction coefficient of species s on species k ($log\lambda_{ks}$) and $pred_{ks}$:

$$log\lambda_{ks} = a_k + b.pred_{ks} + normal(0, var_{ks}), \quad (2)$$

where a_k was a random intercept for each target species (drawn from a normal distribution of parameters a and var_a, because each target species can have a different tolerance to neighbourhood) and b is the overall slope parameter. $log\lambda_{ks}$ was used because λ_{ks} follow a lognormal distribution. We accounted for the uncertainty associated with λ_{ks}, by modelling $\log\lambda_{ks}$ as a normal variable estimated from the MCMC posterior simulation from the previous analysis. Models estimated with either the phylogenetic, the functional, the hierarchical distance of WD, Hmax, LMA, or SD, or with the multi traits absolute distance were compared against each other using the DIC.

We then explored whether the sign of the correlation observed when pooling all target species was similar to that observed when each target species was considered separately. To do so, we ran a random-slope model allowing the slope of the linear relationship to vary among target species, assuming that for target species k, the slope b_k was drawn from a random normal distribution of mean b and variance var_b (i.e. the hyper-distribution). The variability of the slope estimates for individual target species was represented by plotting the hyper-distribution and the distribution of the slope estimates for each target species for all models.

Variation in the community functional and phylogenetic structure with forest age

We analysed variation in phylogenetic and functional structure of forests with respect to their age, testing whether patterns of successional change were consistent with what might be expected from our results on links between interaction coefficients and traits. We thus restricted our analysis to the traits identified as the best predictors of tree interactions in the previous analyses. We calculated changes in three community properties with forest age: phylogenetic structure using a Net Relatedness Index (NRI; Webb *et al.* 2002), average trait values using community-weighted mean trait values (CWMT, Garnier *et al.* 2004) and the spread of trait values using the Traits Similarity Index (TSI; Uriarte *et al.* 2010). We excluded from the analysis coppice-managed plots, plantations and plots older than 120 years (because the latter were too rare). NRI is an index of relative phylogenetic diversity based on the mean pairwise phylogenetic distance of species in a plot, standardised by the mean expected phylogenetic distance (given the number of species in the plot) to correct for the effect of plot species richness (see Webb *et al.* 2002 for details). TSI was computed in a similar way, except that the distance matrix was computed as species pairwise functional trait distance. The analyses were carried out using the *picante* package in R (Kembel *et al.* 2010) with a null model generated by species-label randomisation. CWMT was computed from species relative basal area per plot. Variation in CWMT, TSI and NRI with plot age was evaluated against a null model based on a plot age randomisation (represented by the 95% quantile of 1000 randomisations). As CWMT, TSI and NRI co-varied with environmental variables correlated with plot age, we used the residuals of their ordinary least squares regression against the bioclimatic variables (*DD* and *WB*), rather than their actual values. The phylogenetic dependences of functional traits were computed using Pagel's λ, which measures the phylogenetic signal of quantitative biological characters (Pagel 1997). We calculated Pagel's λ and tested the estimated value against 0 (indicating no phylogenetic signal), using a likelihood ratio test (Harmon *et al.* 2008).

RESULTS

Species effects and goodness-of-fit of the neighbourhood models of tree growth

For all 22 target species, the inclusion of neighbouring trees effects into the models resulted in a large drop of DIC (> 10 for 19 species; Table 1), indicating strong statistical support that neighbourhood effect on tree radial growth. For all target species except *Pinus cembra*, the best-supported model had separate interaction coefficients for each of the neighbouring species (ΔDIC > 10 for 19 target species; Table 1). Even for *Pinus cembra,* there was similar statistical support for models including and excluding species effects (ΔDIC = 1.3) and therefore, for consistency, we used separate interaction coefficients for this species as well. The percentage of deviance explained by the models, which included separate interaction coefficients for each neighbouring species ($M_{\text{neighbour species}}$), was in the range 0.25–0.73.

Do interaction coefficients correlate with absolute or hierarchical functional trait distances, or with phylogenetic distances?

We found strong statistical support for a relationship between interaction coefficients and hierarchical trait distances among pairs of species (Table 2), but no support for a relationship with absolute trait distances (whether calculated with a single trait or with multiple traits) or phylogenetic distances (DIC more than 190 points greater than the best-fitting model, Table 2). The best-fitting model included LMA hierarchical distance, whilst the second-best included WD hierarchical distance (Table 2). For LMA, the negative posterior density of the slope parameter indicates that species with lower LMA than a target species have a greater competitive effect than species with higher LMA (Fig. 1, left-hand panels). For WD, the positive posterior density of the slope parameter indicates that species with higher WD values than the target species have greater

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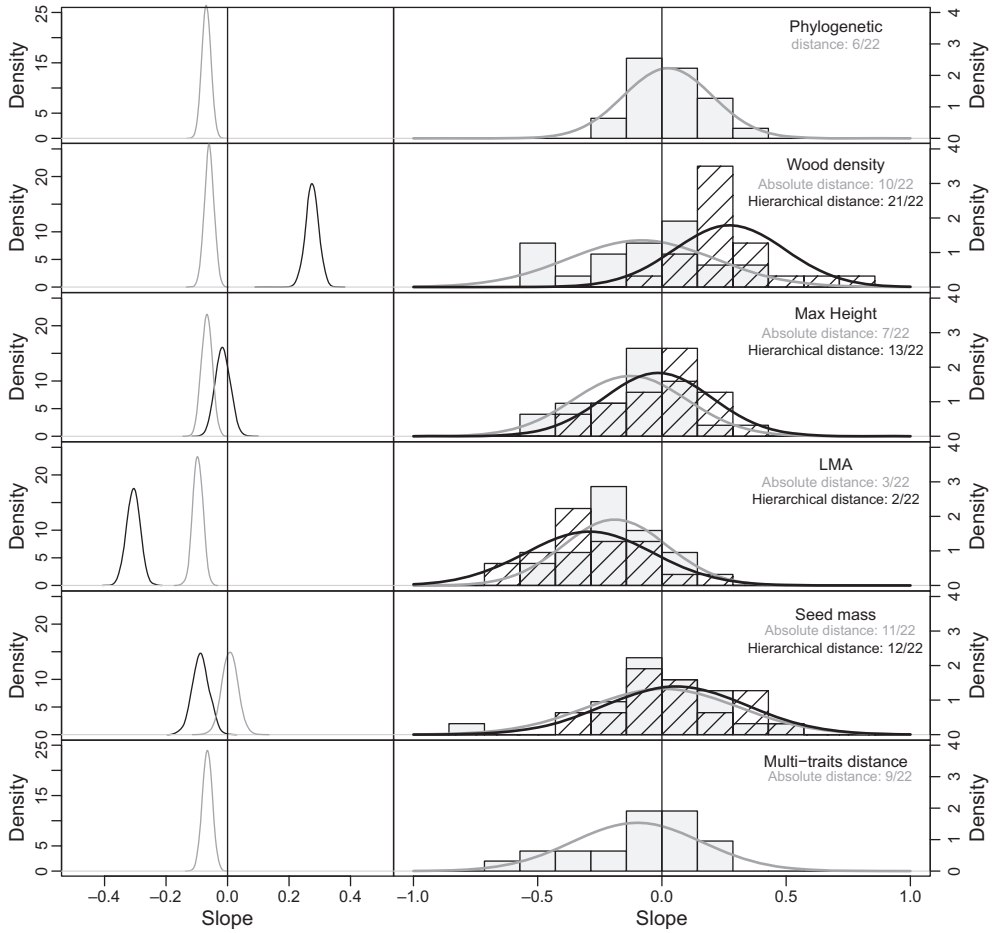

Figure 1 Left-hand panels: posteriors of the slope parameter of the regression between the interaction coefficients between pairs of species and their functional trait absolute distance (based on single trait or multiple traits) or phylogenetic distance (grey line) or functional trait-hierarchical distance (black line) fitted with a model assuming the same slope for all target species (eqn [2]). Right-hand panels: hyper-distributions of the slopes and histograms (grey bar for distance and hatched bars for hierarchy) of slope estimates for each target species estimated with a model assuming a random slope for each target species. The hyper-distribution of the target species slopes is given as Gaussian curves with mean and standard deviation estimates. The proportion of species with positive slope is indicated after the model label.

competitive effects than species with lower WD values (Fig. 1, left-hand panels).

The effect of trait-hierarchical distance on interaction coefficients was similar across species. The correlations observed when all target species were analysed simultaneously were also conserved when each target species was considered separately: the random-slope models revealed hyper-distributions that strongly deviated from zero for both LMA and WD (negatively for LMA and positively for WD). For 20 of the 22 target species, the slope of the LMA hierarchical distance model was negative (Fig. 1 right-hand panel; the exceptions being *Pinus nigra* and *Pinus uncinata*; but these species had interaction coefficients estimated for only six and five species respectively). For 21 of the 22 species, the slope of the WD hierarchical distance model was positive (the exception being *Pinus nigra*). In contrast, most models based on functional traits absolute distance (based on single trait or multiple traits) or phylogenetic distance showed much less consensus on the sign of the slope among the 22 target species. These results support the competition-traits hierarchy hypothesis rather than the competition-traits similarity or competition-relatedness hypotheses.

Variation in functional and phylogenetic structure with forest age and phylogenetic signal

We focused on changes in the functional structure of LMA and WD with forest age, given that growth analyses had identified these traits as important determinants of tree–tree interactions. The mean trait values (CWMT values) decreased systematically with plot age for LMA and increased systematically for WD (Fig. 2). The similarity index for both traits (TSI) was lower for young forest plots (Fig. 2), signifying a decrease in trait diversity with age (because lower TSI values indicate higher trait diversity). These changes in functional trait structure in early forest successional stages are consistent with a successional increase in the dominance of species with high competitive ability, with low LMA and with high WD.

We found that LMA, WD and SM had significant phylogenetic signals, but not H_{max} (see Fig. 3), with Pagel's λ being 0.604 for LMA, 0.483 for WD and 0.113 for SM (all P values < 0.001). The fact that more closely related species had more similar LMA and WD values means that increases in phylogenetic similarity with forest plot age (see Fig. 4) are probably associated with trends in the functional traits (in Fig. 2).

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Table 2 Model selection statistics (DIC) for the 10 candidate models of the relationship between the interaction coefficients between pairs of species and their phylogenetic distance, functional trait absolute distance (based on single trait or multiple traits) or functional trait-hierarchical distance

Model	DIC
Phylogenetic distance	*972.1*
WD	
Absolute distance	*981.4*
Hierarchical distance	839.5
LMA	
Absolute distance	*958.9*
Hierarchical distance	**784.8**
H_{max}	
Absolute distance	*981.1*
Hierarchical distance	*996.3*
SM	
Absolute distance	*998.4*
Hierarchical distance	*985.4*
Multi-traits distance	
Absolute distance	*976.2*

DIC, Deviance Information Criterion; H_{max}, tree maximum height; LMA, leaf mass per unit area; WD, wood density; SM, seed mass.
The best-fitting model is highlighted in bold black and the second best-fitting model in bold grey.

DISCUSSION

Neighbour effects on tree growth are driven by hierarchical trait distances

We found strong support for the hypothesis that competition between pairs of tree species is linked to hierarchical distances in LMA and WD, but not to their functional or phylogenetic similarity. The fact that interaction coefficients are related to the hierarchy of these two traits strongly suggests that competition for light is a major driver of tree interaction, and community structure. Indeed, the result that species with low LMA are strong competitors agrees well with the idea that low LMA species have greater shade tolerance and superior ability to harvest light (Valladares & Niinemets 2008; Niinemets 2010). The relationship between WD and competition for light is less well understood, but several studies indicate that shade-tolerant species have higher WD (Muller-Landau 2004; Nock *et al.* 2009; Uriarte *et al.* 2010 but see Russo *et al.* 2010). Among plant species, H_{max} is often considered a key determinant of competitive ability (Westoby *et al.* 2002). Yet, for tree species, we found no evidence of this, in agreement with other recent studies (Keating & Aarssen 2009; Uriarte *et al.* 2010). Fundamental differences in leaf life span and cellular wood structure between angiosperms and conifers may lead to distinct correlations between the

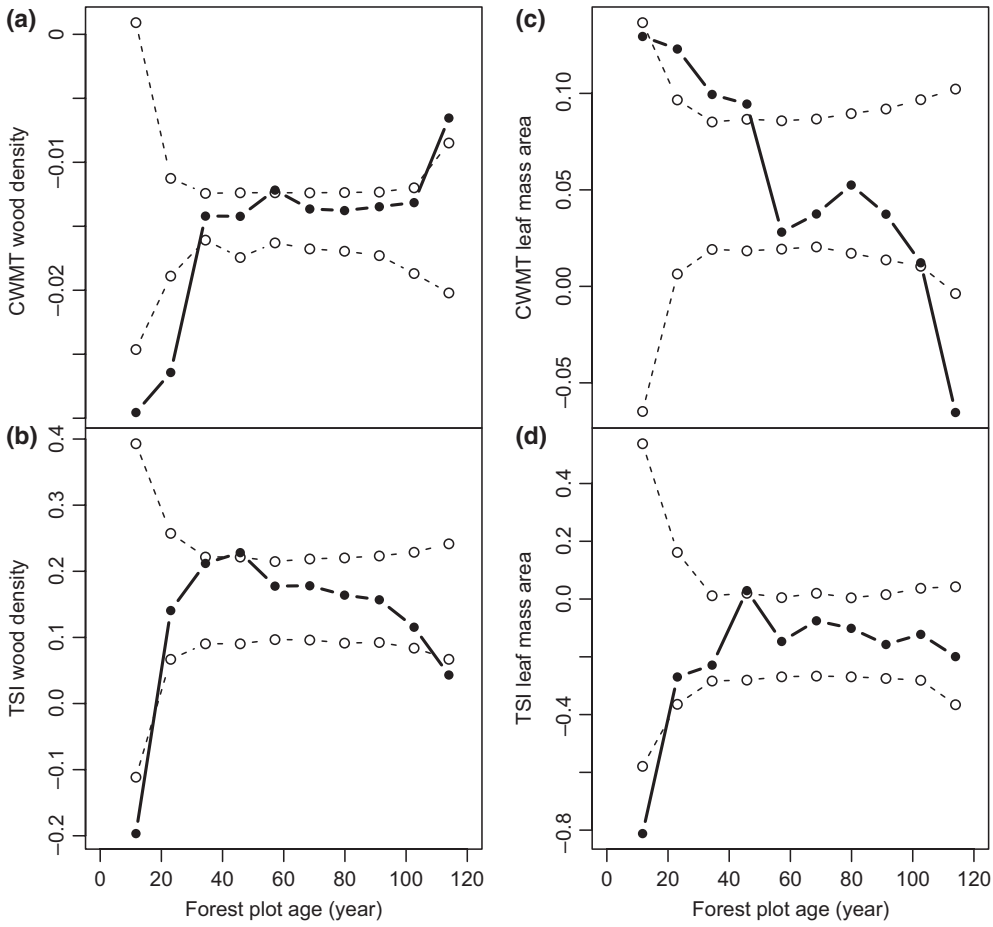

Figure 2 Variation of community-weighted mean traits (CWMT) and traits similarity index (TSI) with plot age for wood density (WD; a and b) and leaf mass per area (LMA; c and d). Black lines represent mean CWMT and TSI for 10 forest age classes and the dashed lines represent the 95% confidence intervals of 100 randomisations of plot age. To control for the effect of environmental variables, we used residual of regression of CWMT or TSI against bioclimatic variables (*DD* and *WB*).

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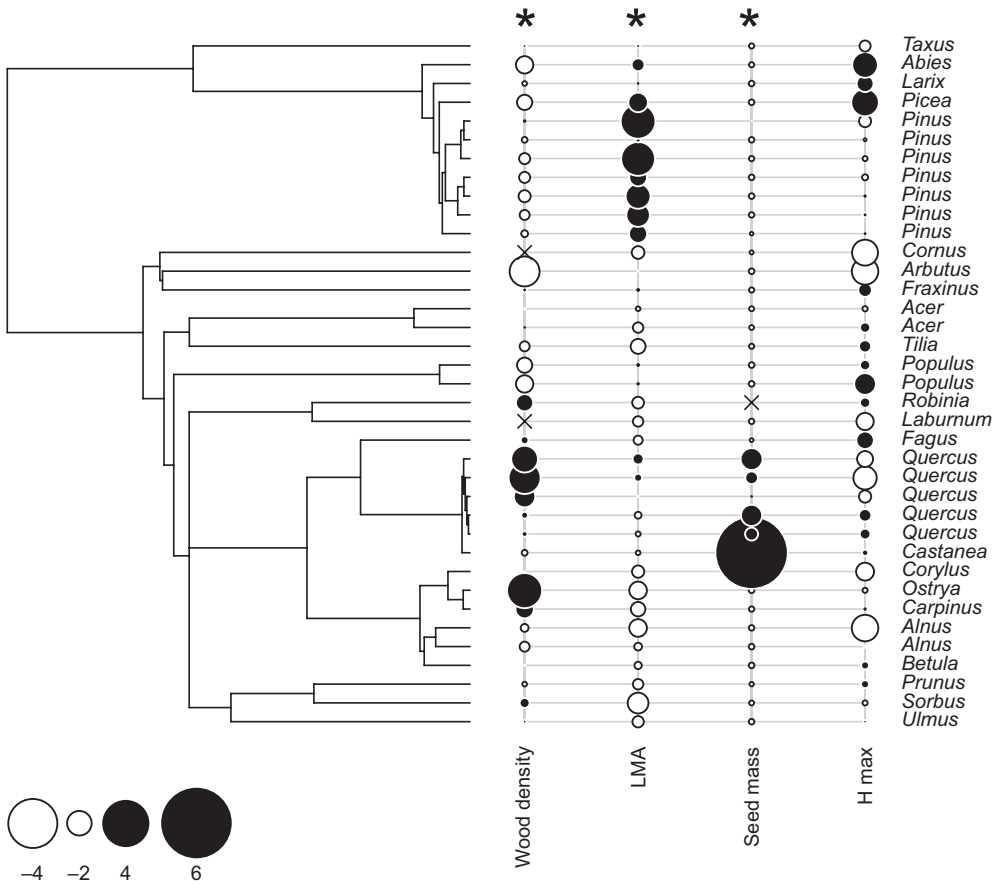

Figure 3 Phylogeny of the tree species (only species genus is given) from the French Alps and Jura Mountains. Values of the four functional traits are represented on the tips of the phylogeny (in centred and standardised format). Missing trait values are represented by an X. Traits with a significant phylogenetic signal (Pagel's $\lambda > 0$) are represented by an *.

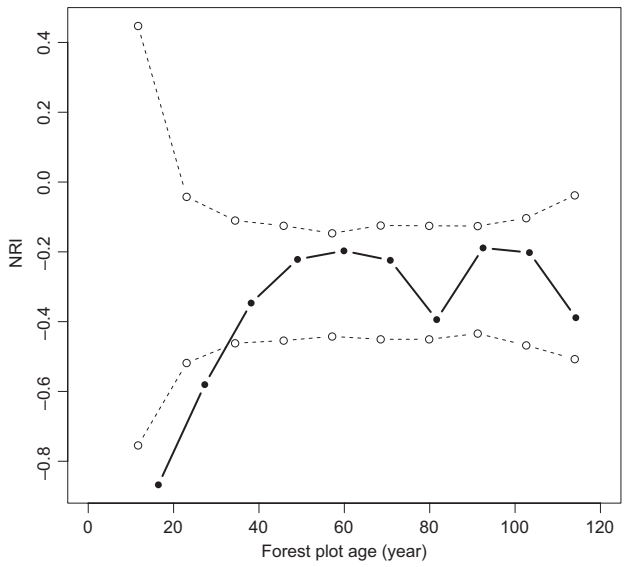

Figure 4 Variation in Net Relatedness Index (NRI) with plot age. The solid black line represents the mean NRI for 10 forest age classes and the dashed lines represent the 95% confidence intervals of 100 randomisations of plot age. To control for the effect of environmental variables, we used residual of regression of NRI against bioclimatic variables (*DD* and *WB*).

shade tolerance and these functional traits in conifers (Lusk & Warton 2007; Chave *et al.* 2009). It might be thought that the relationship we report between trait-hierarchical distance and interaction coefficients is the result of comparing two very distinct clades, but the relationship held when we restricted the analysis to angiosperms only (see Appendix S6; the limited number of conifers in our dataset precluded detailed investigation of this clade).

No evidence for the competition-relatedness hypothesis on tree growth

Our study does not support the hypothesis that niche similarity is the primary driver of local interactions among adult trees because absolute trait distances did not represent good predictors of tree interaction coefficients. Even models built with multi-trait distance as a predictor, which should capture more accurately the species niche similarities, were statistically inferior to the hierarchical trait models. The idea that niche similarity drives plant competition has been widely put forward in the literature on community assembly (Kraft & Ackerly 2010), but previous studies have never empirically tested whether competition is best predicted by functional trait similarities (absolute distance) or by hierarchical trait distances. For instance, Uriarte *et al.* (2010) explored the links between interspecific competition and absolute trait distances vs. phylogenetic dis-

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tances, but did not test for links with hierarchical distances. Conversely, Freckleton & Watkinson (2001) found evidence for a link between competition and the hierarchical distance of the maximum weight of herbaceous plants, but did not test models based on trait similarity or phylogeny.

Our observation that interaction coefficients did not correlate with phylogenetic relatedness, which could indirectly account for unmeasured functional traits, also supports the lack of strong effects of niche similarity in the forest communities we analysed. Similarly, two recent studies performed on adult plants also failed to support the 'competition-relatedness' hypothesis (Cahill *et al.* 2008; Uriarte *et al.* 2010). However, support for the competition-relatedness hypothesis has come from studies that have focused on recruitment stages (Webb *et al.* 2006; Burns & Strauss 2011; Paine *et al.* 2012). This may indicate that recruitment is more sensitive to natural enemies than are adult trees. It is also important to bear in mind that our lack of strong phylogenetic signal may be explained by the long time of divergence between most European tree taxa, which limits the number of closely related species with similar functional traits (although we reach the same conclusions when analysing only within the angiosperms, the clade with species the more closely related; see Appendix S6). Our results are crucial for the phylogenetic community assembly approach because the competition-relatedness hypotheses used in this approach has to hold for the regional species pool analysed and not only within a clade of closely related species.

We explored the role of niche similarity on competition at the tree neighbourhood scale (within 15 m of the target tree), a scale at which competitive interactions are decreased by differences in species' nutrient requirements or rooting depths (Coomes & Grubb 2000). Our results indicate that such local resource partitioning may not have a strong effect on tree growth. Owing to the evidence of species coexistence at the regional scale, it is, however, likely that other types of stabilising niche differences play a significant role. This role may only become apparent through other traits or other processes (recruitment, fecundity) or at other spatial or temporal scales. For instance, the effect of stabilising niche differences through storage effects (*sensu* Chesson 2000) will only become apparent when analysing variations in competitive interactions with temporal or spatial variations in environmental conditions (e.g. climate or soil). For such analyses, it would be crucial to add to our analysis the intraspecific variability of functional traits (particularly if this variability were correlated to the environment). However, such data are rarely available for large spatial scales, such as the scales represented by National Forest Inventories. Finally, identifying stronger stabilising niche mechanisms may require analysing the covariance of several fitness components, such as the trade-offs between colonisation and competition and to relate these to trade-offs between several functional traits to accurately measure species' niche similarities (Chesson 2000).

Temporal changes in functional and phylogenetic structure of forest communities

Long-term changes in the functional structure of forests with plot age for LMA and WD were in agreement with our results on the short-term effect of tree interaction on radial growth. We observed a decrease in community-weighted LMA and an increase in community-weighted WD with plot age. This probably originates from an increase in the dominance of competitive, shade-tolerant species (with low LMA and high WD), as predicted by classical theories of forest succession (Pacala *et al.* 1996). In line with these changes in community-weighted traits, the progressive decrease in trait diversity over time for very young forest plots indicates an exclusion of species with low competitive ability (i.e. shade-intolerant species). This pattern is reminiscent of the old concept of initial floristic composition (Egler 1954), which states that all species are present at the start of the succession and are then differentially selected. An increase in trait similarity with stand age is generally interpreted as an effect of environmental filtering, with a progressive sorting of the species best adapted to the local abiotic conditions (Uriarte *et al.* 2010). Given our results, we would propose that an alternative interpretation is that this increase is primarily driven by competition for light, which selects species with traits conferring greater competitive ability (Navas & Violle 2009).

Our results showing an increase of NRI with succession taken together with our results on local tree interaction and forest functional structure are consistent with the explanation provided by Mayfield & Levine (2010) that competition leads to a gradual increase in community NRI with successional stage. This is in sharp contrast to previous studies in which an increase of NRI was interpreted only as evidence of environmental filtering (Uriarte *et al.* 2010). So far, relatively few studies have analysed the change in phylogenetic relatedness through succession. Most studies of tropical forests have found a decrease in phylogenetic relatedness (NRI) with increasing successional stage (Letcher 2010; Letcher *et al.* 2012; Norden *et al.* 2012; but not Uriarte *et al.* 2010). In contrast, a study in a fire-prone Mediterranean system (Verdú *et al.* 2009) found an increase in NRI at the final succession stage, which they interpret as the result of competitive exclusion as in our study. The contrasting results on the variation of phylogenetic overdispersion with succession between tropical (Letcher 2010; Letcher *et al.* 2012; Norden *et al.* 2012) and temperate or Mediterranean ecosystems (this study and Verdú *et al.* 2009) may be best explained by the higher frequency of enemy-mediated density dependence in tropical climate (Mangan *et al.* 2010) leading to a more determinant role of niche similarity for tree interactions.

Implications for community assembly rules

Both species similarity and competitive ability determine the outcome of competition, and as a function of their relative importance, competition may either lead to an overdispersion or a clustering of functional traits within communities (Navas & Violle 2009). Our work suggests that the role of niche similarity in community assembly cannot be quantified simply by analysing the overdispersion of single traits or phylogenetic relatedness. The mechanisms by which plant–plant interactions can lead to coexistence of species have been synthesised several years ago (Chesson 2000), but niche assembly models have so far failed to incorporate these mechanisms. As recently proposed by Spasojevic & Suding (2012), we can now move on to a next generation of community assembly models that: (1) separate the effect of niche and competitive ability differences in plant interactions and (2) understand what trade-off axis among multiple traits underpins plant competitive ability or stabilising niche differences. This is crucial to understand how the importance of these two processes changes among community types (e.g. forests vs. protist communities; Violle *et al.* 2011) and along climatic gradi-

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ents (e.g. tropical vs. temperate forests). With such improved insights, opportunities will emerge for models of community assembly to be incorporated into tools forecasting global change impacts on plant biodiversity (Lavergne *et al.* 2010).

AUTHORSHIP

GK conceived the project while working with DAC in Cambridge, and designed the study following discussions at a workshop attended by all authors except JK; formatted the data, performed modelling work and analysed output data; wrote the first draft of the manuscript. SL performed phylogenetic analyses. All authors substantially contributed to revisions.

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