Intraspecific trait variability of trees is related to canopy species richness in European forests

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ABSTRACT

Functional diversity informs about biodiversity-ecosystem functioning relationships. The intraspecific component of functional diversity (i.e. the phenotypic space of each species) depicts individual differences in the resource use and fitness among conspecifics, and gives valuable information about the functional similarity (competition) or dissimilarity (complementarity) of coexisting species. Here, we quantified trait differences within tree species along local diversity gradients to shed light on the role that this intraspecific variability exerts on functional complementarity of tree species. We measured architectural traits in 5,036 individuals and leaf traits in 1,403 individuals from nine dominant tree species, surveyed in 92 plots located in three major European forest types (Mediterranean, temperate and boreal forests). In each forest type, plots were positioned along a canopy richness gradient, with every study species present in different species richness levels, including monocultures. Our results showed that the relative magnitude of intraspecific trait variability to community-level variability is high in these forests. At the species level, we found adjustments of species leaf traits (mean shifts) in response to neighbouring trees, suggesting the existence of processes that limit niche overlap. We also found higher variability in architectural traits of conspecific individuals in more diverse canopies, suggesting greater niche packing and a more efficient use of available space as the number of species in the canopy increases. Altogether, our results support the hypothesis that differential responses of individuals within a species promote species complementarity, suggesting that biodiversity-ecosystem functioning relationships cannot be properly estimated without accounting for the intraspecific level of functional variation.

1. Introduction

An increasing body of work shows the positive effect that plant diversity exerts on different ecosystem functions and services, accounted either individually (e.g. productivity, stability or resilience against pests or pathogen outbreaks) (Allan et al., 2013; Balvanera et al., 2006; Cardinale et al., 2012) or together (the so-called 'multi-functionality') (Gamfeldt et al., 2008; Lefcheck et al., 2015; van der Plas et al., 2016). For individual ecosystem functions, two additive mechanisms have been identified supporting this positive relationship: niche complementarity and selection effects (Loreau and Hector, 2001; Turnbull et al., 2013). The former assumes that diverse communities comprise species with different resource use (i.e. differences in resource

requirements or spatial/temporal distribution); the latter assumes that competition leads high-yielding species to dominate in mixtures.

Including functional diversity, in addition to the number of species, gives further information about the biodiversity effect on ecosystem functioning as it can better capture species interactions in a community (Cadotte, 2017; Cadotte et al., 2011; Ebeling et al., 2014). Traits determine how individuals use resources from their environment (McGill et al., 2006), and provide information about species niche and fitness differences (Kraft et al., 2015). Species trait differences are therefore directly linked to the complementarity and competitive ability of coexisting species (Carroll et al., 2011; Loreau et al., 2012), key components of biodiversity that influence how an ecosystem operates or functions (Tilman, 2001). Since approximately 25% of total estimated

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trait variation in plant communities worldwide is found within species (Albert et al., 2010a, b; Siefert et al., 2015), intraspecific variability should not be ignored when quantifying biodiversity effects on ecosystem functioning (Aschehoug and Callaway, 2014; Ashton et al., 2010; Zhu et al., 2015). Accordingly, an increasing number of studies is revealing the importance of intraspecific variability for different ecological questions, including functioning of plant communities (Crutsinger et al., 2006; Lecerf and Chauvet, 2008), community assembly (Jung et al., 2010; Siefert, 2012), species distribution forecasting (Cochrane et al., 2015; Valladares et al., 2014), and mechanisms ruling species interactions and coexistence (Lichstein et al., 2007; Roscher et al., 2015).

Traits are measured at the individual level, and the distribution of trait values within a species identifies its functional trait space. Hence, considering trait variability between and within species entails that the functional space can be occupied continuously by all the individuals making up the community. Approaches based on species mean traits underestimate species interactions (by ignoring functional overlaps) and the utilisation of available resources (de Bello et al., 2013; Violle et al., 2012). The functional overlap among coexisting species reveals their similarity, i.e. the functional space they share (Violle et al., 2012). Thus, low trait overlaps in rich communities would support that species exploit different niches and are thus complementary in their resource use. Meanwhile, large overlaps would imply functional redundancy among coexisting species. Despite the large effort required to quantify and collate trait variation within species, several studies have tackled the relationship between species richness and trait distributions and overlaps in order to elucidate mechanisms that underpin the structure of natural communities (Bastias et al., 2017; Kumordzi et al., 2015; Le Bagousse-Pinguet et al., 2014). However, results are contrasting and there is no clear evidence of similar species-specific responses (trait adjustments) to changes in species richness and composition. Insights from biodiversity experiments (carried out primarily with herbaceous species) have revealed a potential role of intraspecific variability for fostering species complementarity (Ashton et al., 2010; Mitchell and Bakker, 2016; Zuppinger-Dingley et al., 2014; Zhu et al., 2015). For instance, Zhu et al. (2015) assessed that 64% of the total net biodiversity effect measured on light capture compared to monocultures in wheat and maize intercrops was due to species plasticity.

Here, we have quantified trait variation within tree species along diversity gradients of canopy trees in mature, European forests to address whether intraspecific trait variability enhances species complementarity. We have compared the intraspecific trait variability (hereafter ITV) of trees growing in pure vs. mixed stands in three contrasting forest types: a continental-Mediterranean, a mountainous mixed temperate and a boreal forest. First, we have evaluated the magnitude of ITV at the community level relative to the variability among species (intErspecific Trait Variation, hereafter ETV) across the forest types, and analysed its relationship with species richness of the canopy tree layer. We further analysed how this component of the variability at the community level varies with species richness.

Subsequently, we analysed the relationship between species richness and ITV at the species level, i.e. trait mean and variance among conspecific individuals, searching for species-specific responses to the diversity gradient. Given the contrasting results found in previous studies of how species richness affects ITV (Bastias et al., 2017; Kumordzi et al., 2015; Le Bagousse-Pinguet et al., 2014; Siefert et al., 2015), we posit three alternative hypotheses for this relationship (Fig. 1): i) species richness and ITV are not correlated, suggesting either full complementarity among species or non-saturated communities; ii) species richness and ITV are negatively correlated, implying a reduced ITV due to resource partitioning and avoidance of niche overlap with increasing species richness (McGill et al., 2006; Tilman, 1982); iii) species richness and ITV are positively correlated, entailing higher temporal or spatial heterogeneity in the community that provides new opportunities (new niche availability) and wanes competition among individuals (Stein

et al., 2014). This positive correlation might arise either by an increment of intraspecific trait variability at the community level (changes in trait variance among conspecifics in two different communities), or by trait mean shift of a species.

2. Methods

2.1. Study sites

The three study sites belong to a network of plots established for the European project FunDivEUROPE (*Functional significance of forest biodiversity*; www.fundiveurope.eu), which comprise some of the major European forest types (Baeten et al., 2013). In particular, this study was located in a continental-Mediterranean mixed forest in the Alto Tajo Natural Park (Spain), a mountainous beech forest in Râşca (Carpathian Mountains, Romania) and a boreal forest in North Karelia (Finland). Hereafter, we refer to them as 'Mediterranean', 'temperate' and 'boreal', respectively (Table 1).

In each site, plots (30 x 30 m) were established following a diversity gradient of regional dominant tree species in different combinations (replicated at least twice), ranging the species richness (SR) of the canopy from 1 to 3 in Finland, and from 1 to 4 in Romania and Spain. Every dominant species was present in all species richness levels (see in Appendix A, Table A.1 the detailed species combination design). The total number of sampled plots were 92 and the tree species were *Pinus nigra* Arnold, *Pinus sylvestris* L., *Quercus faginea* Lam. and *Quercus ilex* L. in the Mediterranean forest with 36 plots in total; *Abies alba* Mill., *Acer pseudoplatanus* L., *Fagus sylvatica* L. and *Picea abies* [L.] Karst. in the temperate forest; and *Betula pendula* Roth., *Picea abies* [L.] Karst. and *Pinus sylvestris* L. in the boreal forest, both with 28 plots. Criteria for plot selection are explained in detail in Baeten et al. (2013) and relied on two main principles: 1) mixed plots had high evenness, i.e. species had similar relative abundances; 2) variation of environmental conditions among plots within a region (e.g. soil, topography) was minimised, reducing the covariation between environmental gradients and species richness.

2.2. Study traits, sampling and measuring

We considered traits at the leaf and at the whole-plant levels. At the leaf level, we chose two morphological leaf traits associated with resource acquisition-conservation trade-off (Wright et al., 2004), namely specific leaf area (SLA, the area of an individual fresh leaf divided by its dry mass) and leaf dry matter content (LDMC, the oven-dry mass of an individual leaf divided by its water-saturated fresh mass). Both traits are variable and sensitive to variations in nutrient and water supply (LDMC and SLA) and light conditions (SLA), constituting main factors of adjustment in whole-plant response. Hence, variation in resource availability drives leaf traits in a way that is generally reflected in establishment of individuals with acquisitive traits (high SLA and low LDMC) in nutrient rich environments and conservative traits (low SLA and high LDMC) in nutrient poor environments (Wilson et al., 1999; Wright et al., 2004).

We harvested leaves from ten individuals per species (dbh > 10 cm) in each plot in the boreal and Mediterranean forests, and from at least six (monocultures) and three (mixed forest) trees in the temperate forest, due to the canopy height and difficulty sampling. We selected randomly the surveyed trees to maximise trait variability within species. We cut two branches at the most contrasting crown positions from each of the target trees, one located at the top and facing south, and the other at the bottom of the crown and facing north, and we collected five leaves/needles in each branch. Final sample size totalled 13,990 leaves from 1,403 trees (Appendix A, Table A.2). Leaf collection, storage, processing and trait measurement followed Garnier et al. (2001) and Pérez-Harguindeguy et al. (2013). We weighed rehydrated leaves, scanned them and measured their area using WinFOLIA and
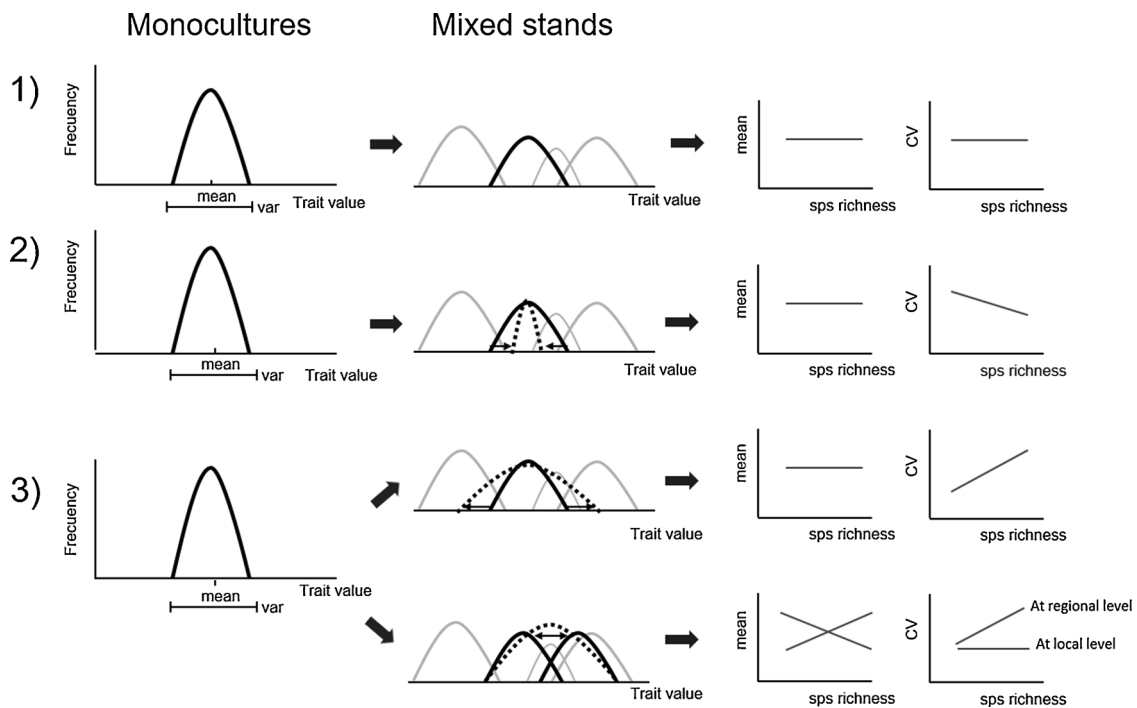
Fig. 1. Alternative hypotheses for the relationship between intraspecific trait variability (ITV) and species richness (SR) in a forest community. The comparison of a species trait distribution between conspecific (monocultures) vs. heterospecific neighbours (mixed stands) is addressed in terms of mean trait value and trait variance (assessed as coefficient of variation -CV-). 1) Null relationship, ITV does not correlate with species richness (neither its mean value nor the variance); 2) ITV decreases with species richness, i.e. variance diminishes around the optimal value; or 3) ITV increases with species richness either by local variance increment or by trait mean shift and the ensuing increment of the overall phenotypic space at a larger scale.

Table 1
Brief description of the study sites, species and environmental conditions.

	North Karelia, Finland (boreal)	Carpathian mountains, Romania (temperate)	Alto Tajo Natural Park, Spain (continental-Mediterranean)
Coordinates	62.4 °N–29.4 °E	47.3 °N–25.5 °E	40.7 °N–1.9 °W
Dominant species	*Betula pendula*	*Abies alba*	*Pinus nigra*
	Picea abies	*Acer pseudoplatanus*	*Pinus sylvestris*
	Pinus sylvestris	*Fagus sylvatica*	*Quercus faginea*
		Picea abies	*Quercus ilex*
Annual mean T (ºC)*	2.1 (0.3)	5.5 (0.5)	9.7 (0.6)
Annual mean P (mm)*	631.8 (5.9)	691.1 (24.9)	537.4 (27.3)
Elevation range (m)	87–233	655–1062	960–1404
Soils	Podzols and glacial tills, histosols on peatlands	Tertiary sandstone and clay, loamy sediments	Calcareous, reddish Terra rossa
Main forest types (EEA-code)*	Boreal	Carpathian mountainous beech forest	Coniferous and broadleaf Mediterranean forests
Species richness gradient	1-3	1-4	1-4
Number of plots	28	28	36
Plots per richness level	11/14/3	8/10/7/3	12/15/6/3

* T = temperature, P = precipitation, figures in brackets are the standard deviations; EEA: European Environmental Agency (source: EEA Technical Report No 9/ 2006; https://eea.europa.eu).

WinSEEDLE for broadleaves and needles, respectively (Regent Instruments Inc. Canada). Finally, they were oven-dried at 60 °C for 72 h and weighed for dry mass.

At the whole-plant level, we considered two traits from every single tree within the study plots (5,036 adult trees in total), namely tree height (H) and crown projection area (CP). We calculated crown projection area assuming elliptical areas, using the projection of two perpendicular diameters (the longest one and its perpendicular) of the crown. Height and crown size can be considered individual performance measures (Garnier et al., 2016); but both variables represent the standing phenotypic variation in a tree community and the relative competitive ability of each individual for coexistence (Siefert et al., 2015). Moreover, our experimental design imply negligible ontogenetic differences at the plot level among individuals because our study sites

comprised mature forests at late- to mid-stem exclusion stages with scattered individuals belonging to immature cohorts (Baeten et al., 2013). A summary of sample sizes per trait, species and forest type is shown in Table A.2 (Appendix A in Supporting information).

2.3. Statistical analyses

2.3.1. Relative extent of intra- and interspecific trait variability on total community variability

We followed the approach developed by de Bello et al. (2011) to evaluate the relative contribution of ITV and ETV on total trait variability in every plot. This approach is based on the partitioning of total community (plot) trait variance into within- (ITV) and among-species (ETV) components, which is equivalent to the decomposition of the

dissimilarity between pairs of observations, i.e. the quadratic entropy diversity (Rao index of functional diversity). Hence, the relative contribution of ITV in community i (ITV$_{rel}$, Eq. (1)) is the ratio of the variance within species j (ITV$_{abs}$) over the total community variance, which is the sum of abundance-weighted ITV and ETV. Similarly the relative contribution of ETV$_{rel}$ in community i is the ratio of the variance among the species j (ETV$_{abs}$) over the total community variance (Eq. (2)),

$$ITVrel_i = \frac{ITVabs}{ITVabs + ETVabs}$$
$$= \sum_j^{Nsp} \frac{p_{ij}\frac{1}{Nind_{ij}}\sum_k^{Nind}(T_{ijk}-T_{ij})^2}{\sum_j^{Nsp} p_{ij}\frac{1}{Nind_{ij}}\sum_k^{Nind}(T_{ijk}-T_{ij})^2 + \sum_j^{Nsp} p_{ij}(T_{ij}-T_i)^2} \quad (1)$$

$$ETVrel_i = \frac{ETVabs}{ITVabs + ETVabs} =$$
$$\frac{\sum_j^{Nsp} p_{ij}(T_{ij}-T_i)^2}{\sum_j^{Nsp} p_{ij}\frac{1}{Nind_{ij}}\sum_k^{Nind}(T_{ijk}-T_{ij})^2 + \sum_j^{Nsp} p_{ij}(T_{ij}-T_i)^2} \quad (2)$$

where Nsp is the number of j species and $Nind$ the number of k individuals sampled in a community (plot) i, p_{ij} is the relative abundance of species j in community i, T_{ijk} is the trait value of the individual k of the species j in community i, T_{ij} the mean trait value of the species j in community i, and T_i the mean trait value in community i. We used the relative species basal area in a plot (i.e. ratio of the sum of cross-sectional area of stems at breast height of each species over the sum of all species present in a plot) as the relative abundance. For foliar traits, we used SLA and LDMC per tree as the average of the ten harvested leaves. We chose the mean value among the most dissimilar leaves in each tree (collected from the two most light-contrasting locations in the crown) instead of leaves exposed to full sunlight, frequently used (Pérez-Harguindeguy et al., 2013), to have a fairer comparison across individuals as our sample included non-dominant individuals with no sun-exposed leaves. Note that ITV or ETV is used for intraspecific and interspecific trait variability in general terms, ITV$_{abs}$ and ETV$_{abs}$ for the absolute value of variability (variance expressed as squared units) assessed for each component, and ITV$_{rel}$ and ETV$_{rel}$ for the relative contribution (%) of each component to the total variability at the community level.

We also evaluated the trait overlap at plot level using the R function 'trova' (de Bello et al., 2013). It assesses the overlapping area between two trait distribution curves with kernel density estimators, not assuming any particular shape of the trait distribution (Mouillot et al., 2005).

2.3.2. Relationship between intraspecific trait variability and species richness

We checked the relationship between species richness (SR) and the ITV assessed at the community (plot) level (ITV$_{abs}$) (Eq. (3)). Then, we scaled down to the species level and analysed the relationship between species richness (SR) and trait mean (T) of conspecific individuals (Eq. (4)), and between species richness (SR) and trait variance at plot level per species, assessed as the coefficient of variation (CV) (100 × (standard deviation/mean)) (Eq. (5)). We fitted linear mixed models (LMMs) for the different response variables, which were log-transformed, as appropriate, to meet the assumptions of inferential statistics (normally distributed errors).

$$ITV_{abs} \sim TF*SR + (1|combination) + \varepsilon \quad (3)$$

$$T \sim Sp*SR + HCanopy + TD + BA + BAcon + (1|combination/plot) + \varepsilon \quad (4)$$

$$CV \sim Sp*SR + TD + BA + BAcon + (1|combination) + \varepsilon \quad (5)$$

Analysing ITV at the community level (ITV$_{abs}$), we included the

interaction between type of forest (TF) and species richness (SR) for analyses as fixed effect, allowing different responses to species richness among forest types. Analysing species trait responses, we included the interaction between species identity (Sp) and species richness, allowing different species responses for analyses at the species level. We ran models for each forest type separately, avoiding triple interactions and complex outcome interpretations. In addition, we included four covariates that describe the structure of the stand and account for any within-region variability due to historical management: i) tree density or number of adult trees in the plot (TD); i) plot basal area (BA), i.e. the sum of the basal area of all trees within a plot (m^2); iii) proportion of basal area considering only conspecific individuals (BAcon); and iv) the hierarchical position of each tree in the canopy (HCanopy) with a visual estimation into: 1) predominant; 2) dominant, 3) co-dominant; 4) dominated; 5) completely suppressed (Kraft, 1884). The latter was not considered when tree height was analysed, as they were highly correlated. Regarding the random structure, *combination* (i.e. species present in a plot) accounted for the variance among observations derived from specific species interactions in a community (see detailed species combinations in Table A.1, Appendix A), and *plot* for the expected correlation among trait observations within plots.

We assessed the significance for each fixed effect by stepwise backward model selection, in which models of increasing complexity were compared to simpler ones using likelihood ratio (L-ratio) tests (Zuur et al., 2009), and we selected our optimal models following the principle of parsimony. For the analyses at the species level, we always retained the species identity and species richness (Sp and SR) in the models, to derive effect sizes for all models, but we removed non-significant covariates. Model parameters were estimated using a Restricted Maximum Likelihood approach, while Maximum Likelihood estimates were used when comparing models with L-ratio tests. LMMs were performed using the package 'lme4' (Bates et al., 2014) in R (R Core Team, version 3.3.1, 2016).

To compare the sole effect of species richness on study traits, we used the mean predicted values from the optimal LMMs of each trait at both extremes of the species richness gradient to assess the d effect size (Cohen, 1988), i.e. the mean difference standardised by the pooled standard deviation of the two groups. We combined firstly the effect sizes by forest type, and secondly we pooled all to provide the grand mean effect size using fixed-effect models (Hedges and Vevea, 1998). We represented these effect sizes using the package 'metafor' in R (Viechtbauer, 2010).

3. Results

3.1. Relative extent of intraspecific variability at the community level

Comparing the relative extent of intra- vs. interspecific trait variability (ITV$_{rel}$ vs. ETV$_{rel}$) showed that the contribution of ITV$_{rel}$ was substantial in the three studied forests (Fig. 2), although the magnitude depended on the trait. Specifically, architectural trait variability (tree height and crown projection area) remained mainly within species (i.e. ITV$_{rel}$ was always over 50%); while for leaf traits, the contribution of ITV$_{rel}$ was smaller, especially for SLA with contributions below 50%.

Regarding patterns along the species richness gradient, we found some expected trends. All the variability found in monocultures was due to ITV by definition. Gradually, as the species richness increased, the variability at the community level (absolute values) increased, due to increments in both, inter- and intraspecific components (Fig. 3; Appendix B, Fig. B.1).These results are in accordance with Kumordzi et al. (2015) (see their Supporting information) who evidenced a mathematical correlation between species richness and both components of the community trait variance. However, we found that the relative importance of ITV$_{rel}$ decreased with species richness for both leaf traits, while the relationship depended on the forest type for architectural traits (Fig. 2). Finally, we also studied the relationship between SR and
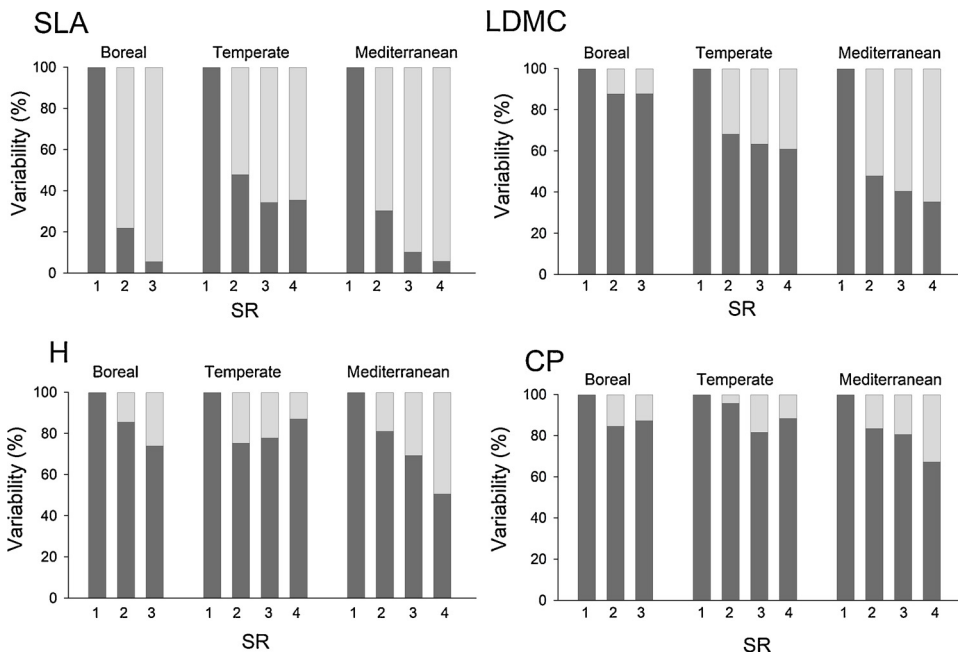
Fig. 2. Mean relative contribution of intraspecific (dark grey) and interspecific (light grey) variability to the community-level functional trait variability (in %) assessed for the study traits (SLA: specific leaf area; LDMC: leaf dry matter content; H: tree height; CP: crown projection area). Each bar represents the average of communities (plots) with the same species richness level (SR) within each forest type.

the species overlap for the four study traits, obtaining no significant effect (see SI; Appendix C, Fig. C.1).

3.2. Species trait patterns in relation to species richness

Focusing on species-specific responses, we analysed the relationship between species richness (SR) and both mean trait values of conspecific individuals and trait variability at community (plot) level. The analyses showed divergent trends for leaf traits among forest types, and similar for architectural ones (Fig. 4; Table 2).

In the temperate forest, we found a clear positive relationship between species richness and SLA, and a negative relationship with LDMC. In the Mediterranean forest, species richness was positively correlated with LDMC, while in the boreal forest no significant pattern was found (Fig. 4a; Table 2; SI Appendix B Fig. B.2). Regarding the architectural traits, values of tree height and crown area did not show clear relationships with species richness, with species-specific responses (significant interaction between species richness and species) in the

boreal and Mediterranean forests. However, trees were taller as the proportion of conspecific individuals (in basal area) increased, and as tree density decreased in the three study cases (Table 2; Fig. B.2). Moreover, trees generally had larger crown in less dense communities (Table 2).

The relationship between species richness and species trait variability at plot level (CV) was clearer in architectural than in leaf traits (Table 2). Despite the lower sample size, which implied wider confidence intervals (Fig. 4b), conspecific individuals in richer communities were more variable than in monocultures, at least in the boreal and temperate forests; while it was species-specific in the Mediterranean forest (Fig. 4b; Table 2; Fig. B.2).

4. Discussion

We explored two main questions regarding the relevance of intraspecific trait variability of tree species in European forests. First, we have observed an important contribution of ITV_{rel} to the total
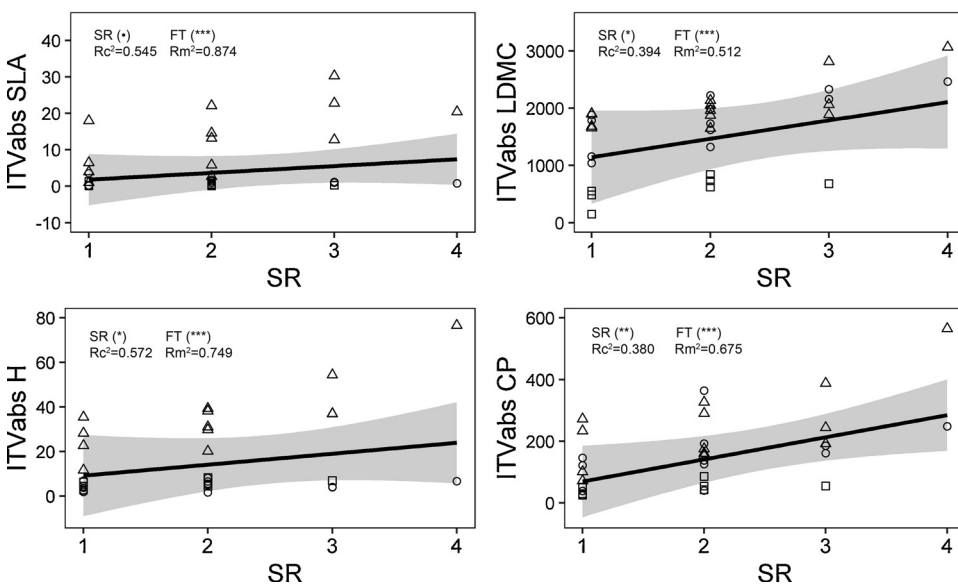
Fig. 3. Relationship between predicted ITV at community level (ITV_{abs}) for the four study traits (SLA: specific leaf area; LDMC: leaf dry matter content; H: tree height; CP: crown projection area) and species richness (SR) with 95% confidence intervals for fixed effects. R^2 marginal and conditional of the models are shown, and significant SR and/or forest type (FT) effects are indicated (• p-value ≤ 0.1; * p-value ≤ 0.05; ** p-value ≤ 0.01; *** p-value ≤ 0.001). Squares are predicted values for the boreal forest, triangles for the temperate forest, and circles for the Mediterranean forest.
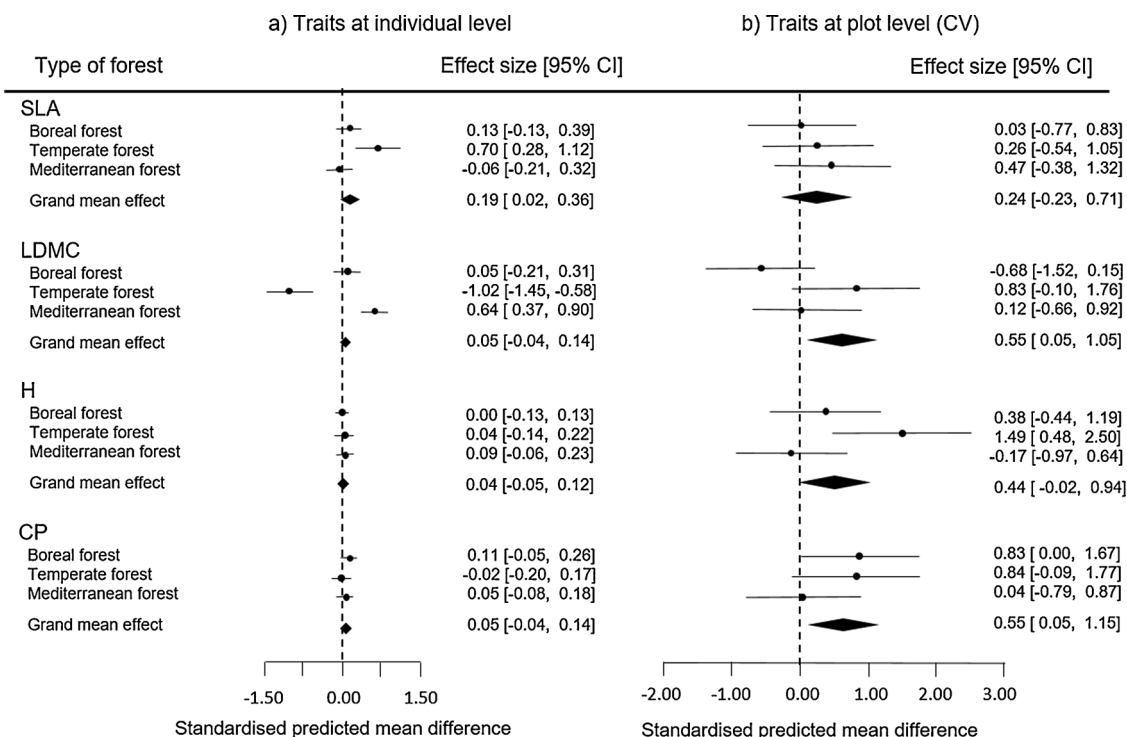
Fig. 4. Standardised effect sizes of species richness on: a) individual trait values; and b) trait variability at community (plot) level expressed as coefficient of variation -CV- of the four study traits (SLA: specific leaf area; LDMC: leaf dry matter content; H: tree height; CP: crown projection area), using linear mixed models. Error bars represent 95% confidence intervals.

variability at the community level for all the study traits, supporting the need for its incorporation in trait-based approaches to community ecology. Second, we have also found a slight adjustment of species traits in responses to the species richness of the neighbours that may promote species complementarity, although it varied among traits, species and forest types. Our results generally supported our third proposed

hypothesis that trait variability increases in more diverse European forest communities, and that this increment is driven either by increased variability of conspecific individuals with more variable phenotypes or by shifts of mean trait values at a larger scale.

Table 2

Optimal linear mixed models for individual trait values and trait variability at plot level (CV, coefficient of variations) as response variables. The columns show the χ^2 values from likelihood-ratio tests and the direction of each explanatory term selected.

		Sp	SR	Sp*SR	Hcanopy	TD	BA	BAcon	n	ΔAIC	R^2 marginal/conditional	
Boreal	SLA	1514.14***	0.34		(+) 37.23***				460	5.73	0.972	0.978
	LDMC	243.05***	0.49		(-) 8.3 **			(-) 3.44 •	460	5.7	0.485	0.638
	H	233.57***	0.63	32.32***		(-) 17.24***		(+) 23.42***	1824	1.8	0.407	0.564
	CP	16.57***	0.51		(-) 874.41***	(-) 12.25***		(-) 8.63***	1824	1.4	0.646	0.574
Temperate	SLA	484.95***	5.24*		(+) 45.96***				226	2.97	0.921	0.929
	LDMC	154.3***	7.65**						224	6.65	0.537	0.571
	H	59.79***	0.17			(-) 20.27***	(+) 9.34**	(+) 16.37***	1227	2.9	0.199	0.335
	CP	118.45***	0.04		(-) 672.34***	(-) 3.81 •			1205	7.7	0.433	0.551
Mediterranean	SLA	1901.6***	0.55	10.48*	(+) 33.58***			(+) 2.78 •	700	3.76	0.947	0.959
	LDMC	682.08***	4.78*						686	10.5	0.644	0.729
	H	293.35***	3.10 •	28.07***		(-) 6.71**	(+) 24.18***	(+) 28.57***	1951	0	0.522	0.679
	CP	107.81***	0.63	10.79*	(-) 1084.22***	(-) 11.21 ***			1944	9.2	0.421	0.665
Boreal	CV SLA	102.36***	0		nc				48	2.72	0.882	0.895
	CVLDMC	110.24***	3.5 •	4.82 •	nc			(-) 4.28*	48	3.22	0.905	0.905
	CV H	47.14***	3.33 •		nc				48	3.6	0.622	0.625
	CV CP	6.82***	4.32*		nc	(-) 5.28*			48	5.9	0.236	0.311
Temperate	CV SLA	16.44***	0.18		nc				61	7.55	0.218	0.304
	CV LDMC	40.40***	2.32		nc				61	5.31	0.478	0.501
	CV H	19.39***	5.60*		nc				61	3.94	0.363	0.456
	CV CP	17.73***	1.36		nc				60	10.13	0.235	0.296
Mediterranean	CV SLA	64.44***	2.58	9.58*	nc	(+) 9.57**			72	3.49	0.636	0.666
	CV LDMC	75.46***	0.05		nc				71	2.71	0.639	0.728
	CV H	10.93*	0.16		nc		(-) 5.17*		72	4.65	0.174	0.311
	CV CP	23.91***	0.12	8.04*	nc	(-)12.8***			72	3.52	0.378	0.58

SLA: specific leaf area; LDMC: leaf dry matter content; H: tree height; CP: crown projection area; Sp: species; SR: species richness; HCanopy: hierarchical position in the canopy; TD: tree density in the plot; BA: basal area of the plot; BAcon: proportion of BA of conspecific individuals; n: sample size; ΔAIC: difference in AIC referred to the saturated model; nc: not considered in the saturated model. Significance: •10%, *5%, **1%, ***0.1%.

4.1. Relative extent of intraspecific trait variability in European forests

Trait variation within and among species may reach comparable magnitudes (Auger and Shipley, 2013; Fajardo and Piper, 2011), especially in species-poor communities where ITV contribution to community-level trait variability is expected to be larger than in highly diverse communities (Siefert et al., 2015). Our study forest communities, which are examples of the most representative and extensive types of European forests, are poor in terms of tree species richness compared to forest ecosystems in other regions. Our findings showed that ITV$_{rel}$ comprises a large amount of the community-level trait variability (often over 50%), supporting our expectations. However, the magnitude depended on the trait considered, in agreement with previous studies (Auger and Shipley, 2013; Siefert et al., 2015). Tree height and crown size variability mainly encompassed dissimilarities at the species level (higher ITV$_{rel}$ than ETV$_{rel}$). This outcome is consistent with the fact that plants are modular organisms so whole-plant traits can accumulate more variability according to the local conditions where each module develops (Herrera, 2009; Marks, 2007; Siefert et al., 2015) than organ-level traits. Moreover, asymmetric competition for light enhances trait variability among individuals, regardless of the species, which accumulates throughout the lifespan of the plant.

Crucially, we found contrasting results for the two leaf traits. Variability in SLA was greater among species than within, and the opposite was true for LDMC. This finding can be explained by the fact that both traits are influenced by soil fertility and moisture but SLA is more influenced than LDMC by light conditions, which can vary enormously within a crown (Pérez-Harguindeguy et al., 2013; Wilson et al., 1999). Several studies have documented large variability in SLA within individuals conferring this variation on self-shading effects and complex interactions between soil fertility and light conditions (Reich, 2014; Wilson et al., 1999). However, in this study we omitted this component of the variability (within individuals), as we used averaged leaf traits per individual, and most of the remaining SLA variability was found between, instead of within, species. Contrasting variability patterns between these two traits are not new (Hulshof and Swenson, 2010; Roche et al., 2004) further supporting that the relative importance of ITV to ETV rely on the trait considered, species identity and communities.

4.2. Relationship between species richness and species trait patterns

We found that species richness correlated with ITV at the species level, although the strength and sign of the relationship depended on the study trait and forest type. Previous studies with grasslands also detected diversity-induced differences in species trait means (Gubsch et al., 2011; Roscher et al., 2015; Zuppinger-Dingley et al., 2014). Here, we found smaller conspecific individuals and with more variable architectures in richer communities (coefficient of variation of height and crown size at plot scale), which agrees with studies that report competition release, increased niche packing and a more efficient use of aboveground space in mixed stands compared to monocultures (Jucker et al., 2015; Pretzsch, 2014; Swenson and Weiser, 2014). In particular, Jucker et al. (2015), working in the same study sites, found greater vertical stratification and higher species crown variability in mixed stands compared to monocultures.

Leaf trait means also correlated with species richness but the direction varied among forest types. In the temperate forest, individuals had higher SLA and lower LDMC in more diverse communities as typically shown in resource-rich environments (Wright et al., 2004). Increasing nutrient or water availability in soils of mixed vs. monospecific tree stands has often been postulated based on positive diversity effects on litter decomposition and nutrient cycling, and based on below-ground resource use complementarity through niche partitioning and/or facilitation (Ashton et al., 2010; Richards et al., 2010; Rothe and Binkley, 2001). On the contrary, individuals in more diverse stands in the boreal and Mediterranean forests had leaves with higher LDMC than in monocultures, suggesting more stressful conditions for individuals in high diverse plots submitted to higher interspecific than intraspecific competition. Although we have no fitness measurements to confirm this assumption, previous studies in our boreal and Mediterranean study sites indicated that stressful conditions (e.g. droughts) boost competition for belowground resources in more diverse communities (Grossiord et al., 2014a,b; Jucker et al., 2014).

4.3. Implications for biodiversity effect

We have shown that plant individuals adjust some of their traits, and therefore the species functional space, to the biotic environment (see also Aschehoug and Callaway, 2014; Berg and Ellers, 2010; Callaway, 2003), namely to the richness of species. This is in agreement with results derived from biodiversity experiments (Gubsch et al., 2011; Lipowsky et al., 2015; Mitchell and Bakker, 2016; Roscher et al., 2015; Zuppinger-Dingley et al., 2014), which negates our first hypothesis (Fig. 1). Moreover, we did not detect a pervasive shrinking of species trait breadths (variability at the community level) in mixed forests compared to monocultures, nor an increasing trait overlap with increasing species richness (see Appendix C, Fig. C.3), as would be predicted by the niche-based theory hypothesises – thus rejecting our second hypothesis- (Tilman, 1982). On the contrary, our results support the third hypothesis, as we found some increments of trait variability and trait mean shifts as species richness increased. Moreover, we found that species overlaps remained steady at increasing richness suggesting both highly dissimilar or barely redundant species, as expected in poor-species communities (Valladares et al., 2015), and an expansion and packing of the functional space with increasing diversity in accordance to studies conducted in other forest communities (Pretzsch, 2014; Swenson and Weiser, 2014).

Our results suggest that intraspecific trait variability, no matter the origin (either phenotypic plasticity or genetic diversity), provides species with the flexibility to avoid competition with coexisting species promoting complementarity instead (Aschehoug and Callaway, 2014; Ashton et al., 2010). Responses at the individual level to the presence of heterospecifics reduce functional similarity, favouring complementarity and resulting biodiversity effect on ecosystem functioning through two complementary ways. Firstly, shifts of leaf trait means along richness gradients would imply species short- and mid-term responses to canopy diversity, similar to the trait shifts found within herbaceous experiments (Gubsch et al., 2011; Roscher et al., 2015). Secondly, assuming the modular nature of plants, these differential short-term responses among conspecifics would imply cumulative variation, resulting in more variable phenotypes (architectures) in the long-term (Herrera, 2009). Furthermore, individuals with contrasting phenotypes create larger spatial heterogeneity, which in turn promotes associated biodiversity due to greater habitat availability (Stein et al., 2014). A limitation of our study is that we cannot fully remove the actual effect of historical management on these long-term responses, a common limitation when surveying long-lived organisms. However, results from biodiversity experiments in grasslands have reported similar cumulative phenotypic variability and species complementarity, augmenting the biodiversity effect through time (Reich et al., 2012; Tilman et al., 2006; Zuppinger-Dingley et al., 2014).

Collectively, our results demonstrate the relative importance of intraspecific trait variability to the functional diversity of plant communities highlighting its relevance for alleviation of competition and promotion of species complementarity.

Acknowledgements

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.ppees.2018.12.002.

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