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# Linkage of plant trait space to successional age and species richness in boreal forest understorey vegetation

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## Summary

**1.** Determining the changes in within- and between-species functional diversity in plant communities, and their contribution to overall species trait overlap, can enhance efforts at understanding mechanisms of species coexistence. However, little is known about how variation in species functional diversity influences variation in species trait overlap among contrasting environments.

**2.** Here, we studied the understorey vegetation in a well-characterized 5000-year-old chronosequence involving 30 forested islands that differ greatly in size, soil fertility and species diversity. Across this chronosequence, we expected consistent changes in both within- and between-species functional diversity that would lead to decreasing overall species trait overlap with increasing successional age, species richness, understorey vegetation density and spatial heterogeneity of soil resources.

**3.** For each island, we measured specific leaf area (SLA) of each of ten individuals of each plant species present. Using a variance decomposition method, we partitioned the total community functional diversity of SLA on each island into within- and between-species functional diversity. Further, we estimated overall species trait overlap as the ratio of within-species functional diversity to total functional diversity. Using regression analyses, we then explored relationships of within- and between-species functional diversity, and of overall species trait overlap, with several environmental variables across the 30 islands.

**4.** Consistent with our hypotheses, overall species trait overlap decreased with successional age due to a statistically significant decrease in within-species functional diversity, and decreased with species richness due to a simultaneous decrease in within-species functional diversity and increase in between-species functional diversity. Against our predictions, overall species trait overlap increased in more competitive environments and did not change with increasing spatial heterogeneity of soil N or P.

**5. Synthesis.** Our study suggests niche packing as a key mechanism for species coexistence in plant communities. Using SLA as an integrator of plant ecological strategy, we show that community successional age and species richness are significantly linked to trait space distribution of plant individuals of boreal forest understorey vegetation and therefore to local species coexistence. Our results also suggest that the trait space of dominant and subordinate species may respond differently to local environmental variables.

**Key-words:** community assembly, determinants of plant community diversity and structure, functional diversity, niche packing, plant competition, spatial heterogeneity, trait overlap, variance partitioning, within- and between-species variability

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## Introduction

The challenge of understanding how local plant communities are assembled in nature has a long history in ecology (Gleason 1926; Hutchinson 1957; MacArthur & Wilson 1967). Several studies over the past two decades have highlighted the importance of both niche- and non-niche-based processes that influence community assembly and functional diversity (Weiher & Keddy 1995). While non-niche-based models assume that species are ecologically equivalent and that species assembly is largely driven by stochastic processes (Hubbell 2001; Alonso, Etienne & McKane 2006), niche-based models assume non-equivalence between species and suggest that functional characteristics of species regulate their coexistence (Weiher, Clarke & Keddy 1998; Chesson 2000; Mayfield & Levine 2010). In the case of niche-based models, functional trait (dis-)similarity within and between coexisting species can shed light on how available resources are shared (Weiher & Keddy 1995; Cornwell & Ackerly 2009; Mason *et al.* 2011).

Considering patterns of species trait overlap among contrasting plant communities, for example those differing in successional status, can provide insights about mechanisms that underpin community structure (see Violle *et al.* 2012; Le Bagousse-Pinguet *et al.* 2014). As such, in early successional communities, abiotic filtering has been shown to favour the occurrence of species with functionally similar acquisitive traits, that is that would enable rapid growth and resources capture under conditions of high resources availability (Gaudet & Keddy 1995; Diaz, Cabido & Casanoves 1998; Lagerström, Nilsson & Wardle 2013; Lasky *et al.* 2014). However, as succession progresses, a decrease in trait overlap driven by factors such as biotic interactions and resource partitioning can occur (Ingram & Shurin 2009; Bhaskar, Dawson & Balvanera 2014). Therefore, and consistent with niche-based theory of species coexistence (Chesson 2000; Chase & Leibold 2003; Walker *et al.* 2010), species trait overlap is expected to decrease with community successional age because species will show increased functional dissimilarity in order to coexist (Stubbs & Wilson 2004; Violle *et al.* 2012; Laliberte, Norton & Scott 2013b; Laliberte *et al.* 2013a).

Parallel to the influence of community successional age, species in the community (and especially the most abundant ones) could become functionally differentiated as the number of interacting species increases in a community, which would enhance niche packing, or the capacity for coexisting species to partition and thus fill the available niche space along important niche dimensions (Kraft *et al.* 2007; Mayfield & Levine 2010; but see Maire *et al.* 2012). Additionally, increasing competition between coexisting plants can limit their functional similarity within a community via competitive exclusion (Maire *et al.* 2012) or can conversely increase their similarity by promoting the dominance of species with optimal competitive trait values (Schamp, Chau & Aarssen 2008; Mayfield & Levine 2010; HilleRisLambers *et al.* 2012; Spasojevic & Suding 2012). Following these contrasting expectations, both a decrease in the overall functional

diversity of communities and an increase in niche packing of the dominant species could be expected in communities with strong competitive interactions (Chesson 2000).

Further, spatial heterogeneity of soil resource availability can greatly influence species coexistence and can therefore serve as a powerful mechanism for promoting community functional diversity (Reynolds *et al.* 2007; Gundale *et al.* 2011; Gazol *et al.* 2013). It is well recognized that spatial variation in such resources can increase diversity in available niches, allowing species with contrasting resource requirement to coexist (Chesson 2000; Adler *et al.* 2013). Consequently, local communities which have the greatest spatial heterogeneity of soil N and P, both of which are important limiting plant nutrients in many ecosystems world-wide, would be expected to show higher niche packing (Grime 2001).

In this study, we apply analytical approaches that have recently been developed to better understand trait-based ecology. These approaches enable us to better understand how functional trait diversity within- and between-species can affect community assembly (Mason *et al.* 2005, 2011; Villegger, Mason & Mouillot 2008; Ackerly 2009; Lepš *et al.* 2011) and how environmental drivers influence these components of community structure (Le Bagousse-Pinguet *et al.* 2014). Of particular interest, Violle *et al.* (2012) proposed a method of trait variance decomposition both within- and between-species that enables assessment of how the trait breadth of coexisting species varies across different communities. This method focuses on the  $T_{IP/IC}$  metric, that is the ratio of trait variance within single species belonging to a community relative to the total trait variance of that community. Low values of  $T_{IP/IC}$  generally indicate communities with low trait overlap, which in turn suggest increased niche packing between species (Violle *et al.* 2012). This variance ratio provides an operational framework that explicitly incorporates within-species variance, a component that has largely been ignored in studies of plant community assembly (Albert *et al.* 2011), to understand primary forces that structure communities. The  $T_{IP/IC}$  metric is advantageous in that it measures an overall overlap in functional trait space within a community, which can be related to niche-based assembly processes. A further benefit of this metric is that when it is decomposed into its components, it allows for simultaneous examination of how different components of community functional diversity (i.e. within- and between-species trait variation) respond to environmental changes or along gradients (Le Bagousse-Pinguet *et al.* 2014).

We studied a well-characterized post-fire chronosequence of 30 forested lake islands in northern Sweden, each of which serves as a discrete independent community, and that differ greatly in successional age, species composition and intensity of understorey plant competition, soil fertility and spatial heterogeneity of limiting soil nutrients (Wardle *et al.* 1997, 2003, 2012; Gundale *et al.* 2011). Using the trait variance decomposition approach proposed by Violle *et al.* (2012), changes in within- and between-species functional diversity of understorey vegetation were assessed across the 30 communities in response to key aspects of local

environmental variables, that is ecosystem successional age, plant species richness and density of understorey vegetation, and spatial heterogeneity of soil N and P. We selected these five environmental variables because they usually change considerably across communities (including in our system) and their effects on plant community assembly are well established (Gundale *et al.* 2011; Kumordzi, Wardle & Freschet 2015). We focused on specific leaf area (SLA), a key plant functional trait that is strongly indicative of plant ecological strategy and can be easily measured for many individuals (Diaz, Cabido & Casanoves 1998; Evans & Poorter 2001). We hypothesize that species trait overlap would decrease with increasing (i) successional age, (ii) species richness, (iii) density of understorey vegetation and (iv) spatial heterogeneity of soil extractable N and P. This decreasing pattern of trait overlap may be a result of decreasing within-species functional diversity and increasing between-species functional diversity.

Overall, by assessing how the different environmental variables drive the distribution of trait of species within communities, we seek to better understand niche-based local assembly processes that play a significant role in how co-occurring species share available niche space.

## Materials and methods

### STUDY SYSTEM

This study was conducted in a post-fire chronosequence consisting of 30 islands (see Table 1 for environmental properties of the islands) in lakes Hornavan and Uddjaure in northern Sweden (65°55'N to 66°09'N; 17°43'E to 17°55'E). The mean annual precipitation over the past 30 years is 750 mm, and the mean monthly temperature is +13°C in July and -14°C in January. The islands, which vary in size (large >1.0 ha; medium 0.1–1.0 ha; small <0.1 ha 10 in each size class), were all formed following the retreat of land ice about 9000 years ago. The only major extrinsic factor that varies among islands is the history of lightning-ignited wildfire, with larger islands

having burned more frequently than smaller islands because of their larger area to intercept lightning (Wardle *et al.* 1997, 2003). As such, the islands range in time since the most recent fire from 60 to 5350 years. Despite this difference in historic disturbance regime, there is no current variation among islands in the disturbance regime that they experience (Gundale *et al.* 2011; Wardle *et al.* 2012). Previous studies on these islands have shown that as they become smaller and time since fire increases, they enter a state of 'ecosystem retrogression' (Peltzer *et al.* 2010) in which there is a reduction in soil fertility [notably a reduced availability of plant-available nitrogen (N) and phosphorus (P)], plant biomass, and ecosystem productivity (Wardle *et al.* 1997, 2003; Lagerström *et al.* 2009; Lagerström, Nilsson & Wardle 2013).

The overstorey vegetation is dominated by *Pinus sylvestris*, *Betula pubescens* and *Picea abies*, which have their greatest relative biomass on large, medium and small islands, respectively; these three species constitute >99.8% of all tree biomass. The ground layer vascular vegetation, which is the focus of this study, is dominated by the dwarf shrubs *Vaccinium myrtillus* (which is deciduous) and *Vaccinium vitis-idaea*, and *Empetrum hermaphroditum* (both of which are evergreen); these species dominate the large, medium and small islands understorey, respectively (Table S1; Wardle *et al.* 2003). However, all three species occur ubiquitously on all islands. Other understorey species that occur as subordinate species and that occur on only some islands are *Vaccinium uliginosum*, *Trientalis europaea*, *Pyrola rotundifolia*, *Cornus suecica*, *Linnaea borealis*, *Melampyrum* sp., *Rubus chamaemorus* and *Rhododendron tomentosum* (formerly *Ledum palustre*) (Kumordzi, Wardle & Freschet 2015; Table S1).

### SPECIES ABUNDANCE AND ENVIRONMENTAL VARIABLES

Consistent with some other studies in this system (Gundale *et al.* 2012; Kumordzi *et al.* 2014; Wardle & Jonsson 2014), we focused on the understorey or ground layer vascular plant vegetation. Understorey layer is responsible for over half of total net primary productivity in the system (Wardle *et al.* 2012), represents 78% of the vascular plant species present, and plays an important role in the functioning of the boreal forest (Nilsson & Wardle 2005). Previous studies on the

**Table 1.** Range and variability (coefficient of variation; CV) of different environmental variables measured across the 30 islands, and correlation coefficients among these variables.

Ecosystem property	Range	Variability (CV)	Pearson correlation coefficient			
			Successional age	Spatial heterogeneity of soil extractable N	Spatial heterogeneity of soil extractable P	Density of understorey vegetation
Successional age <sup>1</sup>	40–5330	0.78	–	–	–	–
Spatial heterogeneity of soil extractable N <sup>2</sup>	0.71–2.57	0.34	0.03	–	–	–
Spatial heterogeneity of soil extractable P <sup>2</sup>	0.35–1.04	0.29	–0.13	–0.08	–	–
Density of understorey vegetation <sup>3</sup>	0.39–1.0	0.14	–0.09	–0.13	–0.09	–
Species richness <sup>4</sup>	3–13	0.27	0.32	0.14	–0.22	–0.25

None of these correlations coefficients are statistically significant at  $P < 0.05$ .

<sup>1</sup>Time since last fire (years).

<sup>2</sup>Sample variance (semi-variogram sill) derived from 49 samples points on each island (Gundale *et al.* 2011).

<sup>3</sup>The proportion (%) of the total number of plants hits per total intercept of 200 points, representing a relative measure of understorey shrub density (Kumordzi, Wardle & Freschet 2015).

<sup>4</sup>Number of species in a 314-m<sup>2</sup> plot.

islands (Lagerström, Nilsson & Wardle 2013; Kumordzi, Wardle & Freschet 2015) have shown that in the current system, overstorey and understorey vegetation structure and composition are controlled by different environmental factors. For each island, we used a 10-m-radius plot area established directly adjacent to a set of pre-existing experimental plots used for previous studies on the islands (Wardle *et al.* 2003; Wardle & Zackrisson 2005; Gundale *et al.* 2011) for both vegetation measurements and sample collection, which were performed from 24 July to 10 August, 2011. All plots were located at similar distances from the shore (i.e. *c.* 10–15 m) regardless of island size to prevent edge and microclimatic effects confounding the results (Wardle *et al.* 1997, 2003). Species abundance data were obtained on each island using the point intercept (or point quadrat) method (Goodall 1952) where we determined the total number of times the vegetation of each species was intercepted by a total of 200 downwardly projected points; this has been previously shown to be closely related to biomass at least for the three dominant shrub species that comprise over 97% of understorey plant biomass (Wardle *et al.* 2003). Consistent with Kumordzi, Wardle & Freschet (2015), we used the total number of intercepts of all understorey species as a measure of total vegetation density which is interpreted as a relative measure of the level of competition exerted by the whole understorey plant community (Al-Mufti *et al.* 1977). Further, the total species richness of all understorey vascular plant species present was determined for each plot on all islands.

Data on spatial variability of soil nutrient availability within islands were obtained from Gundale *et al.* (2011). These data include measurements of soil extractable P ( $\text{PO}_4^-$ ) and N ( $\text{hboxNH}_4^+$ ) made in 49 sampling points (placed 1–10 m apart) across a semi-randomized grid within the 10-m-radius plot established on each island. Soil samples were extracted with 1 M KCL;  $\text{hboxNH}_4^+$  in these extracts was measured colorimetrically while  $\text{PO}_4^-$  was measured on an Auto-Analyser III (Omni Process, Solna, Sweden). For each island, spatial heterogeneity of soil extractable N and P was estimated as the semi-variogram sill (total variance which includes both spatially structured and unstructured variability) derived from the 49 sampled points (Gundale *et al.* 2011). Data on successional age of each island were obtained from Wardle *et al.* (1997, 2003). This age was determined as the time in years since the most recent major fire on that island through  $^{14}\text{C}$  dating of charcoal; fire is the primary agent of stand-level disturbance in the study area (Wardle *et al.* 1997, 2003).

#### SAMPLE COLLECTION AND LEAF TRAIT MEASUREMENTS

In each 10-m-radius plot in each island, we sampled 10 individual plants of each of the understorey vascular species present (with each individual at least 4 m from all other sampled individuals of that species); between 3 and 13 species (with a mean  $\pm$  SD of  $8.6 \pm 2.23$  species) were sampled in each plot depending on the island. For each individual plant, we collected at least 10 leaves from at least five separate shoots and these leaves were bulked and kept separately from those of other individual plants. We measured specific leaf area (SLA;  $\text{m}^2 \text{kg}^{-1}$ ) on all the leaves for each individual plant following Cornelissen *et al.* (2003), to obtain a single value for each plant. We focused our study on SLA because of the critical importance of this trait in plant economics and plant resource acquisition. The leaf economic spectrum emphasizes an evolutionary plant trade-off that is indicative of the growth strategy of species in contrasting environments (Wright *et al.* 2004). In this regard, variation in above- and below-ground resource availability drives leaf traits in a manner that

is generally reflected in establishment of species with acquisitive traits (including high SLA) in nutrient-replete environments and conservative traits (low SLA) in nutrient poor environments (Diaz, Cabido & Casanoves 1998; Wright *et al.* 2004). Further, SLA is significantly positively correlated with plant relative growth rate (Poorter, Lambers & Evans 2014) and can be used to capture changes in the functioning of plant species during succession (Garnier *et al.* 2004). Specific leaf area has also been shown to constitute the main factor of adjustment in whole-plant response to variations in light and nutrient supply (e.g. more than twice as important as changes in biomass allocation; Freschet, Swart & Cornelissen 2015). Another reason why this study focused primarily on SLA was that previous studies in this particular study system (e.g. Wardle *et al.* 1997, 2003, 2012; Lagerström, Nilsson & Wardle 2013; Kumordzi *et al.* 2014; Kumordzi, Wardle & Freschet 2015) have confirmed that with decreasing island size, plant community shifts from species with acquisitive traits to those with conservative traits, with trait patterns consistent even at the within-species level. Importantly, these studies also showed that SLA of these plant communities was consistently the most responsive trait to variation in above- and below-ground resources and is consistent within- and between-species for both the over- and understorey plant communities that occur on the gradient.

#### ESTIMATES OF COMMUNITY FUNCTIONAL DIVERSITY COMPONENTS

We quantified four functional diversity components, that is within-species functional diversity, between-species functional diversity, total community functional diversity, and species trait overlap ( $T_{\text{IP/IC}}$ ) for each of the 30 islands using a set of R codes developed by de Bello *et al.* (2011). We used the method of variance partitioning (de Bello *et al.* 2011), being tantamount to the decomposition of the quadratic entropy diversity (Pavoine & Dolédec 2005). This method can be applied both for single and multitrait approaches (de Bello *et al.* 2011). We estimated the total community functional diversity (total variance) as the variance in trait values among all individuals collected in a given community (i.e. on each island). The within-species functional diversity was first calculated as the variance of trait values within each species (within-species variance). Then, a weighted average of all within-species trait variances was computed for each island, with the weight of each species being determined by its relative abundance (see de Bello *et al.* 2011 for details). The between-species functional diversity was calculated as the difference between total community and within-species trait diversities, whereas the  $T_{\text{IP/IC}}$  metric was calculated as the ratio of within-species variance to total community variance (Violle *et al.* 2012). We verified the assumption and behaviour of each of the functional diversity components, by running simulations (see Appendix S1 in Supporting Information for R script) to assess the influence of species richness on within-species functional diversity, between-species functional diversity, total community functional diversity and  $T_{\text{IP/IC}}$  (see Appendix S1, Figs S1 and S2 in Supporting Information). Most importantly,  $T_{\text{IP/IC}}$  was found to be independent of species richness, thus supporting its use in this and other studies.

All these components of functional diversity were computed for three sets of species; the first set was based on data for all species, the second was based on only the three dominant species in the system (which are each present and occur abundantly on all islands; Table S1), and the third was based on only subordinate species (each of which is present on at least 13 of the 30 islands but were sometimes too infrequent to be recorded by the point quadrat

**Table 2.** Results of linear regression analyses ( $R^2$  values) of community functional diversity component measures (for all species in the community) in relation to environmental variables (successional age, spatial heterogeneity of soil extractable P and  $hbox{NH}_4^+$ , density of understorey vegetation and species richness) across all 30 islands. FD: functional diversity. TIP/IC: observed community trait overlap. ‘+’ and ‘-’ signs indicate direction of the relationship between the variables

Ecosystem property	TIP/IC <sup>1</sup>	Within-species FD	Between-species FD	Total community FD
Successional age	(-) <b>0.27**</b>	(-) <b>0.36***</b>	(+) 0.05	(+) 0.02
Spatial heterogeneity of soil extractable N	(-) <b>0.02</b>	(-) 0.03	(+) 0.01	(+) 0.01
Spatial heterogeneity of soil extractable P	(+) 0.02	(+) 0.02	(-) <b>0.02</b>	(-) 0.03
Density of understorey vegetation	(+) <b>0.12*</b>	(+) 0.05	(-) 0.04	(-) 0.01
Species richness	(-) <b>0.30***</b>	(-) <b>0.22**</b>	(+) <b>0.24**</b>	(+) 0.09#

Numbers in bold indicate statistically significant relationships. \*\*\* $P < 0.001$ , \*\* $P < 0.01$ , \* $P < 0.05$ , # $P < 0.1$

<sup>1</sup>All functional diversity component values are log-transformed.

measurements; Table S1). Dominant versus subordinate species were categorized based on the frequency of occurrence and relative abundance of each of the species across the whole island gradient (Table S1; see Grime 1998; Kumordzi, Wardle & Freschet 2015). Dominant species occurred on all the islands and had high cumulative relative abundances (i.e. >12%, as proposed by Mariotte 2014), while subordinate species had lower (<12%) cumulative relative abundances and occurred on fewer islands (see Olf & Bakker 1998).

To confirm that patterns of the observed responses of  $T_{IP/IC}$  to different environmental variables were non-random, a null modelling approach was used to estimate an expected trait overlap for each of the 30 island communities (Mason *et al.* 2011). For each of these communities, we computed an expected trait overlap (i.e.  $T_{IP/IC}^{expected}$ ) by randomizing trait values between all individuals in the community, irrespective of the species and while keeping species richness, species composition and species relative abundance constant. A standardized effect size of species trait overlap was then computed separately for each island as:

$$T_{IP/IC}SES = (T_{IP/IC}^{observed} - \text{mean}(T_{IP/IC}^{expected})) / \text{sd}(T_{IP/IC}^{expected})$$

where  $T_{IP/IC}^{observed}$  is the observed  $T_{IP/IC}$ ,  $T_{IP/IC}^{expected}$  is expected species trait overlap under the null model mentioned above, and  $\text{sd}$  is the standard deviation of various results from individual simulations of the null model. We decided to present the results for both  $T_{IP/IC}$  and  $T_{IP/IC}SES$  although their values are naturally correlated as in other null models (de Bello 2012) to illustrate the strength of patterns of both the observed communities and their deviations from the null communities.

#### DATA ANALYSIS

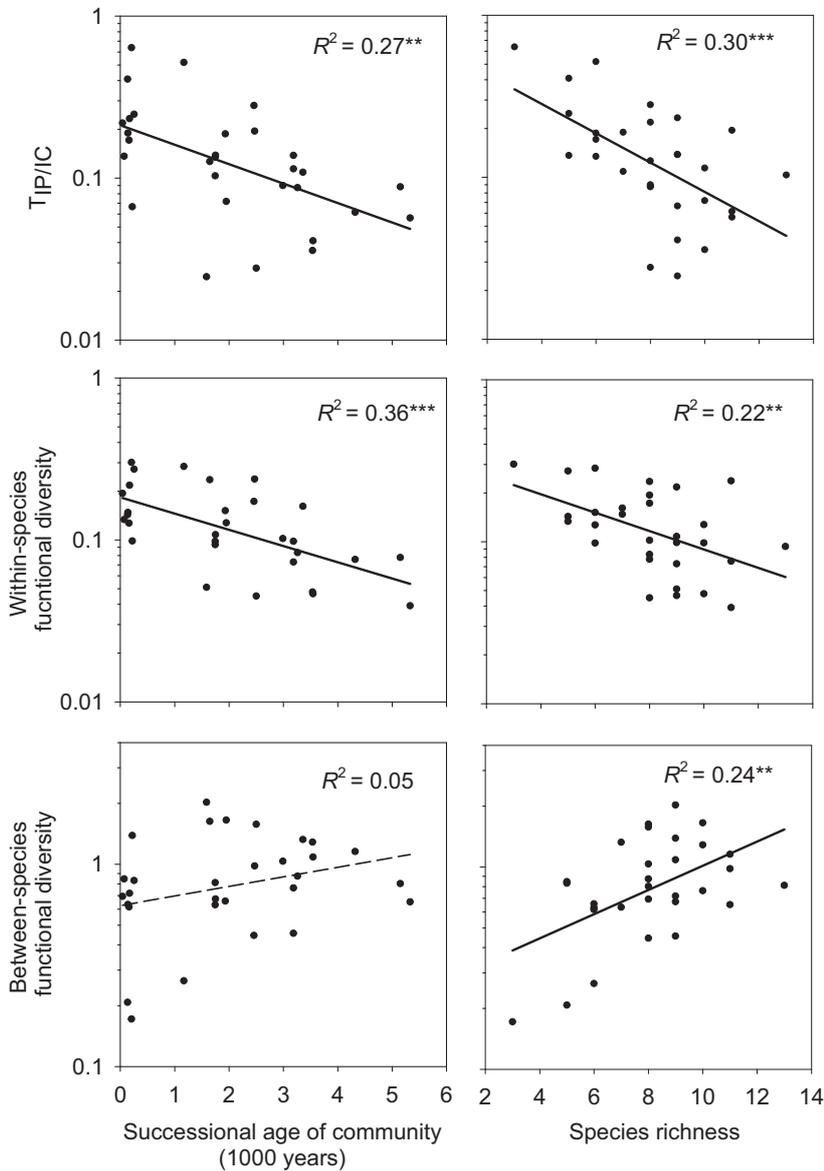
We first used Pearson's correlation coefficients to check for possible dependence between the environmental variables across the 30 islands, that is successional age, spatial heterogeneity of soil extractable N and P, density of understorey vegetation and species richness. We then evaluated the marginal effects of individual predictor by conducting separate linear regression analyses to test the relationship between each of the functional trait diversity components as response variables and each of the environment variables as predictor variables across all 30 islands, with each island serving as a separate data point. We then performed separate multiple linear regressions to determine the combinations of environmental variables that best predicted each of the functional trait diversity components. The response variables were log-transformed to improve normality and homoscedasticity.

The most parsimonious multiple regression models were selected based on the corrected Akaike information criteria (AICc), and all models within two units of the lowest AICc were retained (Burnham & Anderson 2002).

To understand how the different environmental predictors drove within-species variability of both the dominant and the main subordinate species (i.e. those occurring on at least 13 islands) across the 30 islands, we computed the coefficient of variation (CV; standard deviation/mean) of each of these species on each island using data from the 10 individuals of that species. Then, we performed linear regression analyses, with the CVs for each of these species as response variables, and each of the five environmental variables as predictors. All statistical analyses in this study were conducted with the R statistical program (R Core Team 2013).

#### Results

There were no statistically significant relationships between any pair of ecosystem variables used to predict community trait variation across the 30 islands (Pearson correlations; Table 1), and these variables can therefore be presumed to be independent of one another. When univariate regressions were used, successional age and species richness were the best overall predictors of community trait variation measures (Table 2). As such, we found a statistically significant negative relationship of both species trait overlap ( $T_{IP/IC}$ ) and standardized effect size of trait overlap ( $T_{IP/IC}SES$ ) with successional age and species richness (Tables 2, Fig. 1, Table S2 in Supporting Information). The statistically significant decline in species trait overlap with increasing successional age was almost entirely driven by a decline in within-species functional diversity, whereas the decline in species trait overlap with increasing species richness was simultaneously driven by declining within-species functional diversity and increasing between-species functional diversity (Table 2, Fig. 1). Understorey vegetation density was statistically a significant predictor of species trait overlap ( $T_{IP/IC}$  but not  $T_{IP/IC}SES$ , Table 2, Table S2 in Supporting Information). Total community functional diversity showed no relationships with any of the environmental variables. Spatial heterogeneity of soil extractable N and P was never a significant predictor of any community functional diversity measure. Multiple



**Fig. 1.** Relationship of functional diversity components (for all species in the community) with ecosystem successional age and species richness across 30 islands. TIP/IC = community trait overlap. Vertical axis is log-transformed; levels of statistical significance; \*\*\* $P < 0.001$ , \*\* $P < 0.01$ .

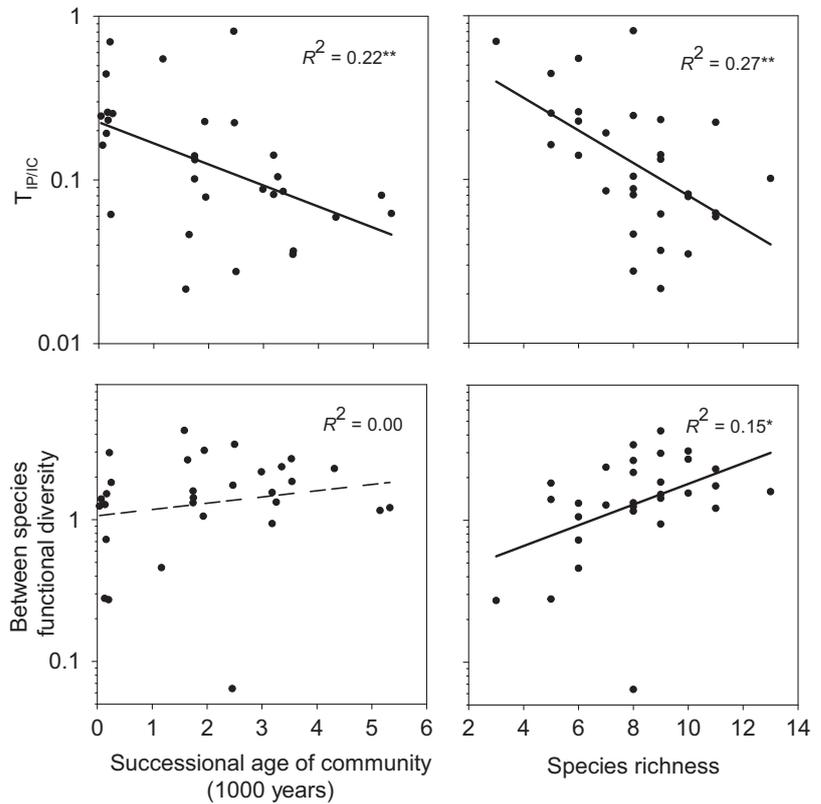
regression analyses showed that species richness was the single most important environmental predictor of species trait overlap ( $T_{IP/IC}$  and  $T_{IP/ICSES}$ ), between-species functional diversity, and total community functional diversity, while successional age was the best predictor of within-species functional diversity (Table S3 in Supporting Information).

Similar relationships, as detected at the community level, were found when only dominant species in the community were considered. Species trait overlap ( $T_{IP/IC}$ ) of dominant species declined with both successional age and community species richness (Fig. 2). There was also a statistically significant positive relationship of between-species functional diversity with species richness, but not with successional age (Fig. 2). Further, we found statistically significant declines in within-species CVs of the three dominant species (*Vaccinium vitis-idaea*, *V. myrtillus* and *Empetrum hermaphroditum*) with both increasing successional age and increasing species richness ( $P < 0.05$  in all cases; Fig. 3). For subordinate species,

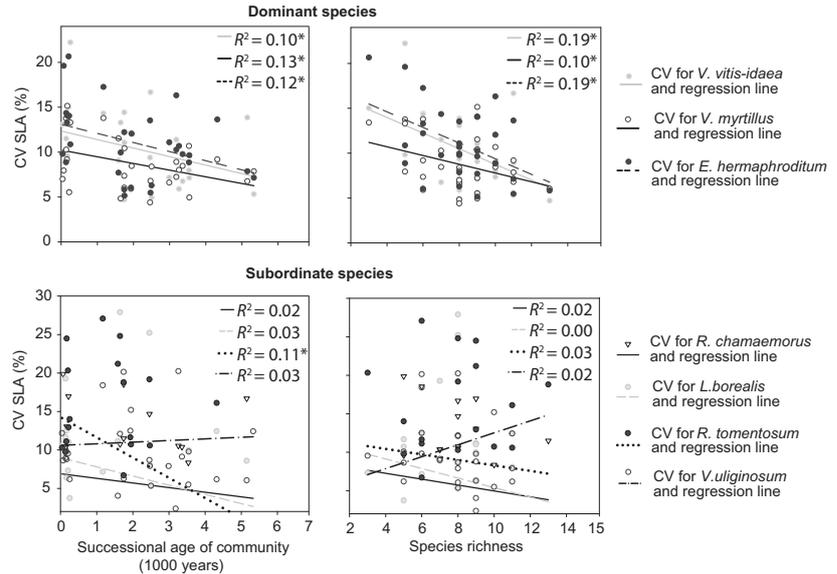
there were no statistically significant relationships between the various components of community functional diversity and environmental variables (Table S4 in Supporting Information). Further, we found no consistent pattern of within-species CVs in response to successional age or species richness; only *Rhododendron tomentosum* showed a statistically significant decrease with successional age (Fig. 3). However, we note that the  $R^2$  of regression models between functional diversity components and the most important environmental predictors of community trait variation (i.e. successional age and species richness) were generally slightly lower when only dominant species rather than all species in the community were considered (Fig. 1 vs. Fig. 2).

## Discussion

Our results highlight the importance of assessing trait overlap between species in plant community assembly along



**Fig. 2.** Relationships of  $T_{IP/IC}$  (a measure of species trait overlap) and between-species functional diversity with ecosystem successional age and species richness for dominant species only.  $T_{IP/IC}$  = community trait overlap. Vertical axis is log-transformed; levels of statistical significance;  $**P < 0.01$ ,  $*P < 0.05$ .

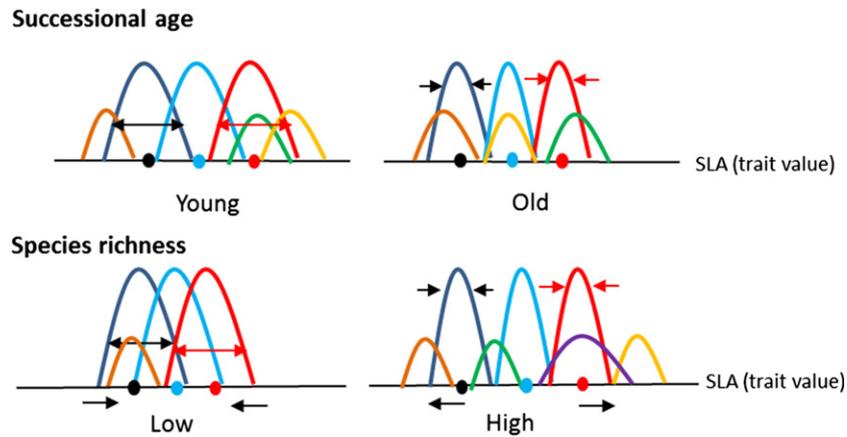


**Fig. 3.** Relationships between coefficient of variation (CV) for each of the dominant and main subordinate species and successional age and species richness. Level of statistical significance;  $*P < 0.05$ .

environmental gradients. The relationships that we found of within- and between-species components of functional diversity with succession and species richness across the island chronosequence point to niche packing as an important mechanism for species coexistence.

Consistent with our first hypothesis, we found that species trait overlap decreased as community successional age increased; we also found that this pattern was mainly related to a decrease in within-species functional diversity. Several

earlier studies have shown that amounts of limiting plant resources such as soil nutrients and photosynthetic available light decrease with succession (Connell & Slatyer 1977; Wardle *et al.* 1997, 2003; Walker & del Moral 2003). Resource limitation may therefore underlie part of the response of species niche overlap to succession (Connell & Slatyer 1977; Pickett & McDonnell 1989). Specifically, our results provide support for the view that species from late successional communities are more specialized in their resource acquisition



**Fig. 4.** Summary of observed changes in dominant and subordinate species trait (SLA) variance and overlap in response to two major environmental drivers across 30 local boreal forest communities. For each panel, each curve represents a different species and the area of each curve represents the relative abundance of that species in the community. Arrows above the line represent changes in within-species functional diversity while those below the line represent changes in between-species functional diversity in response to successional age and species richness. Overall, observed statistically significant changes in community trait overlap in response to successional age and species richness are mainly driven by dominant species. Between-species functional diversity does not change with increasing successional age but does change with increasing species richness.

through taking up only a specific portion of the total available resources (Bazzaz 1979; Walker & del Moral 2003; Walker *et al.* 2010). The fact that we did not find a statistically significant decrease in between-species functional diversity with increasing successional age indicates that in our study system later-successional species neither occupy more trait space nor are better at occupying marginal niche spaces relative to early successional species. This contradicts a widespread idea that changes in species composition as succession proceeds lead to an increase in species functional trait diversity and therefore a progressive shift towards wider use of niche space at the interspecific level (Walker *et al.* 2010).

We found both a decrease in within-species functional diversity and an increase in between-species functional diversity with increasing species richness, supporting our second hypothesis that species trait overlap would decrease with increasing species richness. The opposing relationships of within- and between-species functional diversity of dominant plant species with species richness suggest that dominant species shift their niche position and limit their spread around this niche position as the number of interacting species increases in a community. This finding is consistent with the niche overlap hypothesis which suggests that co-occurring species may show systematic shifts in interspecific niche separation and intraspecific niche width along the same resource utilization axis (May 1972; Pianka 1974). Our finding that between-species functional diversity increases with species richness indicates that co-occurring species show marked differences in their niche requirement in species rich communities to coexist (Silvertown 2004; Maire *et al.* 2012). The decrease in within-species functional diversity with increasing species richness indicates that individuals of a species tend to have similar trait values that minimize average fitness difference (Chesson 2000). This finding is in contrast to that of Le Bagousse-Pinguet *et al.* (2014) who found an increase in within-species functional diversity in plant height with

increasing species richness in calcareous grassland communities. This finding emphasizes the need to measure within-species trait variability to understand patterns of species niche differentiation and coexistence. Overall, these contrasting responses of within- and between-species functional diversity with increasing species richness reveal species niche packing as an important mechanism for the maintenance of functional diversity in plant communities (MacArthur & Levins 1967; Pianka 1974).

The slightly steeper decrease in species trait overlap when both dominant and subordinate species were considered (as opposed to only dominant species) indicates that patterns of community trait distribution along successional and species richness gradients are not driven entirely by dominant species. Therefore, by also considering the functional traits of subordinate species and not just dominant species, it is possible to improve the detection of patterns and processes that underlie community assembly (Mariotte 2014). Further, our finding that within-species trait variability of mainly the dominant but not subordinate species declined statistically significantly as succession proceeds and species richness increases suggests that the coexistence of dominant and subordinate species is at the expense of dominant species niche space breath (Fig. 4; Grime 1998; Fargione & Tilman 2006). This supports previous findings that functional response of plant assemblages are not necessarily 'homogenous', in that different components of the community, such as dominant versus subordinate species, can respond differently to the same environmental factor (Kumordzi *et al.* 2014).

We found no support for our third and fourth predictions that species trait overlap would decrease in an increasingly competitive environment or with greater spatial heterogeneity of soil extractable N and P. On the contrary, species trait overlap was greater with increasing competitiveness of the environment (i.e. the density of understorey vegetation; Kumordzi, Wardle & Freschet 2015), indicating that when

competition is greater, traits of coexisting species become more functionally similar, which may occur through genetic adaptations or plastic responses to environmental conditions. Notably, plants in denser communities with higher competition for light have lower access to light, which would allow less plasticity in SLA to be expressed. Our results support earlier findings that strong plant competition, such as occurs commonly in productive environments, can lead to a convergence of species trait values (e.g. Grime 2006; Bernard-Verdier *et al.* 2012; HilleRisLambers *et al.* 2012). Further, the finding gives credence to the assertion that functional trait differentiation between competitive species may not be the sole prerequisite for species coexistence (Chesson 2000; Schamp, Chau & Aarssen 2008; Mayfield & Levine 2010), or that trait differentiation acts at the level of plant individuals rather than species (Clark 2010).

Consistent with the results of Le Bagousse-Pinguet *et al.* (2014), the spatial heterogeneity of soil extractable nutrients was not related to any of the components of community functional diversity that we measured, and this contradicts the idea that greater spatial heterogeneity in limiting soil resources should lead to an increase in niche availability and promote trait differentiation in coexisting species (Tilman 1982; Huston & DeAngelis 1994). In our study system, most species are clonal (including all the dominant ones) and the ability of their root systems to forage for nutrients at large spatial scales and to redistribute nutrients across ramets within a single clone can downplay the importance of small-scale spatial heterogeneity on community assembly and functional diversity (Hutchings & De Kroon 1994; Wijesinghe & Hutchings 1996, 1997; Gundale *et al.* 2011). Further, we acknowledge that although SLA is responsive to environmental factors, consideration of other traits (e.g. stature traits, below-ground traits) may have reflected other mechanisms that cannot be assessed through using measures of SLA only.

## Conclusion

Our study, based on measures of functional diversity both within- and between-species, provides new insights into how ecological drivers influence local species assembly and species coexistence. First, while our results support the role of niche-based processes in structuring the assembly of plant communities and promoting species coexistence (MacArthur & Wilson 1967; Chesson 2000; Mariotte *et al.* 2013), it also suggests that the trait space of dominant and subordinate species may respond differently to local environmental variables. Accounting for the within-species trait response of both dominant and non-dominant species may therefore enhance our attempts to better understand the mechanisms underlying species coexistence. Second, while at the local scale, plant coexistence is simultaneously driven by multiple environmental factors (Chesson 2000; Lasky *et al.* 2014; Le Bagousse-Pinguet *et al.* 2014); our results suggest that successional age and species richness of communities are key factors that underlie species coexistence through their effects on within- and between-species functional diversity. Finally,

few studies have characterized within-species variability of all component species within each of several contrasting plant communities in order to test how difference among individual species contributes to community assemblage, in the manner that we have done here. Thus, further work is needed to determine the importance of genotypic versus phenotypic contributions to within-species variability as well as to ascertain whether the patterns that we observed hold for other traits and in other types of environments in order to better understand what drives species niche packing and community assembly.

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## Data accessibility

Data are available from the Dryad Digital Repository <http://dx.doi.org/10.5061/dryad.373mg>

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## Supporting Information

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

**Table S1.** Changes in the abundance of dominant and subordinate species across the island size gradient.

**Table S2.** Linear regressions between functional diversity measures and environmental variables.

**Table S3.** Multiple regressions between functional diversity measures and environmental variables.

**Table S4.** Linear regressions between functional diversity measures and environmental variables for subordinate species only.

**Appendix S1.** Simulation analysis for assessing relationship between functional diversity and species richness.