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Scale-dependent effect of biotic interactions and environmental conditions in community assembly: insight from a large temperate forest plot

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Abstract In forested ecosystems, it remains unclear whether environmental conditions, resource competition or their joint effects explain non-randomly distributed species pattern. Recently, trait-based approaches have been recognized as an important tool to infer processes governing community assembly patterns. In this study, we quantify patterns of functional composition and diversity to study how tree species coexistence is influenced by abiotic factors and biotic interactions in a species-rich temperate old-growth forest. In a 25 ha (500 × 500 m) fully mapped forest plot, we calculated functional composition (community weighted mean) and diversity of five key traits considering two spatial scales (20 × 20 and 50 × 50 m quadrats). We compared the observed patterns in functional diversity with randomly generated null communities to test for the presence of non-random patterns in community assembly, and studied the variation of functional composition and diversity along gradients of soil conditions to test for the shift in assembly processes along resource gradients. Functional diversity differed from null expectations depending on the spatial scale considered. In broad-scale quadrats (50 × 50 m), functional diversity in wood specific gravity (WSG) and leaf area (LA) was lower than expected by chance, whereas functional diversity in specific root length (SRL) was greater than expected. In small quadrats (20 × 20 m), functional diversity was lower than expected by chance in specific leaf area (SLA) and when considering all traits in combination. Functional composition and diversity varied along the soil resource gradient but the results were dependent on

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the scale considered. We found an increase in functional composition in maximum height (H) and WSG and a reduction in the functional diversity in most of traits suggesting an increase in competition with the increase in soil water content at small scale. The trait dispersion pattern for all traits in combination had no directional changes with some of individual traits generating more clear dispersion trend when the dominant competitor *Pinus koraiensis* was removed from the community dataset. The results presented here suggest that community assembly is governed by non-random processes in the studied forests. Interestingly, the choice of quadrat size seems to be crucial to describe community patterns and infer the forces governing community assembly. The consideration of different traits and environmental gradients allowed us to discover that different assembly mechanisms operate simultaneously in the studied forest.

Keywords Coexistence · Limiting similarity · Functional trait · Tree maximum height · Null model · Rao · Community-weighted mean

Introduction

Community assembly depends ultimately on a combination of biotic and abiotic factors that influence species performance at different spatial and temporal scales (HilleRisLambers et al. 2012; Mayfield and Levine 2010; Kraft et al. 2015). Biotic interactions (niche partitioning, limiting similarity) that prevent coexisting species from being too similar is among the most important and best studied of these processes (MacArthur and Levins 1967; Chesson 2000). On the other hand, environmental filtering that decreases species dissimilarity through physical environment constraints is assumed an opposing force structuring tree assemblages (Cornwell et al. 2006). Dissecting the relative contribution of these complex processes in hyper-diverse forest systems is a current area of study in ecology (Wright 2002; Mayfield and Levine 2010; Adler et al. 2013; Münkemüller et al. 2014; Long et al. 2015).

Plant functional traits can offer a mechanistic link between fundamental biological processes and community dynamics by capturing essential aspects of species' morphology, and ecophysiology and life-history strategies (McGill et al. 2006), which have the potential to reveal general, synthetic, and predictive relationships that studies of species-specific responses have failed to identify (Kraft et al. 2008; Kraft and Ackerly 2010; Götzenberger et al. 2012; Shipley et al. 2012; Adler et al. 2013; Yang et al. 2014). Currently, trait-based approaches in community ecology have been used to infer community assembly mechanisms primarily through describing the trait diversity in an assemblage and comparing it to null models (Kraft et al. 2008; Swenson et al. 2012; Liu et al. 2013; Coyle et al. 2014). An environmental filtering mechanism is generally inferred when trait diversity is less than expected (i.e. trait clustering or convergence) and the importance of biotic interactions is inferred when diversity is higher than expected (trait overdispersion or divergence; Swenson and Enquist 2009; de Bello 2012; Swenson et al. 2012). For example, Liu et al. (2013) found trait clustering prevailed over several traits in a subtropical forest in China, which provided direct evidence for an abiotic filtering mechanism. However, other studies have demonstrated that trait clustering can be indicative of not only strong environmental filtering, but also other assembly processes such as competitive exclusion (Grime 2006; Mayfield and Levine 2010; Kraft et al. 2015). Similarly, an increase in the number of habitat types (enhanced environmental heterogeneity) will result in an increase of available niche space, resulting in trait overdipsersion similar to patterns from resource competition (Macarthur and Levins 1967). Thus, there may be a risk in inferring assembly processes by solely observing functional trait patterns (Spasojevic and Suding 2012; Adler et al. 2013; Liu et al. 2013). Recent studies have shown that the footprint of these processes in community assembly may change across spatial scales and environmental gradients (Swenson et al. 2012; Yang et al. 2014; Shiono et al. 2015). Scale effect has been a focus of investigation because the imprint of abiotic filtering should be more evident on larger spatial scales, whereas the imprint of biotic interactions on the composition of tree assemblages is likely to be more evident on the spatial scales on which individuals interact (Weiher and Keddy 1995). For example, Yang et al. (2014) proved that trait dispersion varied across habitat types in a 20-ha tropical forest dynamics plot in southwest China, and suggested that biotic determinism is more important on smaller scales while abiotic determinism is more important at larger scales. Stronger inferences regarding the role of environmental filtering would come from directly assessing the degree to which the underlying abiotic environment predicts trait convergence and divergence patterns (Liu et al. 2013).

Moreover, patterns in functional diversity depend on the compilation of patterns of many individual traits. Interpreting mechanisms without understanding these underlying patterns may be misleading (Cornwell et al. 2006; Weiher et al. 2011). As different traits are often associated with different ecological processes which relate to different niche axes (Violle et al. 2007), research focusing solely on multivariate functional diversity may mask community assembly processes when traits are associated with opposing niches axes. For example, as a result of trade-offs among traits of water use and transport, multivariate functional diversity did not change in wet and dry chaparral sites (Cornwell et al. 2006). Thus, exploring the patterns of individual functional traits at multiple spatial scales is helpful to disentangle the multiple processes driving community assembly (Adler et al. 2013; Coyle et al. 2014; Münkemüller et al. 2014).

The broad-leaved Korean pine (*Pinus koraiensis*) mixed forest is the dominant vegetation type in northeastern China. The forest is well-known for high species richness and a unique species composition for temperate forests (Stone 2006). Our previous results suggested that the dominant competitor (*P. koraiensis*), a coniferous tree species, is a key factor explaining canopy variation, and subcanopy diversity and shrub diversity. This dominant competitor acts directly through shading and indirectly through the modification of the soil on the community. Here, we study community assembly though the lens of functional traits by analysing trait patterns and their variation along a soil resource gradient in a 25 ha (500 × 500 m) fully stem mapped plot of the Changbai temperate forest. Firstly, we examined the presence of non-random patterns of community assembly by comparing the observed patterns of functional diversity with those obtained using randomly generated null communities for all trees measured. Secondly, we quantified the variation of functional composition and diversity along gradients of soil conditions in order to test for the influence of abiotic filters and biotic processes on community assembly. Finally, we evaluated the role of dominant competitor on community assembly by comparing traits dispersion pattern with and without the presence of *P. koraiensis*.

Methods

Study site and field measurements

The Changbai Mountain Natural Reserve is located in northeastern China and is dominated by large temperate old-growth forest (Hao et al. 2007). The Changbai forest plot is located in a core zone of broad-leaved Korean pine mixed forest (42°23′N and 128°05′E), where the mean canopy tree age is around 300 years (Hao et al. 2007; Zhao et al. 2014). The region has a temperate continental climate with long, cold winters and warm summers. Rainfall averages 700 mm year^{-1}, most of which occurs from June to September (480–500 mm). Mean annual temperature is 2.8 °C, with a January mean of −13.7 °C, and a July mean of 19.6 °C.

The CBS (Changbaishan) plot was established in the summer of 2004. It is a 25-ha (500 m × 500 m) rectangular plot in which all free-standing woody stems $\geq$1 cm in trunk diameter were mapped, measured and identified to species following standard field protocol (Condit 1998). This work was conducted based on Forestry Standards “Observation Methodology for Long-term Forest Ecosystem Research” of People’s Republic of China (LY/T 1952-2011). The censuses found 52 species with stem DBH $\geq$1 cm, belonging to 32 genera and 18 families (Hao et al. 2007). To study within-community functional composition and diversity at different spatial scales, we consider two spatial grains by dividing the study site into 625 plots of 20 × 20 m and into 100 plots of 50 × 50 m (hereafter referred as small- and broad-scale quadrats, respectively). In each quadrat, species composition was obtained by counting the number of stems of all species with a DBH $\geq$1 cm, and we calculated the basal area for each of the species present as a measure of species abundance. In the small-scale quadrats, the average number of species was 11.5 ± 2.3 (standard error) and ranged between 5 and 19, whereas in the broad-scale plots, the number of species per plot was 20.2 ± 3.1 ranging between 13 and 29 (Yuan et al. 2011).

Plant material for trait measurements was obtained by selecting 10 individuals per species when possible, but sample sizes were lower for the rarest species (Table S1). In order to estimate functional composition and diversity, we quantified 5 functional traits (Table S1) that reflect different plant strategies (Cornelissen et al. 2003; Wang et al. 2013): maximum height (H), wood specific gravity (WSG), leaf area (LA), specific leaf area (SLA) and specific root length for absorptive root (SRL). We followed protocols presented in Cornelissen et al. (2003). H is one of the best indicators of tree competitive ability (Kunstler et al. 2012). SLA is an important feature of light economic spectrum and tends to be negatively correlated with shade tolerance (Cornelissen et al. 2003). LA reflects a plant's strategy to obtain resources and invest them in leaf production (Wright et al. 2004; Mason et al. 2012). SRL reflects the plant ability to capture resources and tends to be negatively related to mychorrizal symbiosis (Kothari et al. 1990). Plant wood specific gravity is related to competitive ability and tolerance to disturbance (Kraft and Ackerly 2010). All the traits were measured following standard protocols.

To account for the variation in abiotic and biotic conditions between plots, several stand features and environmental conditions were considered. We used a total station to survey the entire forest area and determine the elevations of the four corners of all 20×20 and 50×50 m quadrats. After that, we calculated the elevation and slope of each plot. In October 2007, several soil features were measured following standard protocols. Soil samples were collected using a grid of 967 points designed to capture fine scale variations in soil nutrients (Yuan et al. 2011). We considered two soil factors, volumetric soil water content (%) and available Nitrogen, that were found to be important predictors of patterns of diversity in the Changbai forest (Yuan et al. 2012). In each sample location, the volumetric soil water content (%) was measured using a TDR probe at a depth of 20 cm and three soil samples were taken with a cylinder, air-dried and processed in the laboratory. Available N was alkali digested into NH_3 with 1 mol NaOH L^{-1} and followed by H_2BO_3 absorption, then the content was detected using hydrochloric acid titration method. In previous studies, we found that available Nitrogen and soil water content were the main soil conditions influencing diversity patterns in the Changbai forest and that their variation depends on elevation (Yuan et al. 2011, 2012). In addition, soil water content and available N are positively related ($r = 0.61$; $p < 0.01$ and $r = 0.69$; $p < 0.01$ in the 20×20 and 50×50 m quadrats, respectively). Thus, we used soil water content as variable reflecting gradients of soil features and nutrient availability across the studied forest.

Statistical analyses

We used community-weighted mean (CWM) trait values to describe the functional composition in each of the small- and broad-scale quadrats (Lavorel et al. 2008). CWMs represent trait values across all species weighted by the relative abundance of each species and can be used to examine shifts in mean trait values among communities due to selection for certain functional traits (Ricotta and Moretti 2011). For each species, mean trait values were obtained by calculating the average of the different individuals measured. Basal area of each species per plot was used as a measure of abundance. CWMs were calculated separately for each trait using the following equation (Lavorel et al. 2008):

$$\mathrm{CWM} = \sum_{i=1}^{n} p_i \times \mathrm{trait}_i, \quad (1)$$

where p_i is the relative abundance of species i in the treatment, trait_i is the mean trait value of species i in the treatment and n is the number of species. In previous studies, we found that the dominant competitor (*P. koraiensis*), a coniferous tree species, had a strong influence on canopy species diversity (Yuan et al. 2012). Thus, in order to discover the impact of *P. korainesis* in community assembly patterns, we performed the analyses with and without considering this species.

In order to estimate functional diversity within each plot, we computed Rao quadratic entropy (Q; Rao 1982; Laliberté and Shipley 2011). Q quantifies functional diversity as the sum of pairwise distances between species weighted by the relative abundance of each species. We used Gower distance to calculate the trait-based pairwise distance between species. Rao quadratic entropy has the following equation:

$$Q = \sum d_{ij} \times p_i \times p_j, \quad (2)$$

where d_{ij} is a measure of dissimilarity or distance between species i and j, and p_i and p indicate the relative abundance of species in the community.

This index summarizes variations in both functional richness and divergence (Mouchet et al. 2010). Thus, Q can vary as a function in the change in species richness or in species evenness and these effects are difficult to separate (Mason et al. 2013). For each small- and broad-scale quadrat, we calculated Q for all traits in combination and for each trait individually. The functional composition and diversity indices presented above were calculated using the function *functcomp* developed by Laliberté and Legendre (2010) in “FD” package and the Rao function provided by de Bello et al. (2009). As for CWM, the analyses were performed with and without considering the presence of *P. koraiensis*.

In order to detect the influence of assembly processes on species occurrences and/or relative abundances, the trait dispersion was quantified using the observed values of Rao quadratic entropy (Q) and compared to what is expected by chance (Mason et al. 2013; Yang et al. 2014). Null communities were generated by a matrix-swap null model that randomizes species occurrences 999 times but maintains species occurrence frequency and abundance (Gotelli 2000). During each of 999 shuffling, mean Q for the pooled traits and single trait was calculated as explained above. This randomization procedure allowed us to get a standardized effect size for the Q as follows (SES, Gotelli and McCabe 2002):

$$\mathrm{SES}_Q = \frac{Q_{obs} - Q_{exp}}{\sigma_{exp}}, \tag{3}$$

where Q_{obs} is the observed Q for all traits and for each single trait, Q_{exp} is the mean Q value of the randomizations and σ is its standard deviation. For the whole plot scale, a positive SES value indicates that a community is functionally overdispersed, whereas a negative value indicates that a community is functionally clustered.

To disentangle the relative influence of abiotic filters and biotic interactions on community assembly, we studied the variation of CWM and SES_Q along environmental gradients in the small-scale and broad-scale forest quadrats. For the small and broad scale, we studied whether the patterns in CWM and SES Q for each plot were influenced by environmental conditions using ordinary generalized least-square regression (Venables and Ripley 2002). We used a multi-model inference approach based on information theory (Burnham and Anderson 2002). First, we calculated four models containing water content as an explanatory variable and different correlation structures to account for the potential spatial autocorrelation in the data (Dormann et al. 2007). Specifically, we tested a model without correlation and structure and three models with a spherical, exponential, or Gaussian correlation structure. Finally, we selected the model with the lowest AIC as the best model. All calculations were performed in the R environment (R Development Core Team 2014).

Results

The standardized effect size of the Rao quadratic entropy (Q) for the entire set of traits in combination varied from being lower than expected by chance at small scale (20 × 20 m) to not significantly different from random at broad scale (50 × 50 m) (Fig. 1). For traits individually, functional diversity in WSG and LA was lower than expected by chance at the broad scale, whereas functional diversity in SRL was greater than expected by chance. In small-scale quadrats, functional diversity in SLA was lower than expected by chance while no differences were found in functional diversity in the rest of functional traits.

Community-weighted means (CWMs) and functional diversity often exerted significant associations with soil water content at both spatial scales (Table 1; Fig. 2, 3). In the small plots, CWMs for H and WSG were significantly positive correlated with soil water content while LA and SLA showed negative relationships with water content. In the broad-scale quadrats, CWMs for H and LA were negatively related with water content, whereas WSG and SRL were positively related with water content. Furthermore, SES_Q in all traits excluding SRL, showed significant negative relationships with soil water content in the small plots. In the broad scale, SES_Q in WSG and SRL showed negative relationships with soil water content, whereas SES_Q in H and SLA were positively related with soil water content.

The trait dispersion pattern for all traits in combination had no directional changes when the dominant competitor *P. koraiensis* was removed from the community dataset (Table 1). However, functional

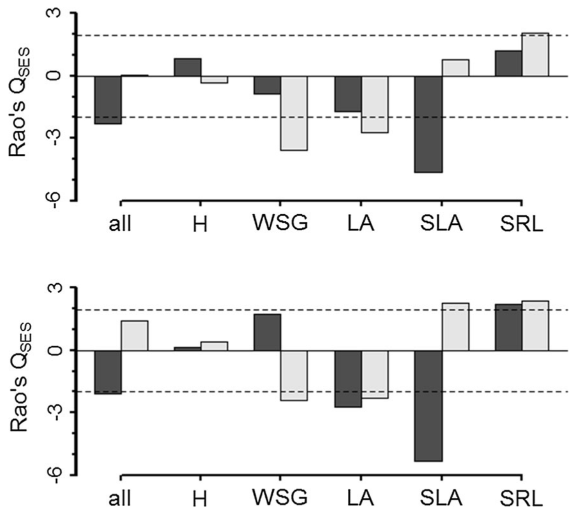

Fig. 1 Standardized effect size of mean Rao functional diversity for the entire set of traits in combination and for each trait at the two spatial scales studied and with (*above*) and without considering *P. koraiensis* (*below*). Different colours are used for each quadrat size: *light grey* (50 × 50 m plots) and *dark grey* (20 × 20 m plots). Values above zero line indicates functional diversity greater than expected by chance (trait divergence) and values below the zero line functional diversity lower than expected by chance (trait convergence). Values lower or greater than ±1.96 indicate patterns in trait convergence or divergence are significant

diversity in LA and SRL at small scale and functional diversity in SLA at broad scale turned to significantly different from expected diversity. Without considering the *P. koraiensis*, the slopes of regressions between soil resources and CWM, functional diversity become much steeper at both scales (Table 1).

Discussion

Non-random trait dispersion pattern

Community ecologists have sought to link patterns of functional trait dispersion to local-scale environments in order to infer assembly mechanisms. Much of this work has inferred that abiotic filters (Weiher and Keddy 1995; Swenson and Enquist 2009) would influence plant community assembly at broad spatial scales to a greater degree than biotic interactions (Kraft and Ackerly 2010; HilleRisLambers et al. 2012). When considering single trait diversity, we found that the majority of traits (LA, SLA, and WSG) have less diversity than expected inside 20 × 20 m quadrats, which is in line with previous findings (Kraft and Ackerly 2010; HilleRisLambers et al. 2012; Swenson et al. 2012; Coyle et al. 2014). For example, Liu et al. (2013) demonstrated that these three traits, LA, SLA and WSG, had significantly lower diversity than expected given the species pool and null model in a species-rich subtropical Chinese forest plot. Mayfield and Levine (2010) also suggested that traits related to resource acquisition ability, such as leaf traits, are more likely to have a lower diversity than expected in contrast to traits related to plant stature (plant height). This pattern is often considered evidence of abiotic filtering within and between quadrats, highlighting a dominant role for this process at the scale of this study (Kraft et al. 2008; Swenson and Enquist 2009). Meanwhile, two traits, H and SRL, have the opposite pattern of higher than expected diversity, which is consistent with studies from temperate and tropical plant community work that have shown overdispersion in these two traits believed to be linked to competition for light and soil resources (Grime 2006; Spasojevic and Suding 2012; Liu et al. 2013). Similarly, Morin et al. (2011) suggested that the coexistence of tree species in temperate forests was driven primarily by competition for light because of vertical stand structure resulting in larger heterogeneity in tree height and leaf display.

Lower functional diversity in LA and WSG than expected and higher diversity in SRL in the broad-scale quadrats (50 × 50 m) makes the imprint of abiotic filter and biotic interactions more clear (Weiher and Keddy 1995; Kraft and Ackerly 2010; HilleRisLambers et al. 2012; Yang et al. 2014). Our previous studies have suggested that habitat filtering and other biotic processes such as dispersal work together to build up diversity patterns (Yuan et al. 2012) with habitat filtering becoming more important at the broader scale (Yuan et al. 2011; Wang et al. 2012). However, larger than expected functional diversity in SLA at the broad scale may arise as a consequence of environmental heterogeneity enhancing light partitioning (limiting similarity) (Chesson 2000). The broader the quadrats size, the greater the probability to contain more stems and functionally similar species, which will increase the biotic interactions that lead to competition (niche partitioning, limiting similarity). It also may suggest that tall large-leaved species may facilitate the persistence of other smaller species, possibly due to protection from wind

Table 1 Summary of the regression models proposed to study the variation of functional composition (CWM) and functional diversity (SES) along the soil resource gradient

		With *P. koraiensis*				Without *P. koraiensis*			
		Water content (%)	Range	Weight	Pseudo-r^2	Water content (%)	Range	Weight	Pseudo-r^2
20 × 20 m									
CWM	H	3.31**	2.42	0.98	0.04	4.21**	2.69	1.00	0.05
	WSG	4.92**	2.58	1.00	0.10	4.68**	2.50	1.00	0.07
	LA	−2.78**	2.62	0.94	0.03	−7.01**	2.64	1.00	0.19
	SLA	−6.57**	2.49	1.00	0.14	−7.56**	2.67	1.00	0.24
	SRL		2.70	0.69			2.52	0.71	
SES	pooled	−5.22**	2.28	1.00	0.07	−5.67**	2.15	1.00	0.07
	H	−2.78**	2.19	0.94	0.02	−1.86	2.10	0.66	0.01
	WSG	−9.26**	2.83	1.00	0.38	−8.96**	2.91	1.00	0.41
	LA	−4.38**	2.72	1.00	0.11	−3.02**	2.77	0.94	0.07
	SLA	−3.34**	2.50	0.98	0.04	−2.02*	2.42	0.72	0.02
	SRL	7.83**	2.28	1.00	0.16	6.81**	2.74	1.00	0.20
50 × 50 m									
CWM	H	−2.38*	3.70	0.76	0.15	−4.60**	3.40	0.98	0.33
	WSG	1.50	3.27	0.50	0.04	1.80		0.64	0.03
	LA	−4.19**	3.43	1.00	0.24	−6.39**	3.12	1.00	0.38
	SLA		3.18	0.73				0.74	
	SRL	3.52**		0.99	0.11	4.72**		1.00	0.19
SES	pooled			0.74		−2.66**		0.92	0.07
	H	9.64**		1.00	0.49	9.21**	3.20	1.00	0.58
	WSG	−3.07**		0.97	0.09	−4.36**		1.00	0.16
	LA			0.64			3.61	0.70	
	SLA	5.89**		1.00	0.26			0.69	
	SRL	−2.65**		0.92	0.07	−2.76**		0.94	0.07

Significance level: * $P < 0.05$; ** $P < 0.01$

For each variable, we show the influence of the water content (%) the presence of spatial autocorrelation in the data (and its range), the weight of the model, and the squared multiple correlation

or cold exposure or increasing ground water acquisition ability (Spasojevic and Suding 2012). These findings support the idea that multiple assembly processes can work simultaneously along different niche axes at different scales (Katabuchi et al. 2012; Spasojevic and Suding 2012; Yang et al. 2014).

Changes in functional diversity across soil nutrients

A shift in the functional composition (CWM) across the soil gradient indicates that habitat filtering is occurring. While this filtering could be due to abiotic environmental constraints, as is often assumed in assembly (Weiher and Keddy 1995), it also can be due to biotic filtering through constraining a community to specific traits and likely results from selection for local competitors (Chazdon 2008; Spasojevic and Suding 2012). At the small spatial scale, the finding that an increase in WSG and H and a reduction in leaf traits along soil resource availability indicates tree species with strong competitive abilities were often filtered into fertile sites (Ackerly et al. 2002; Katabuchi et al. 2012). Previous work with natural old-growth forest has confirmed that species with longer life spans and low growth rates, which are often characterized by a high WSG, might respond less rapidly to environmental changes, conferring them greater survival ability through resistance to disease, drought and physical damage (Baker et al. 2004; Chave et al.

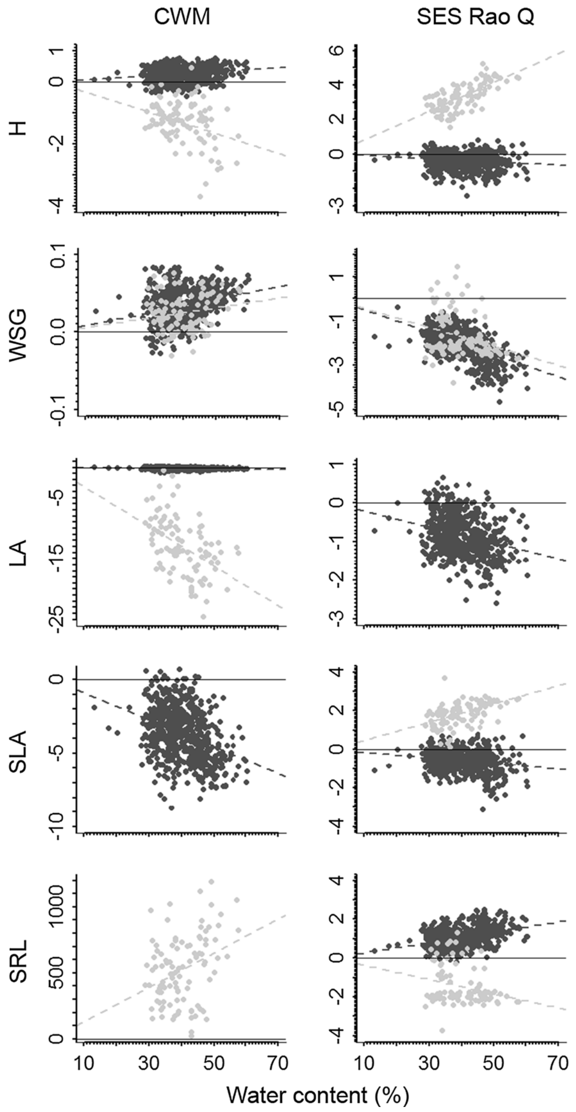

Fig. 2 Community-weighted mean (CWM) and standardized effect size of Functional diversity (SES_Q) for the five traits considered along the soil gradient. For each trait, the figure shows the residual variation of CWM and SES in each trait after removing its spatial structure. Different colours are used for each quadrat size: *light grey* (50 × 50 m quadrats) and *dark grey* (20 × 20 m quadrats)

2009). In our plot, we hypothesize that these results are the consequence of the increase in the abundance of *P. koraiensis*, a dominant canopy species (Yuan et al. 2012), in the resource-rich end of the gradient. *P. koraiensis* acts as a superior competitor in the studied forest and modifies soil conditions which in turn can result in the exclusion of species that cannot tolerate the conditions imposed by the superior competitor (Grime 2006). Thus, there existed a negative relationship between *P. koraiensis* abundance and diversity of the sub-canopy layer in our plot due to shading effect (von Härdtle et al. 2003; Yuan et al. 2012; Wu et al. 2016). A more statistically significant effect of soil moisture on functional diversity and CWM was detected without considering the *P. koraiensis*, highlighting the importance of this coniferous species on community assembly. Furthermore, the regions dominated by *P. koraiensis* are probably very stable and do not suffer from frequent periodic disturbances and this stability results in higher values of tree height and wood density (Baker et al. 2004). In the 50 × 50 m scale, we found a similar pattern for CWM in leaf area and a reversed pattern for CWM in tree height (i.e. a decrease along the soil moisture gradient), which can be a consequence of the increase in habitat types with the increase in grain size. These results suggest that some trait patterns can be consistent across different spatial scales while others will change (Kraft and Ackerly 2010).

The competition for soil resources may be greater in regions with higher nutrient availability and soil moisture, requiring species to use different strategies to stability coexist (Holdaway et al. 2011). In the small quadrats, we found that the standardized effect size of functional diversity in all traits excluding SRL decreased along the soil moisture gradient (i.e. a trend of decreasing functional diversity towards the resource-rich end of the gradient). Conversely, we found that functional diversity in SRL increased along the soil gradient. We hypothesize that this pattern is the result of two opposing assembly mechanisms that act on different niche axes simultaneously. The strong competition imposed by *P. koraiensis* on the resource-rich end of the gradient results in the competitive exclusion of several species and a reduced functional diversity in tree height and WSG as a consequence of the selection of long-lived canopy species. At the same time, nutrient availability will influence resource use strategy of a species resulting in an increase in functional diversity in SRL with the increase in soil nutrient availability. In the broad-scale quadrats, the greater functional diversity in SLA and tree height in areas of greater soil moisture content and nutrient availability may be the consequence of greater habitat heterogeneity in these areas. It is unlikely that niche differentiation as a consequence of tree competition will occur at this spatial scale (Kunstler et al. 2012;

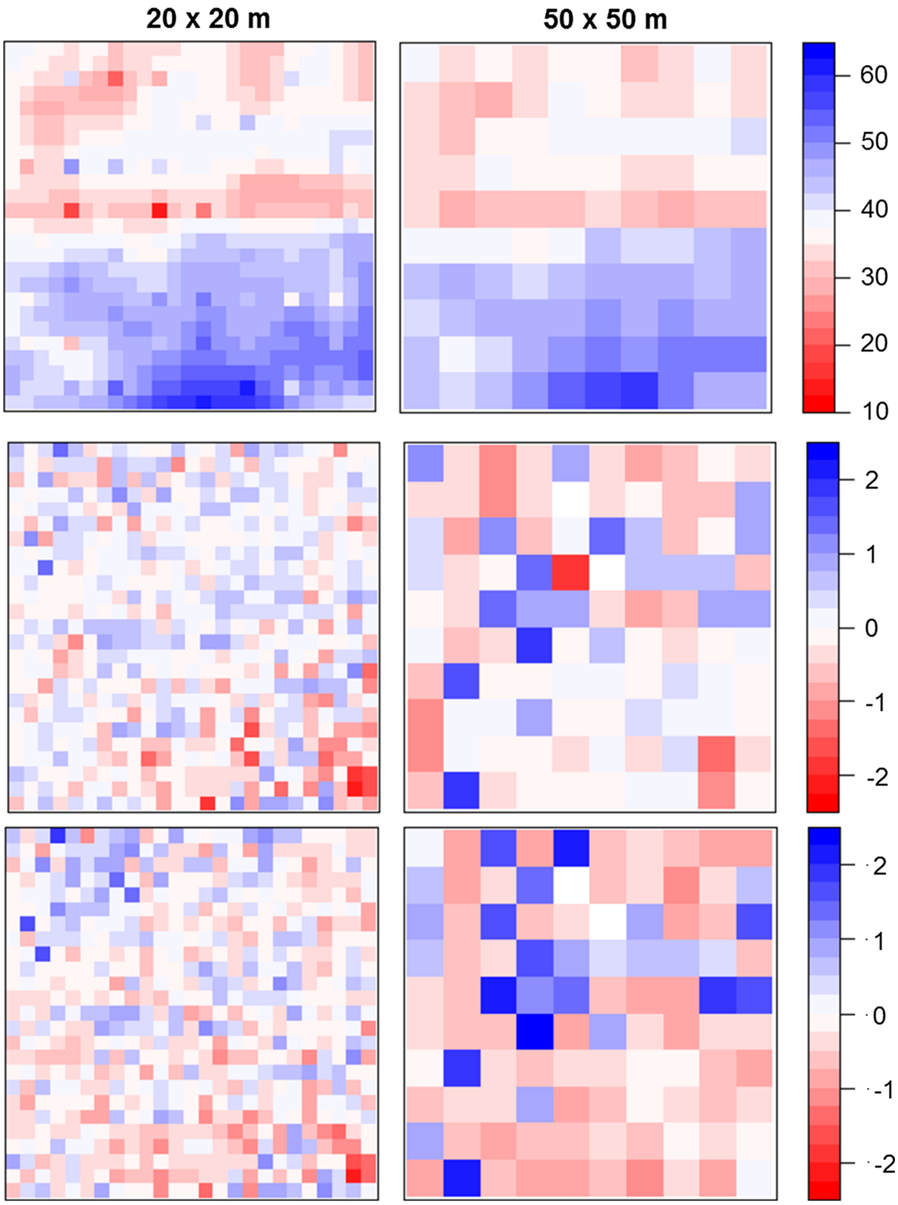

Fig. 3 Soil water content (%) and standardized effect size of functional diversity (SES Rao Q) for the entire set of traits in combination at the two spatial scales studied and with (*above*) and without considering *P. koraiensis* (*below*). The volumetric soil water content (*above*) and the SES Rao Q in each sample quadrat (20 × 20 and 50 × 50 m quadrats) is represented by a colour scheme. The size of the squares is equivalent to the size of the plot

Kraft and Ackerly 2010). Thus, there should be suitable spots for different species to coexist without interacting (Kraft and Ackerly 2010). Why functional diversity in WSG and SRL decrease along the soil gradient is probably a consequence of environmental filter processes (Weiher and Keddy 1995). That is, the increase in the abundance of *P. koraiensis* in that region results in a decrease of the functional diversity in wood specific gravity. Our findings concur with previous knowledge and suggest that the strength and intensity of assembly processes can vary along environmental gradients (Mason et al. 2012; Spasojevic and Suding 2012).

Conclusions

Although inferring community assembly from functional diversity patterns is far from perfect, trait-based approaches are increasingly being utilized to detect the opposing 'signatures' of abiotic environmental filtering and biotic interactions. The present study analysed five ecological important trait dispersion patterns and their relationships along soil nutrients' gradients in a 25-ha (500 × 500 m) temperate mixed forest in northeast China. Our results suggest that deterministic non-random processes drive community assembly in forests, consistent with previous studies (Kraft et al. 2008; Swenson et al. 2012; Shipley et al. 2012). Previous reports have shown a tendency for trait convergence and have attributed it to the presence of strong habitat filters (Swenson 2013), while biotic interactions are presumed to occur at smaller scales (Shipley et al. 2012). Nevertheless, to properly discriminate the relative influence of these processes on trait patterns, they need to be studied in the context of environmental conditions (Adler et al. 2013). Our results show that specific traits displayed different patterns along a gradient of soil conditions, suggesting that different assembly mechanisms operate simultaneously for different traits along soil resource gradients. We also argued that the trait patterns detected and conclusions drawn from them depend on the size of the quadrat studied. These results need to be interpreted with caution, as they can be influenced by selection of the null model and the metrics of functional diversity employed (de Bello 2012; Mason et al. 2013) and because the dominant competitor *P. koraiensis* can determine assembly patterns mostly for leaf traits. However, our results are quite clear on suggesting that community assembly patterns in the studied forest depend on soil moisture conditions and tree interactions at least partially.

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Authors' contributions YZQ, AG and HZQ conceived the study, analysed the data and wrote the paper. YZQ, LF, WXG, YJ and FS performed the research, collected the data and provided extensive revisions on the manuscript. JM provided extensive revisions to the paper.

Compliance with ethical standards

Conflict of interest None of the authors has conflict of interest.

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