Intraspecific trait variation improves the detection of deterministic community assembly processes in early successional forests, but not in late successional forests

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Abstract

Aims

Intraspecific trait variation (ITV) has been increasingly recognized to play an important role in understanding the underlying processes influencing community assembly. However, gaps remain in our understanding of how incorporating ITV will influence the relative importance of deterministic (e.g. habitat filtering, limiting similarity) and stochastic processes in driving community assembly at different successional stages.

Methods

We used data for eight functional traits from 55 woody species in early (24 ha) and late (25 ha) successional temperate forest plot in northeast China. We employed an approximate Bayesian computation approach to assess the relative contribution of stochastic processes, habitat filtering and limiting similarity in driving community structure. We then compared the results with and without intraspecific trait variation to investigate how ITV influences the inferred importance of each process.

Important Findings

We found that when analyzing interspecific trait variation only (i.e. without ITV), stochastic processes were observed most frequently in driving community composition, followed by habitat filtering and limiting similarity in both forests. However, ITV analyses showed that the relative importance of both deterministic processes (habitat filtering and limiting similarity) increased in early successional forest, but remained virtually unchanged in late successional forest. Our study reveals the distinctive influence of ITV on the inference of underlying processes in a context of succession and reinforces the need to estimate ITV for making correct inferences about underlying ecological processes.

Keywords: Changbaishan, community assembly, functional trait, intraspecific trait variation, succession

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INTRODUCTION

A fundamental goal of ecology is to discern the underlying processes that assemble species into communities (Chesson 2000; Götzenberger *et al.* 2012). There has been a surge of interest in quantifying trait similarity among co-occurring species, which can detect whether stochastic or deterministic processes clearly dominate (Chase *et al.* 2011; Spasojevic and Suding 2012). For example when deterministic processes dominate, habitat filtering will select co-occurring species

with similar traits, while limiting similarity will remove species that are too similar in niche requirements and drive co-occurring species possessing dissimilar traits. In contrast, stochastic process will lead to a random local trait composition (Cadotte and Tucker 2017; Macarthur and Levins 1967; McGill *et al.* 2006; Perronne *et al.* 2017; Weiher *et al.* 1998). However, the dichotomous analyses of trait similarity ignored the fact that multiple assembly processes can structure local composition simultaneously and their effects can be interactive (HilleRisLambers *et al.* 2012; Mayfield and Levine 2010; Shipley *et al.* 2012). To untangle their confounding effects, stronger evidence is necessary from trait-based researches that directly examines the relative contribution of each underlying processes (Munoz *et al.* 2018; Perronne *et al.* 2017; van der Plas *et al.* 2015).

The pervasive application of trait-based approaches in previous studies is based on the fact that interspecific trait variability can represent species ecological difference (Adler *et al.* 2014; Cadotte *et al.* 2013; HilleRisLambers *et al.* 2012). However, due to local adaptation or to phenotypic plasticity, functional traits can also express a substantial portion of variability within species, namely, intraspecific trait variation (ITV) (Albert *et al.* 2011; Bastias *et al.* 2017; Bolnick *et al.* 2011; Des Roches *et al.* 2018; Jung *et al.* 2014; Siefert *et al.* 2015; Spasojevic *et al.* 2014; Violle *et al.* 2012). ITV recalls the concept of the niche as a multidimensional hypervolume and can be used to reflect species intraspecific niche width (Blonder *et al.* 2014; Carmona *et al.* 2016). Previous studies have found that considering ITV can increase the inferred importance of dominant deterministic assembly rules, such as environmental filtering or limiting similarity (Chalmandrier *et al.* 2017; Jung *et al.* 2010; Paine *et al.* 2011; Spasojevic *et al.* 2016). However, most researches employed null model approaches to detect whether observed functional diversity deviated from a null expectation and compared the results with and without ITV (Chalmandrier *et al.* 2017; Spasojevic *et al.* 2016). It remains unclear to what extent accounting for ITV will modify the relative contribution of different processes. Further, both field and experimental evidence have suggested that ITV should be more important in species-poor communities (Bastias *et al.* 2017; Kraft *et al.* 2014; Siefert *et al.* 2015). Compared with tropical forest, species richness are lower and deterministic process are often more easily to be detected in temperate forest (Myers *et al.* 2013; Wang *et al.* 2016). Inferences about the influence of ITV on community assembly mechanisms are therefore crucial in temperate forest.

Forest communities at different successional stages can be structured by multiple ecological processes (Lebrija-Trejos *et al.* 2011; Li *et al.* 2015; Lohbeck *et al.* 2013; Meiners *et al.* 2015; Norden *et al.* 2017). For example due to environmental adversity that species experience, habitat filtering is likely to influence early successional communities (Connell and Slatyer 1977; Lohbeck *et al.* 2014). As succession proceeds, co-occurring species are more specialized in their resource acquisition and fulfill the available niche space evenly in order to coexist (Kumordzi *et al.* 2015; May and Mac Arthur 1972; Pianka 1974). Accordingly, we can expect that analyzing functional diversity based on mean species trait values should provide results closer to an analysis acknowledging ITV in late successional stage (Fig. 1). Although considerable ITV have been found in previous successional studies (Derroire *et al.* 2018; Plourde *et al.* 2015), whether and how considering ITV can change the inferred contribution of multiple processes across succession has seldom been explored. Moreover, while a shift from habitat filtering to biotic interactions has been found in many successional studies, several recent studies have found little support of such a progression across succession (Bhaskar *et al.* 2014; Craven *et al.* 2015). Analyzing the relative contribution of different processes by incorporating ITV may thus improve our understanding of community assembly rules during succession. To the best of our knowledge, however, no published study has investigated whether and how incorporating ITV could change the relative importance of different processes on forest community assembly across succession.

In this study, we selected two large temperate permanent monitoring forest plots (24 ha early and 25 ha late successional forest plot) in a typical temperate forest in northeast China, which can permit us to compare our findings with previous studies about ecological processes at different successional stages (Anderson-Teixeira *et al.* 2015). We computed functional diversities based on two most common families of dissimilarity measures: (i) 'Gower' distance, using only species mean value; (ii) 'trait overlap', which considers ITV (de Bello *et al.* 2013). Then we employed an ecological simulation modeling approach to examine how the relative strength of different ecological processes will be changed based on two dissimilarity measures. Specifically, we aimed to answer following two questions:

1) What is the relative contribution of stochastic processes, limiting similarity and habitat filtering process in two successional forests?

We expected that the relative contribution of stochastic processes should be higher than deterministic processes in both forests. Secondly, the effect of habitat filtering will be more important than limiting similarity in two successional forests. This is because previous studies in temperate forests showed that competitive limiting similarity contributed only slightly to species coexistence within small spatial scales (<20 m) (Wang *et al.* 2013, 2015, 2018), while habitat filtering is often seen as a driving force at early successional stage (Lohbeck *et al.* 2014).

2) How will incorporating ITV influence the inferred relative contribution of different processes in two successional forests?

We assumed that the inclusion of ITV should improve the inferred proportion of deterministic processes, since ITV can reflect species adaptation to external biotic and abiotic
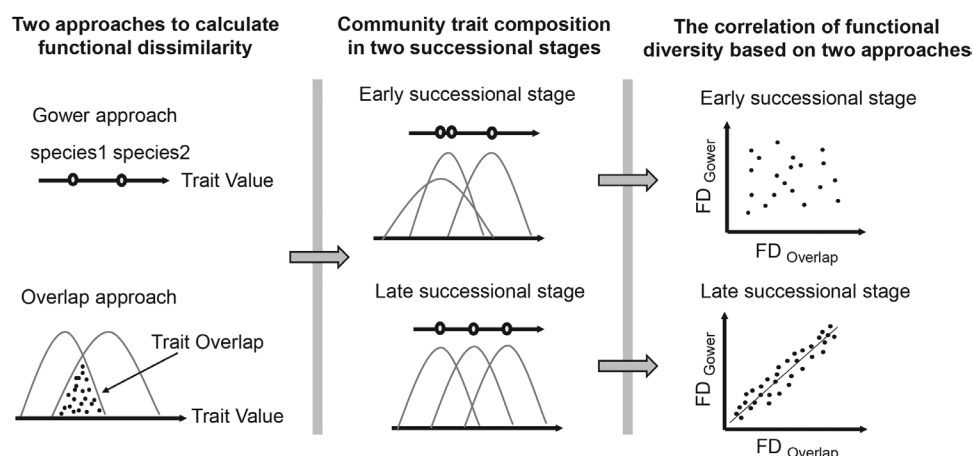
Figure 1: graphical representation of the estimation of functional diversity based on mean trait value (Gower) and trait overlap (Overlap) in two successional forests. Gower approach estimates functional dissimilarity based on the difference among mean trait value, which only considers interspecific trait variation, Overlap approach calculates functional dissimilarity based on overlap between the curves of trait distribution for each pair of species, which further considers intraspecific trait variation. Trait distribution for each species is fitted with mean and standard deviation of trait values. At early successional stage, initial colonization randomly samples the trait distribution of species and species will have different ITV, then functional diversity might be uncorrelated between Gower approach (without ITV) and Overlap approach (with ITV). As succession progresses, species will distribute more evenly along niche axis and ITV will decrease due to limiting similarity, which will cause higher correlation between functional diversity with and without ITV.

environments more precisely (Jung *et al.* 2010). However, due to the increased niche differentiation among co-occurring species, functional diversity with and without ITV should produce similar results at late successional stage. Therefore, the importance of incorporating ITV on the inference of community assembly will decrease over succession.

MATERIALS AND METHODS

Study sites

The two large permanent forest plots were located in Changbaishan (CBS) Nature Reserve in northeast China (42°23′N, 128°05′E). The 24 ha (600 m × 400 m) young growth forest was first established in 2005 at a size of 5 ha and then enlarged to 24 ha in 2016. This forest was subject to logging until 1930s. The elevation of this young growth forest plot ranges from 771.7 to 815.1 m. The late successional plot comprised 25 ha (500 m × 500 m) without logging and other human disturbances for at least 300 years. The terrain of the 25 ha old forest plot is relatively gentle, with elevation ranging from 791.8 to 809.5 m. Censuses for the 5 ha young growth forest plot were conducted in 2005, 2010 and 2015, while the 25 ha old growth forest plot was surveyed in 2004, 2009 and 2014. During each census, all free-standing woody stems with diameter at breast height (DBH) ≥1 cm were identified, tagged and mapped. The 25 ha old growth forest plot contains 52 species, belonging to 32 genera and 18 families. The 24 ha secondary forest plot contains 65 species, belonging to 18 genera and 21 families. Here, based on the latest composition data of two plots, we selected 48 species from 25 ha old growth forest plot and 54 species from 24 ha secondary forest plot for this analysis.

Functional traits collection

We followed standardized protocols (Pérez-Harguindeguy *et al.* 2013) to measure eight functional traits, including six leaf traits (leaf area (LA), specific leaf area (SLA), leaf carbon stable isotope (C13), leaf nitrogen stable isotope (N15), leaf carbon: nitrogen content (LCNC), leaf nitrogen: phosphorus content (LNPC)); one root trait (specific root length (SRL)) and one stem trait (wood density (WD)). These functional traits can provide a reliable description of species life history strategies, such as light capture (leaf area), resource use (leaf stable isotope values and leaf carbon stable isotope (C13), leaf economics spectrum (specific leaf area, leaf nitrogen and leaf phosphorus), and tradeoff between structural investment and growth and mortality rates (wood density) (Laughlin 2014; Westoby *et al.* 2002). We selected 5–20 individuals for each species and collected fully expanded leaves without disease and insect injury from upper branches (online supplementary Table S2). Leaf surface area was scanned using a portable scanner (Canon LiDE 110, Tokyo, Japan) and then measured using WinFLOIA software (Régent Instruments, QC, Canada). After oven-dried at 65°C for 48 h to a constant mass, specific leaf area was calculated as the ratio of leaf area to leaf dry mass. Leaf carbon and leaf nitrogen concentration was determined using an elemental analyzer (Vario EL III, Elementar, Hanau, Germany). Leaf stable carbon and nitrogen isotope composition were analyzed by the isotopic Cavity-Ring Down Spectrometer equipped with the Combustion Module (CMCRDS system, Picarro, CA). Leaf phosphorus content was measured using PERSEE TU-1900 UV spectrophotometer. We collected the trunk cross section from a nearby tree farm during forest logging period in autumn and winter at 2011 and

2012, then oven-dried them at 80°C for 72 h to a constant mass. The ratio of dry weight to volume represented the wood density. Specific root length was calculated as root dry mass divided by root length. Here, the first-order roots, which are primarily responsible for water and nutrient uptake, were included in our analysis.

Constructing local community

We divided each forest plot into adjacent, non-overlapping 20 m × 20 m quadrats, resulting in 600 quadrats in early successional forest and 625 quadrats in late successional forest. The average species number at each quadrat is 16.9 in early successional forest and 11.4 in late successional forest. The selected quadrat size is commonly used in the analysis of forest mega-plots (Swenson *et al.* 2012; Wang *et al.* 2018) and is the typical patch size in some forest gap models (e.g. Fischer *et al.* 2016). Also, the quadrate size is appropriate to capture the effects of tree competition while minimizing the influences of habitat heterogeneity (Wang *et al.* 2010), and it is effective to examine the significant influence of ITV on community assembly (Spasojevic *et al.* 2016).

Functional dissimilarity with and without ITV

We evaluated functional dissimilarity among species in two ways (Fig. 1). The first one is Gower dissimilarity, which calculates the difference in mean trait values among species and only considers interspecific differences (Gower 1971). This approach allows comparisons across different traits since the difference is standardized between 0 and 1 for each trait. The second approach is based on the overlap in trait distribution between species, which we call 'Overlap' (de Bello *et al.* 2013). For each species, we fitted a normal distribution based on the mean value and standard deviation of the measured traits, then we calculated the functional dissimilarity as 1 minus the overlapping area between two trait distributions. To control the influence of sampling intensity differences for different measured traits, we employed a rarefaction analysis by randomly re-sampling five individuals per species and repeated 1000 times, then the mean value and standard deviation for each trait were calculated based on the 1000 randomizations (Bastias *et al.* 2017). Here, we averaged trait dissimilarities across all single traits for a multi-trait estimation of dissimilarity (de Bello *et al.* 2013).

To detect the influence of ITV on the functional diversity measures, we calculated functional richness, functional evenness, functional divergence based on Gower and Overlap approach separately. Then, we calculated the Pearson correlation coefficients between each functional diversity.

Trait-based community assembly

We used STEPCAM model to disentangle the relative importance of three categories of ecological processes driving community assembly, namely: stochastic process, habitat filtering and limiting similarity (Hauffe *et al.* 2016; Janzen *et al.* 2017; Kraft and Ackerly 2010; van der Plas *et al.* 2015). The

STEPCAM model is a STEPwise Community Assembly Model that removes species from the regional species pool (here defined as all observed species in each forest plot) until the observed local species richness. Based on species functional dissimilarity, removal of species occurs according to different rules: (i) stochastic process (S): species are randomly removed by the reverse of the relative frequency of species in the species pool; (ii) Filtering process (F): species that are most dissimilar from the trait optima (community weighted mean) are deterministically removed. This procedure simulate the niche-based selection where species without the appropriate traits can't survive in a particular environment (Cadotte and Tucker 2017; HilleRisLambers *et al.* 2012); (iii) limiting similarity (L): species pairs with lowest functional dissimilarity are identified first. From this species pairs, the one closest to a third species will be removed. This step is consistent with the idea that species with shared resources, predators, or pathogens can't coexist (Götzenberger *et al.* 2012; Macarthur and Levins 1967). In this study, the community assembly processes were considered in the following order: (i) dispersal assembly, (ii) filtering or (iii) limiting similarity, which is most in line with other literature on this topic (Cornwell and Ackerly 2009).

Following van der Plas *et al.* (2015), we employed approximate Bayesian computation within a sequential Monte Carlo (ABC-SMC) framework to infer the relative importance of three assembly processes. By setting each process with different proportion (e.g. 1, 0, 0), the model generate simulated communities with different composition. Then ABC compared four summary statistics (functional richness, functional evenness, functional divergence, and community trait means) between observed and simulated communities. These functional diversities can represent different aspects of community composition (van der Plas *et al.* 2015; Villéger *et al.* 2008). If the data of a simulated community approximates the observed community, we assumed that the performed species removal steps reflects the relative importance of the three assembly processes for the observed community. To control the scale difference among different summary statistics, we divided them by the standard deviation (SD) of the respective index, calculated for all observed local communities.

For each quadrat, we ran STEPCAM models to detect the relative importance of the three community assembly processes in structuring local communities. Specifically, to examine the influence of incorporating ITV on the inferred importance of each process, STEPCAM models were ran based on functional dissimilarity with (Gower approach) and without (Overlap approach) ITV, separately. Then, we used the Wilcoxon sign rank test to compare the difference between results.

Here, we also employed null model approach to quantify whether functional diversities were higher or lower than expected given the observed species richness in the community. This approach can be used to determine whether deterministic or stochastic processes are identified as the dominant processes (Gotelli 2000). For each quadrat, we generated

999 randomized communities by independent swap algorithm (Gotelli and Entsminger 2003). Then, we calculated the standardized effect size (SES) as the difference between the observed functional diversity and the mean of the 999 random values, divided by the standard deviation of the random values. Due to non-normality, we used a Wilcoxon test to test difference of SES with or without ITV and to test for significant deviations of functional diversity from a null expectation (SES = 0).

RESULTS

The influence of ITV on the functional diversity measures

Functional diversity with and without ITV often correlated significantly in two successional forests. However, including ITV can have higher influence on the estimation of local community composition in early successional forest. For example based on multivariate traits (All), the correlation of functional evenness and functional divergence in early successional forest were weaker than in old successional forest. Such trends were also found for functional richness based on individual trait (Table 1).

Relative contribution of ecological processes with and without ITV

Overall, stochastic processes were responsible for 75.4% of all community assembly steps in early successional forest and 58% in late successional forest (Fig. 2). Habitat filtering accounts for 21% and 31% in two forests, respectively. Limiting similarity shown lowest contribution in both forests (Fig. 2).

In early successional forest, considering ITV improved the inferred importance of deterministic processes. Specifically, the average relative contribution of habitat filtering and limiting similarity both increased, from 21.1% to 29.5% and 3.5%

to 14%, respectively (Fig. 2). In contrast, ITV failed to improve the proportion of deterministic processes in late successional forest, while the average relative contribution of stochastic process increased from 58% to 64.9% (Fig. 2).

In addition, all three functional diversity measures deviated from a null expectation (SES = 0) significantly in both successional forests ($P < 0.001$), supporting the dominance of deterministic processes. When including ITV, the standardized effect size of functional divergence shifted from negative to positive in both successional forests. For two other functional diversities, standardized effect size of functional richness was much lower in early successional forest and functional evenness was much lower in late successional forest (Fig. 3; $P < 0.001$).

DISCUSSION

The relative contribution of stochastic processes, habitat filtering and limiting similarity process

In this study, we found the highest contribution of stochastic processes to community assembly in both early and late successional temperate forests, which was consistent with previous studies in tropical (Bhaskar *et al.* 2014), subtropical (Mi *et al.* 2016) and temperate forests (Wang *et al.* 2013, 2015). However, we also found the observed functional diversity significantly departed from random expectations, supporting the dominance of deterministic processes (Götzenberger *et al.* 2012; Pavoine and Bonsall 2011; Swenson 2013). One explanation for this apparently counter-intuitive result might be that the contribution of deterministic processes often exceeded 40%, which was enough to generate nonrandom community structure even though stochastic processes were also strongly influencing community patterns. Similarly, Loranger *et al.* (2018) also found that the predictive power of deterministic constraints on functional composition decreased when stochasticity increased, but the imprint of

Table 1: correlations between three functional diversities with and without ITV in two successional forests

Trait	Functional richness		Functional evenness		Functional divergence	
	YGF	OGF	YGF	OGF	YGF	OGF
All	0.82***	0.84***	0.30***	0.67***	0.18***	0.38***
C13	0.26***	0.67***	0.38***	0.72***	−0.53***	−0.08
LA	0.17***	0.44***	0.58***	0.59***	−0.4***	−0.55***
LCNC	0.34***	0.74***	0.61***	0.6***	−0.63***	−0.44***
LNPC	0.25***	0.65***	0.38***	0.2***	0.11**	0.07
N15	0.32***	0.52***	0.14***	0.4***	0.17***	0.04
SLA	0.36***	0.66***	0.64***	0.55***	0.01	0.25***
SRL	0.61***	0.85***	0.43***	0.6***	0.23***	0.57***
WD	0.74***	0.72***	0.63***	0.75***	0.06	−0.12***

YGF represents the 24 ha young growth forest plot, OGF represents 25 ha old growth forest plot. Values indicate the Pearson correlation index, asterisk represents the statistical significance (***$P < 0.001$; **$P < 0.01$; *$P < 0.05$). All: multivariate traits; C13: leaf carbon stable isotope; LA: leaf area; LCNC: leaf carbon: nitrogen content; LNPC: leaf nitrogen: phosphorus content; N15: leaf nitrogen stable isotope; SLA: specific leaf area; SRL: specific root length; WD: wood density.
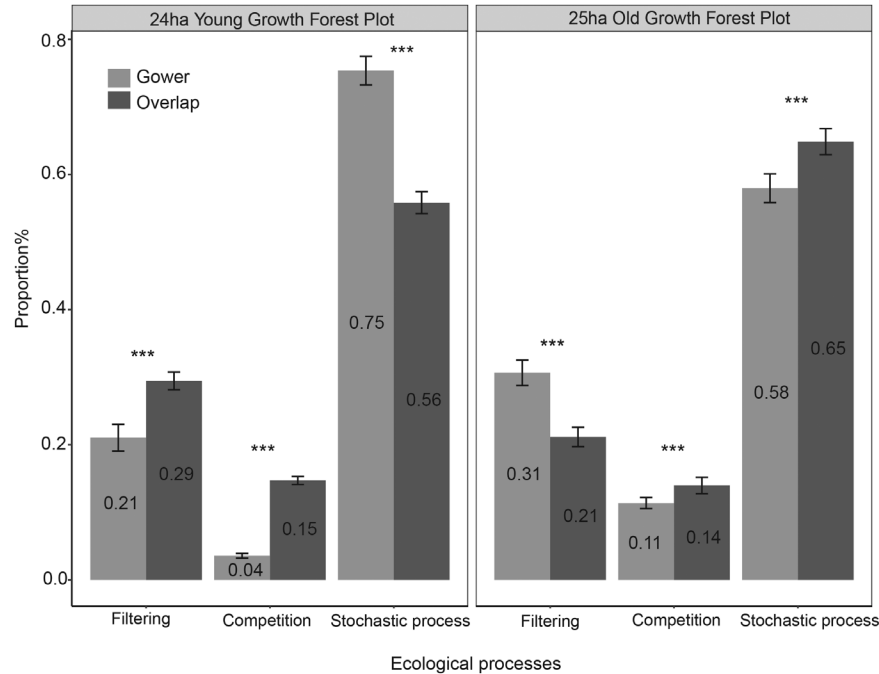
Figure 2: relative contribution of habitat filtering (F), limiting similarity (L) and stochastic process (S) underlying community assembly in two successional forests. Overlap: functional dissimilarity with ITV, Gower: functional dissimilarity without ITV. Bar label is the average contribution of each process. Error bar shows the 95% confidence interval. Asterisks represent the statistical significance of whether there is a difference between the proportions with and without ITV using Wilcoxon sign rank test (***$P < 0.001$; **$P < 0.01$; *$P < 0.05$).
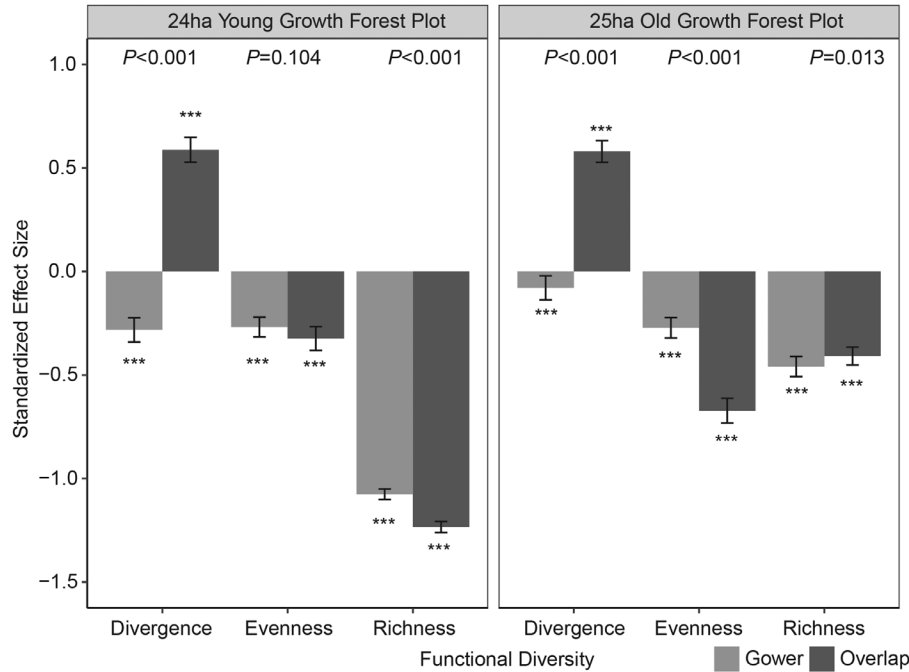
Figure 3: standardized effect size of three functional diversities with (Overlap) and without (Gower) ITV in two successional forests. Error bar is the 95% confidence interval. P values indicate the difference between functional diversities with and without ITV based on Wilcoxon sign rank test. Asterisks represent the statistical significance of whether functional diversity measures deviate from expected by chance (SES = 0) using Wilcoxon sign rank test (***$P < 0.001$; **$P < 0.01$; *$P < 0.05$).

deterministic processes still remained detectable even when it was weaker than stochastic processes. Here, our study suggested that niche-based deterministic processes could exert

their influences well, despite stochastic processes predominated across succession. This finding might provide important evidence to resolve seemingly contrasting results about the

dominance of deterministic processes and stochastic processes (Segre *et al.* 2014; Stegen *et al.* 2013).

In addition, we found that habitat filtering was more important than limiting similarity at two successional stages. There has been extensive debate about whether there was a shift from habitat filtering to limiting similarity during succession (Bhaskar *et al.* 2014; Letcher 2010; Li *et al.* 2015; Purschke *et al.* 2013; Raevel *et al.* 2012). However, most previous studies could only detect the dominance of stochastic or deterministic processes (Cadotte and Davies 2016; Swenson 2013). Here, we quantified explicit proportion of each process and found the consistent dominance of habitat filtering across succession. It has been hypothesized that the strong influence of habitat filtering would select co-occurring species with similar traits (Cadotte and Tucker 2017; Lebrija-Trejos *et al.* 2010). We detected that the observed functional richness was significantly lower than expected, suggesting that habitat filtering would limit the total niche space by excluding maladapted species (Baldeck *et al.* 2013). Although limiting similarity was often considered as a dominant process in structuring late successional communities (Lohbeck *et al.* 2014; Purschke *et al.* 2013), we found little evidence in this old growth forest plot. This supported recent findings, which suggested that species competitive interactions had a relatively minor influence on community assembly (Martorell and Freckleton 2014; Wang *et al.* 2013, 2015). However, different types of interactions (e.g. facilitation, indirect effects mediated through other trophic levels) may concurrently occur (Callaway *et al.* 2002; Chu *et al.* 2009). The interplay or counterbalance among them might not leave a detectable signal on our community-level analysis (Wang *et al.* 2016; Wiegand *et al.* 2012). Therefore, quantifying other types of species interaction may further improve our understanding of biotic driving forces underlying community assembly (Soliveres *et al.* 2015).

The effect of incorporating ITV on the inference of different processes

We found that incorporating ITV can have stronger influence on the inferred strength of deterministic processes at early successional stage than at late successional stage. The improved importance of deterministic processes (environmental filtering and limiting similarity) suggested that incorporating ITV was crucial for quantifying species' response to abiotic or biotic constraints (Jung *et al.* 2010; Violle *et al.* 2012). Several recent studies have found that ITV can act differently across environmental gradients (Lajoie and Vellend 2015) and spatial scales (Chalmandrier *et al.* 2017; Spasojevic *et al.* 2016). To our knowledge, our study provided first empirical evidence that considering ITV had different influences on the inference of assembly processes across succession in temperate forest. The diminishing influence of ITV might result from the changing of niche packing across succession. As succession progresses, the accumulation of limiting similarity can cause increase of species' interspecific niche separation and force co-occurring species to fill the niche space more

evenly (Pianka 1974; Violle *et al.* 2012). Although we didn't find a detectable increase of limiting similarity across succession, the departure of functional richness from expected was greater at early successional stage than at late successional stage. Therefore, co-occurring species at late successional stage would increase niche differentiation by exploiting more functional trait space. Consistent with our findings, Kumordzi *et al.* (2015) also found that the changing niche packing was a key mechanism for species coexistence during succession in a boreal forest. In addition, we found that the correlation between functional diversities (with and without ITV) was weaker at early successional stage than at late successional stage. This suggested that considering ITV could influence the inference of ecological processes by changing the estimation of functional diversity (de Bello *et al.* 2011; Bolnick *et al.* 2011). Therefore, by incorporating ITV, trait value distributions could improve our ability to detect the influence of deterministic processes especially at early successional stage.

In this study, we assessed the effect of ITV on the relative contribution of different processes in shaping community structure in temperate forests. Our results demonstrated that incorporating ITV could increase the inferred contribution of deterministic processes (both habitat filtering and limiting similarity) at early successional communities, but not at the late successional stage. However, three key limitations need to be highlighted. First, we employed two forest plots on very different ends of the successional gradient. Studies based on a more detailed succession sequence can help to verify the generality of our results and determine transitions in the importance of different assembly mechanisms. Second, we used same mean trait value and trait variation for the species that occurred at both successional stages, which might underestimate niche overlap at the early successional stage or overestimate that at later stages. Further study that employs specific trait values or individual-based functional traits would therefore be highly valuable (Liu *et al.* 2016; Yang *et al.* 2018). Finally, the relative contribution of different processes may depend on spatial scale. Here, we only detected the influence of ITV on community assembly at one spatial scale (20 m). Future studies are needed to examine how the influence of incorporating ITV on the relative importance of ecological processes change across spatial scales.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Plant Ecology* online.

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