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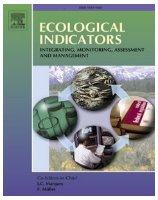

Original Articles

Importance and benefit of incorporating the responses of species mean trait values in trait-based community assembly

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ABSTRACT

Species mean trait values are the common currency of current trait-based community ecology, in which species are approximated by a set of constant mean trait values and are assumed to be passively selected by abiotic and biotic filters according to these values. However, species mean trait values can respond to both species interactions and the environmental context. Do such responses in traits subsequently alter the effect of filters on communities? Can we benefit by incorporating the responses of species mean trait values in trait-based community assembly? We tested the responses of mean values of four key functional traits to reduced light and interspecific competition in a two-year common garden experiment, using 1,584 seedlings of 11 tree species. We quantified the changes in interspecific trait differences, community-weighted means (CWM), and functional diversity (FD) and compared these to their corresponding changes under the assumption of constant mean trait values. Species mean values of most examined traits underwent substantial changes (mean = 18 ± 3%) to shading and interspecific competition treatments, but the direction and extent of these responses varied among traits and species, resulting in significant changes in interspecific trait differences, CWM and FD. Considering these trait responses largely improved our ability to identify these effects of low light and interspecific competition on CWM and FD. Further, we showed that strong abiotic filters could promote trait divergence if trait responses were considered, but that this pattern would be obscured if species mean trait values were considered as constant. Consequently, incorporating the responses of species mean trait values, e.g. using multiple mean values for a trait of a species in a heterogeneous environment, into the current trait-based community ecology offers us a more accurate, sensitive, and time-saving way to identify the underlying ecological mechanisms.

1. Introduction

The search for general rules of community assembly in ecology has led to a persistent focus on functional traits (Calow, 1987; Adler et al., 2013; Funk et al., 2017), those characteristics of species that reflect fundamental physiological and ecological trade-offs in life-history strategy and are believed to directly influence species interactions and adaptation to their abiotic environment (Funk and Wolf, 2016). Trait-based approaches have provided key insights into mechanisms of community assembly and ecosystem functioning (Adler et al., 2013; Báez and Homeier, 2018). However, most trait-based theories and empirical studies have approximated species' traits as constant mean values (e.g. Stubbs and Wilson, 2004; McGill et al., 2006; Kraft et al., 2008; Weiher et al., 2011; Kergunteuil et al., 2018), without considering the responses of mean trait values to their environmental context and local competition (Cornwell and Ackerly, 2009). Despite increasing recognition of the importance of trait response in some observational studies (Bolnick et al., 2011; Des et al., 2018), it has not been tested experimentally whether responses in mean trait values subsequently alter the effect of filters on communities. This deficiency has hindered our ability to precisely understand and predict communities in terms of functional traits.

Species mean trait values are easily altered by both abiotic and biotic factors, possibly to a large extent (Alpert and Simms, 2002). Individual plants, even from the same genotype, can have great phenotypic plasticity (Henneron et al., 2017). For instance, specific leaf area (SLA) can quickly increase from unshaded to shaded environments (Ryser and Eek,

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2000). Thus, species mean trait values, as well as the community-weighted means (hereafter CWM) of their traits across several species, will likely vary among different environments. Alternatively, the different environmental contexts can select genetically different individuals with certain trait values (Abakumova et al., 2016) and result in predictable shifts in the species mean trait values and CWM across environments (Mitchell et al., 2018; Roscher et al., 2018b). Ignoring these trait responses and assuming constant mean trait values help to cover as many species as possible from a variety of environments in large scale biodiversity studies, however, they would limit our ability to detect the influence of abiotic and biotic filters on community trait structures at small scales.

Furthermore, the responses of species mean trait values may be unequal among species. Consequently, species trait differences based on mean trait values and their functional diversity (hereafter FD) will change according to the environmental context as well as competition from neighbors (Bennett et al., 2016; Bittebiere et al., 2019). Specifically, Violle et al. (2012) proposed that species with initially unfit trait values can adjust their traits according to the abiotic environment (Mudrák *et al.* 2019; e.g., A in Fig. 1b); abiotic filters will also select traits or individuals with similar trait values. Both ways will change species trait differences and may lead to the convergence of traits among species and low FD (case 3 in Fig. 1b). Second, an increase in FD (case 4 in Fig. 1b) is expected under the interspecific competition, because this competition will select for traits or individuals with greater trait dissimilarity (Bennett et al., 2016; Roscher et al., 2018a). Considering these potential responses of traits might open a new dimention to understand the effect of abiotic and biotic filters on community assembly. For example, instead of using one mean value per trait for a species, multiple mean values of the trait can be estimated for plots in a heterogeneous environment and their differences can be used to identify the effect of abiotic and biotic filters on either species or communities according to above expectations (Swenson et al., 2011; Luo et al., 2019). Yet no study has experimentally examined these expected changes in CWM and FD.

The perspective of variable mean trait values might offer a more sensitive and time-saving way to detect the signal of the environment on community trait patterns (Jung et al., 2010; Palacio et al., 2019). Since some species trait values can respond more easily and quickly to environmental filtering and competition than species abundance, we suggest that considering the responses of mean trait values has the potential to reveal the changes in community trait structure and the assembly mechanisms over short periods (e.g., two years). Within such period, shifts in the species abundance and the turnover of species composition for perennial species would be relatively small, and any associated changes in CWM or FD will also likely be hard to detect if species' trait values are assumed as constant. In contrast, the consideration of species trait responses might offer a more sensitive and accurate way to detect the changes in CWM and FD due to abiotic and biotic filters, even if the species abundance and community composition remained unchanged. Similar ideas have been proposed in recent attempts to validate theories of community ecology (Molina-Venegas et al., 2018; Roscher et al., 2018b; Palacio et al., 2019). However, no study, as far as we know, has experimentally verified the above potential advantage.

Here we quantified the responses of mean trait values and interspecific trait differences of tree seedlings, CWM, and FD, to experimental manipulations of light and interspecific competition. We chose 1584 seedlings of 11 species for a two-year experiment because functional traits are critical for the demography of this stage in the tree life cycle (Shen et al., 2019), and impact the relative abundance and species composition of mature forests (Umaña et al., 2015). We set up a control group and three treatment groups (reduced light, interspecific competition, and their joint effect, Fig. 2) by manipulating two light intensities (shaded and unshaded environments) and two status of interspecific competition treatments (growing alone and with a heterospecific). Three leaf traits and stem-specific density were measured for every seedling at the end of the experiment. By comparing mean trait values among different treatments, we asked the following questions: i) whether and to what extent do species mean trait values respond to reduced light, interspecific competition, and their joint effect? ii) if so,

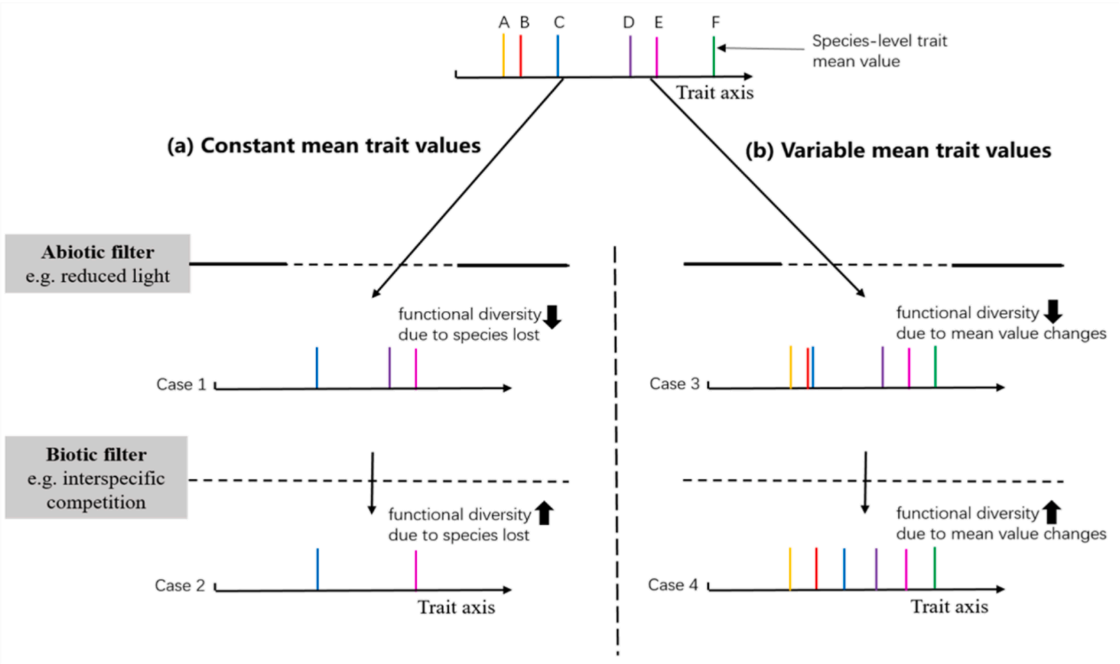

Fig. 1. A conceptual framework illustrating the different trait-based community assembly mechanisms under the assumptions of (a) constant and (b) variable mean trait values. Species (A-F) belonging to a local species pool will be selected by both abiotic and biotic filters. Different colors denote different species, and the positions of these vertical lines represent the species mean trait values. (a) species mean trait values are constant, and species with initially unfit trait values (e.g., B, F in case 1) and very similar mean trait values (e.g., D in case 2) will be excluded by abiotic and biotic filters, respectively. (b) species mean trait values can change under abiotic and biotic filters, which in turn lead to a decrease (e.g., B, F in case 3) or increase in FD (e.g., B, C, D, E in case 4).

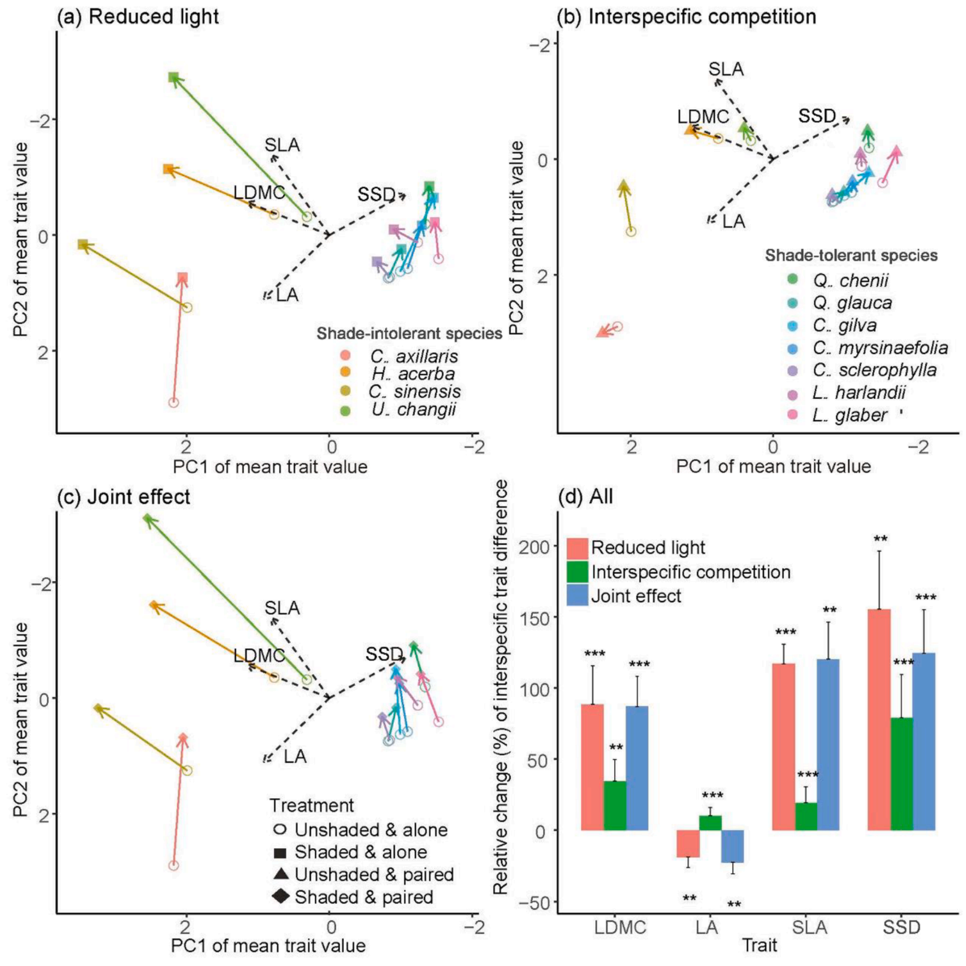

Fig. 2. Observed responses of (a-c) species mean trait values and (d) interspecific trait differences to reduced light, interspecific competition, and their joint effect in our experiment. (a-c) Characters of species mean trait values of 11 tree species were summarized by the first two axes of a principal component analysis (91.2% explained variance). Each solid line arrow represents the overall change of their mean trait values for each species. (d) The relative changes are the percentages of changes of trait difference from experimental to the control relative to trait differences under the control. Vertical line is one standard error bar and asterisks indicate significance (•:<0.1;*: <0.05; **: <0.01; ***: <0.001).

species with initially unfit trait values can adjust their traits to adapt to the abiotic environment, leading to a decrease in FD (e.g., B, F in case 3) under the strong abiotic filter. Meanwhile, species with very similar initial average trait values can also adjust their trait to avoid competitive exclusion, resulting in an increase in FD (e.g., B, C, D, E in case 4). Can we observe the above-expected changes in CWM and FD if the responses of species mean trait values were considered? And iii) if we assume constant mean trait values, do we still find similar changes in CWM and FD?

2. Material and methods

2.1. Experimental site and treatments

The seedling experiment was carried out on a flat of idle field (hereafter called experimental field) at the south foot of the Taibai Mountain in Tiantong National Forest Park, eastern China (29.7959° N, 121.7952° E). This park has a typical subtropical monsoon climate and supports an undisturbed subtropical evergreen broad-leaf forest (Song and Wang, 1995). Annual mean temperature and precipitation are 16.2 °C and 1374.7 mm, respectively.

In the autumn of 2014, 2,000 mature and intact seeds were collected from the park for each of the study 11 tree species, including four shade-intolerant and seven shade-tolerant species (Appendix S1: Table S1). Seeds of each species were collected from a single mother tree as a way to reduce intraspecific genetic differences. In order to select healthy and uniformly growing seedlings for the experiment, the seeds were first sown in a nursery near the experimental field in March 2015. Seedlings emerged in April and were transplanted in May into the nearby experimental field, where the experimental species can naturally recruit if no human disturbance. The whole 1,860 m^2 experimental field was leveled and ditched in April to keep the soil depth and soil water content across the field as homogeneous as possible. The experimental field was then divided into 12 equal-sized blocks to further reduce the bias of potential heterogeneity in soil conditions among blocks.

To examine the response of species mean trait values to reduced light, which is one of the important abiotic factors for plant seedling growth and renewal (Lewis and Tanner, 2000), half of the blocks were randomly selected to be shaded with a black shading net at 3 m height for the two years' experiment, and the remaining blocks were left unshaded (Appendix S1: Fig. S1a). The average midday light intensities of 10 $\mu mol/(m^2 \cdot s)$ and 1800 $\mu mol/(m^2 \cdot s)$ for the shaded and unshaded environments, respectively, are typical light conditions in the understory and canopy of the surrounding forest.

To examine the effects of interspecific competition, within each block, two alone growing seedlings of 11 species and 55 two-species pairs (all combinations of 2 species drawn from 11 species) of heterospecific seedlings were planted (Appendix S1: Fig. S1a). Seedlings growing alone represented individuals without competition; the pair of seedlings grew with each other ($\leq$2 cm apart) in the same planting spot and suffered interspecific competition. A mixed-effect model showed that both shading and competition had a significant effect on seedling growth (Appendix S1: Table S2); thus our treatments were strong enough to simulate the abiotic filter of reduced light and biotic filter of interspecific competition. Other details of the experimental treatments are explained in Appendix S1.

After two years (October 2017), four functional traits, leaf area (LA), specific leaf area (SLA), mean leaf dry mass content (LDMC), and stem-specific density (SSD), were collected and measured for each surviving seedling (average mortality rate 17.0%) according to the standard protocols (Perez-Harguindeguy et al., 2013) (see Appendix S1). The four functional traits are thought to be tightly linked with light acquisition and interspecific interactions(Swenson et al., 2011; Siebenkäs et al., 2016). Trait values were standardized for each trait before analyses.

2.2. *Trait-related indices and their responses to treatments*

Four commonly used trait-related indices were used to quantify the trait structures at both the species and community level for each combination of treatments (Appendix S1: Fig. S1b). The first index was the species mean trait value, $\overline{m}_{i,k}$, for trait k of species i. The second index was the interspecific trait difference, $d_{i,j,k} = |\overline{m}_{i,k} - \overline{m}_{j,k}|$, between species i and j of trait k. These two indices summarize trait structures at the species level. The extent and direction of their responses to different treatments were quantified by the first two axes of a principal component analysis.

The third index was CWM, defined as $\mathrm{CWM}_k = \sum_{i=1}^{S} p_i \overline{m}_{i,k}$, where S is the total number of species in all blocks, and p_i is the relative abundance of species i in the treatment. The fourth index was FD, estimated by Rao's quadratic entropy (Rao, 1982), which is the best for detecting both abiotic and biotic filters (Botta-Dukát et al., 2016). It is defined as $\mathrm{FD}_k = \sum_{i=1}^{S} \sum_{i=1+1}^{S} p_i p_j d_{ijk}$(Botta-Dukát, 2005). These last two indices summarize trait structure at the community level, considering all seedlings within the same treatment as a community, and compared the community trait structure under different treatments.

The responses of these four indices to different treatments (i.e., reduced light and interspecific competition) were defined as their changes and relative changes in the experimental treatments (i.e., shaded and competition conditions) versus the control (unshaded and alone conditions) (Appendix S1: Fig. S1c). Responses of FD based on all the examined traits were also calculated.

Significance of the responses of species mean trait values was tested with pairwise Wilcox tests. For the other three indices, we tested whether the observed response departed from the corresponding random responses, which were generated by randomly shuffling trait values across all conspecifics in the experiment 9999 times. To test whether ignoring a traits' response to abiotic and biotic factors would yield similar results, we also calculated CWM and FD based on constant species mean trait values across all treatments.

A more detailed explanation of the responses of trait structure to treatments is given in Appendix S1. All of the above analyses were done in the R software environment (version 3.6.0, R Core Team, 2018) and all code is in Appendix S2.

3. Results

3.1. *Responses of species mean trait value and CWM*

After the two years of the experiment, species trait values underwent large changes in response to reduced light, interspecific competition, and their joint effect (Table 1). The mean relative change in species mean trait value was 18.0 ± 3.4%. However, the direction and extent of these responses varied among traits (Table 1). Under reduced light or interspecific competition, LDMC, SLA, and SSD were significantly increased, and LA significantly reduced. Under the joint effect of reduced light and interspecific competition, SLA increased by 94.8%, while SSD did not significantly change (Table 1). Similar substantial variation was observed among species as well (Fig. 2a-c). The phenotypic plasticity of seedlings in different treatments also exhibited similar patterns (Appendix S1: Fig. S2).

When we explicitly consider these species- and trait-specific responses, we found significant changes in CWM for most treatments (Fig. 3b). The extent and direction of these CWM changes were generally in line with the changes in species mean trait values (Table 1). However, if we ignored the responses of species mean trait values, no significant change in CWM was detected for any trait or treatment (Fig. 3a).

Table 1

The responses of species mean trait values of seedlings after two years of experimental light reduction, interspecific competition, and their joint effect for four functional traits over 11 species. Shown are the mean change, standard error, and percentage change (in parenthesis).

Trait	Reduced light	Interspecific competition	Joint effect
LDMC†	6.02 ± 2.62**‡ (17.67%)	1.9 ± 0.49*** (5.87%)	7.63 ± 2.21** (22.86%)
LA	−4.19 ± 3.54** (−16.38%)	−0.03 ± 1.03*** (−1.45%)	−4.47 ± 3.52 (−17.11%)
SLA	10.14 ± 2.13*** (79.78%)	2.07 ± 0.42 (18.07%)	11.91 ± 2.66*** (94.81%)
SSD	1.86 ± 2.65*** (2.91%)	2.83 ± 0.97** (7.19%)	1.51 ± 1.84 (1.96%)

†: LDMC: leaf dry mass content; LA: leaf area (cm^2); SLA: specific leaf area (cm^2/g); SSD: stem-specific density (g/cm^3);
‡: •:<0.1; *: <0.05; **: <0.01; ***: <0.001.

3.2. *Responses of interspecific trait differences and functional diversity*

Due to the strong responses of species mean trait values to reduced light and interspecific competition, the trait differences between species within treatments also changed a lot (mean = 17 ± 5% in Fig. 2d). Under reduced light, LDMC, SLA, and SSD of different species became more dissimilar, but LA of different species became more similar. The interspecific competition treatment had a similar and relatively weak ($V = 14708$, $P < 0.01$) effect on interspecific differences of all examined traits.

If we ignored these observed changes in trait differences among species, few significant changes in FD were found (Fig. 4a). However, when the trait changes of species in different treatments were explicitly considered, we found a significant response in FD for most traits (Fig. 4b). Generally, the FD of all measured traits (except LA) significantly increased under reduced light, opposite to our first expectation. However, in line with our second expectation, FD of LDMC (marginally) and SSD (significantly) increased under interspecific competition. Similar patterns were found when multiple traits were used to quantify FD (right bars in each panel of Fig. 4).

4. Discussion

We found large responses of species mean values of all measured traits to reduced light and interspecific competition during the first two years of the life of tree seedlings. Similar variation was observed in the traits of shoots and leaves of grasses (Siebenkäs et al., 2016) and tree leaf (Dwyer et al., 2014; Henneron et al., 2017). These results showed that abiotic and biotic factors can modify species mean trait values once trait differences exist among conspecifics. It clearly supports the idea that species mean trait values do not hold constant but vary substantially depending on the abiotic and biotic context. This subtle change from constant to variable mean trait values offers a more realistic way of detecting the signal of selection on the functional structures of tree communities.

These plastic responses of species mean trait values are essential for individual survival under heterogeneous environments (Molina-Venegas et al., 2018; Roscher et al., 2018b), and have been increasingly considered in trait-based studies (e.g., Fig. 1a) (Valladares et al., 2000; Henneron et al., 2017; Khalil et al., 2019). As shown by our experiment (Figs. 3 & 4), ignoring these trait responses will decrease the detection of functional structure changes under abiotic and biotic filters. These results may partially explain the low predictive power of current mean

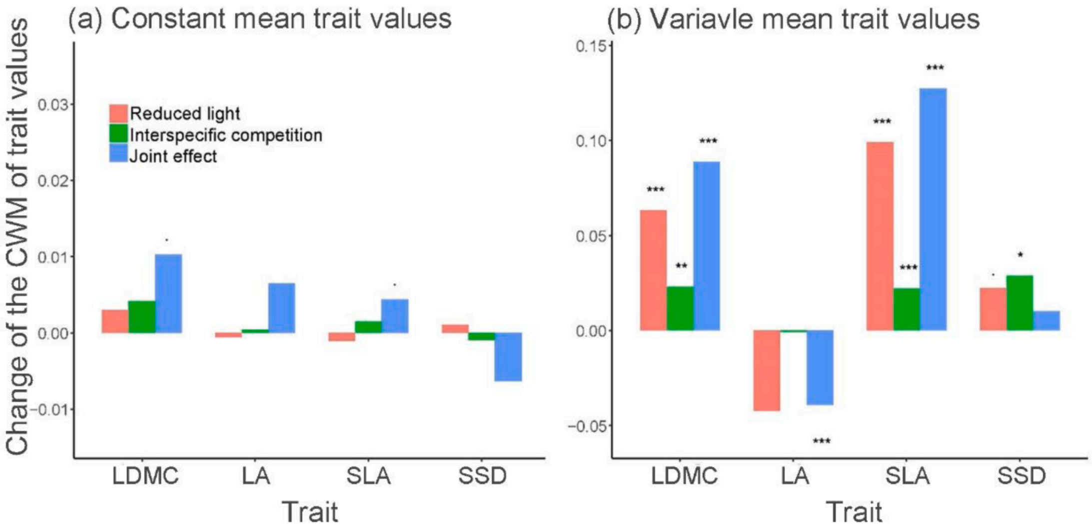

Fig. 3. Changes of community-weighted means (CWM) of trait values to reduced light, interspecific competition, and their joint effect. a) We assumed constant species mean trait values of a species across all treatments. (b) We considered the responses of species mean trait values to the treatments. We showed that considering these responses can improve the detection of the CWM changes to reduced light and interspecific competition (LDMC: leaf dry mass content; LA: leaf area; SLA: specific leaf area; SSD: stem-specific density. •:<0.1; *: <0.05; **: <0.01; ***: <0.001).

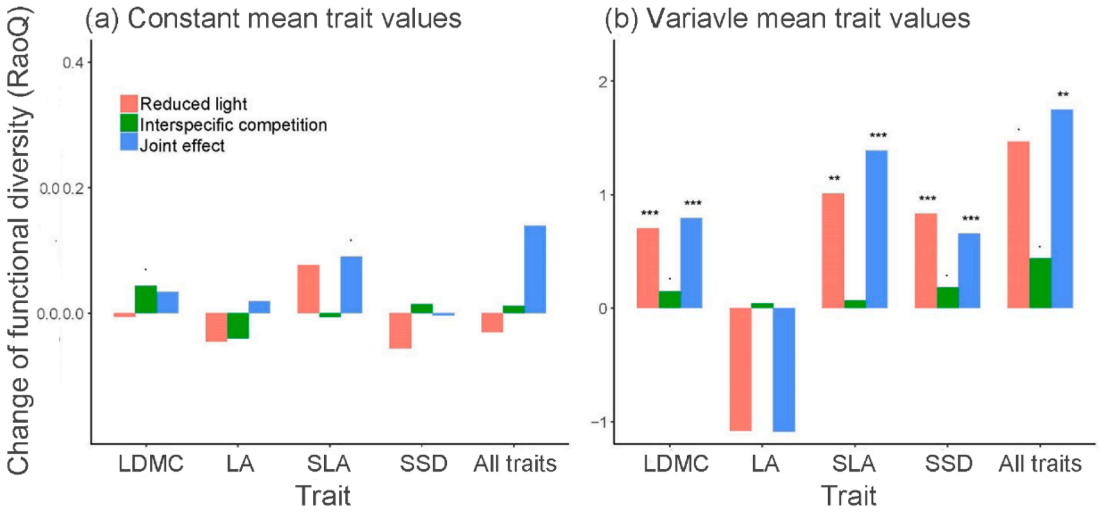

Fig. 4. Changes of functional diversity (quantified by Rao's quadratic entropy) to reduced light, interspecific competition, and their joint effect, by ignoring (a) or considering (b) the responses of species mean trait values to treatments. (LDMC: leaf dry mass content; LA: leaf area; SLA: specific leaf area; SSD: stem-specific density. •:<0.1; *: <0.05; **: <0.01; ***: <0.001).

approach models (Yang et al., 2018) in which the trait values of all individuals of a given species are aggregated to a mean trait value. Therefore, this study provides experimental support for the additional value of considering variable mean trait values. Our results suggest that both environmental and competition contexts can select for traits and that traits of individuals can also respond to these different contexts (Violle et al., 2012). For studies that aim to predict long-term community dynamics in heterogeneous environments or along environmental gradients, a single global mean trait value for a species can identify large changes in community compositional changes, but multiple mean trait values can more closely capture the real means and differences in species' traits, which may lead to more solid understanding about species interactions and coexistence (Turcotte and Levine, 2016).

A new and exciting finding of our study is that strong abiotic filters can increase FD (Fig. 4). This result is opposite to the general expectation that strong abiotic filters will select species with more similar functional traits, reducing FD (Götzenberger et al., 2012). This apparent conflict resulted from whether trait responses were considered or not. If trait responses are ignored and only constant mean trait values used, species with unfit trait values will be filtered out, and a decrease in FD seems the only possible result under strong abiotic filtering. However, if trait responses are explicitly considered, species with initially unfit trait values can modify their trait values. FD might increase under strong abiotic filters when species have substantial differences in their trait responses to the abiotic filters.

The extent and direction of trait responses were different among the studied species, particularly between shade-intolerant and shade-tolerant species (Fig. 2a, Fig. 5 and Fig. S2). This is consistent with the results of previous studies (Valladares et al., 2000; Valladares et al., 2006). Low light conditions created by shade nets not only serves as an environmental filter but also acts to stimulate phenotypic plasticity to compensate for the shading, resulting in huge and different changes in species mean trait values. Meanwhile, tall seedling neighbors also reduce light quanlity and quantity beneath them, so that the effect of shade from neighbors in treatments with interspecific competition may simulate phenotypic plasticity to compensate for the shading too. It is

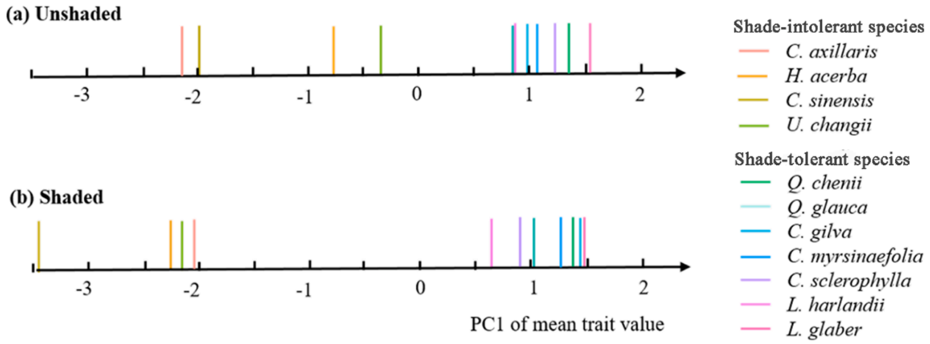

Fig. 5. Observed responses of species mean trait values of single seedlings from unshaded (a) to shaded (b) environments along with the first principal component (63.7% explained variance) axis of all measured traits in our experiment, leading to increased functional diversity under reduced light (Fig. 4). Colored vertical lines represent the real mean trait values of 11 experimental species under unshaded/shaded environment.

these different responses of mean trait values, no matter from environmental filtering or interspecific competition, that increased trait differences among species (Fig. 2d), which directly resulted in the significant increase in FD for all species (Fig. 4). Therefore, considering variable mean trait values offers a more complete view of FD changes under strong abiotic filters. The effects of strong abiotic filters on community trait patterns also depends on the different responses of mean trait values among species. This new finding highlights the theoretical difficulty in distinguishing the signatures of abiotic and biotic filters from community trait patterns. Other nonrandom community structures, not just trait convergence or divergence, are probably needed in order to correctly identify ecological processes in natural communities.

Explicitly incorporating trait responses can also help to reduce the time required to detect and examine the effects of ecological processes. Under the assumption of constant mean trait values, CWM and FD will, according to their definitions, vary largely only when some species are filtered out completely, or when large changes in the relative species abundances have occurred. In our two years' experiment, no tree species varied much in abundance or had been filtered out, thereby no significant result was found (Fig. 3a and 4a). When we incorporated the responses of species mean trait values into our analyses, significant changes in CWM and FD were found just within two years, consistent with our results based on seedling biomass (Appendix S1: Table S2). Certainly, this advantage of considering trait responses is gained at the expense of more trait sampling effect. Fortunately, one doesn't need to measure all individuals of all species for all plots. Standard protocol of trait samplings (Cornelissen et al., 2003) can be applied to estimate species mean value for each trait in each plot.

The advantage in the time required to detect a significant effect of ecological processes may significantly speed up our progress to understand mechanisms of community assembly. By explicitly considering variable mean trait values and monitoring their responses under competition, it becomes possible to avoid space-for-time substitution (Damgaard, 2019) and to quickly establish the links between traits and types of interspecific differences. Further, because CWM and FD based on variable mean trait values appear to be more sensitive and able to identify signatures of abiotic and biotic filters, for studies of environmental gradients, considering variable mean trait values and using different trait means at different locations along environmental gradients may help us to more easily to identify main ecological processes. Finally, this advantage could also help to speed up the validation of theories of species invasion, because it is not necessary to wait for the large changes in species composition after invasion (Li et al., 2016); one may just need to monitor the responses of species mean trait values to the invasion.

Several flaws might limit the generalization of our study but are expected to be solved in the future. First, our results are based on only four functional traits of seedlings over two years. Whether our conclusions are valid for other traits and the later life stages of trees is unknown. Manipulating and maintaining such an experiment beyond the seedling stage is labor intensive and is more difficult from the perspective of avoiding interactions between planting sites and protecting the experiment from disturbance such as extreme weather events (e.g., typhoon). Second, plants in nature may respond to a wide variety of other ecological factors, including herbivory, parasitism, mutualism, the presence or absence of conspecifics, and density of neighbors. Whether and to what extent these ecological factors produce similar effects on species trait means and differences is still mostly unknown or unverified by experiment.

5. Conclusion

Overall, we observed significant responses of species mean trait values, interspecific trait differences, and CWM and FD to experimentally reduced light and interspecific competition for 11 tree species seedlings. Our study provides experimental evidence that mean trait values of seedlings are not constant properties of species and can respond to abiotic and biotic factors. Our findings suggest that explicitly considering these responses (e.g. using multiple mean values for a trait of a species in a heterogeneous environment) not only provides a new angle to understand community assembly from the trait-based perspective but also offers a sensitive and time-saving way to identify the effect of ecological processes and test theories of community assembly.

CRediT authorship contribution statement

Jing Yang: Data curation, Formal analysis, Writing - original draft. **Jiahui Lu:** Formal analysis. **RenRen Wang:** Data curation. **Xihua Wang:** Resources. **Shaopeng Li:** Writing - review & editing. **Guochun Shen:** Conceptualization, Writing - review & editing, Funding acquisition, Supervision.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2021.108095.

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