

Research Article

Explaining variation in productivity requires intraspecific variability in plant height among communities

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Abstract

While recent studies have shown the importance of intraspecific trait variation in the processes of community assembly, we still know little about the contributions of intraspecific trait variability to ecosystem functions. Here, we conducted a functional group removal experiment in an alpine meadow in Qinghai-Tibetan Plateau over 4 years to investigate the relative importance of inter- and intraspecific variability in plant height for productivity. We split total variability in plant height within each of 75 manipulated communities into interspecific variability (TV_{inter}) and intraspecific variability within a community (ITV_{within}). Community-weighted mean height among communities was decomposed into fixed community-weighted mean (CWM_{fixed}) and intraspecific variability among communities (ITV_{among}). We constructed a series of generalized additive mixed models and piecewise structural equation modeling to determine how trait variability (i.e. TV_{inter} , ITV_{within} , CWM_{fixed} and ITV_{among}) indirectly mediated the changes in productivity in response to functional group removal. Community productivity was not only affected directly by treatment manipulations, but also increased with both inter- and intraspecific variability (i.e. CWM_{fixed} and ITV_{among}) in plant height indirectly. This suggests that both the 'selection effect' and a 'shade-avoidance syndrome' can incur higher CWM_{fixed} and ITV_{among} , and may simultaneously operate to regulate productivity. Our findings provide new evidence that, besides interspecific variability, intraspecific trait variability in plant height also plays a role in maintaining net primary productivity.

Keywords aboveground net primary productivity, alpine meadow, interspecific trait variability, intraspecific trait variability, plant height

解释生产力的变异需要考虑群落间植物高度的种内变异

摘要: 已有研究表明, 种内性状变异在群落构建过程中具有重要作用, 但是迄今为止关于种内性状变异对生态系统功能的贡献仍然知之甚少。我们在青藏高原的高寒草甸进行了为期4年的功能群去除实验, 以研究植物高度的种间和种内变异对生产力的相对重要性。将75个控制群落内的株高总变异分为种间变异(TV_{inter})和种内变异(ITV_{within}), 将群落间的群落加权平均高度分解为固定群落加权平均值(CWM_{fixed})和群落间种内变异(ITV_{among})。我们通过广义加性混合模型、模型筛选和结构方程模型评估了性状变异(即 TV_{inter} 、 ITV_{within} 、 CWM_{fixed} 和 ITV_{among})如何间接介导功能群去除后生产力的变化。研究结果

表明, 功能群去除不仅会直接引起生产力变化, 同时还会通过改变种间和种内株高变异间接影响生产力(即 CWM_{fixed} 和 ITV_{among})。 “选择效应” 和 “避荫综合征” 都可能导致更高的 CWM_{fixed} 和 ITV_{among} , 从而起到调节生产力的作用。该研究结果说明, 只考虑种间变异可能会低估植物群落功能结构在驱动生态系统过程中的贡献。

关键词: 地上净初级生产力, 高寒草甸, 种内性状变异, 种间性状变异, 植物高度

INTRODUCTION

Variation in net primary production (NPP) at the global scale is primarily controlled by climatic variables like temperature, precipitation and growing season length (Del Grosso *et al.* 2008; Nemani *et al.* 2003). At small spatial scales, in which variation in both climatic and soil properties is severely reduced, variation in NPP is mainly determined by variation in the functional trait composition of the plant community and yet the capacity to predict ecosystem properties from plant traits has not been fully realized (Lavorel and Garnier 2002). At the level of local plant communities that differ in NPP, variation in functional traits arises from both intraspecific and interspecific variation (de Bello *et al.* 2011; Lepš *et al.* 2011; Violle *et al.* 2012). Although functional plant ecologists have made progress in determining the relative extent of intraspecific and interspecific variation for several traits (e.g. Carlucci *et al.* 2015; Siefert *et al.* 2015), we do not yet know the relative importance of intraspecific and interspecific trait variations in determining ecosystem properties like NPP.

An increasing body of evidence has accumulated in recent decades suggesting that plant functional traits (particularly of dominant species) can predict community assembly (Shipley 2010; Spasojevic and Suding 2012) and ecosystem functions (Des Roches *et al.* 2018; Lavorel *et al.* 2011; Maynard *et al.* 2019; Suding *et al.* 2008). Currently, most such studies employ community-weighted trait means to explain biodiversity and ecosystem functions that are maintained by a community (e.g. Liu *et al.* 2015). Such community-weighted means neglect the ubiquitous intraspecific trait variability, arising from intraspecific genetic variation and/or phenotypic plasticity. Therefore, this mean field approach may underestimate the degree of trait or niche dispersion among species and the resources they exploit and result in misinterpreting the mechanisms of species coexistence and various ecosystem processes (Albert *et al.* 2011; Bolnick *et al.* 2011; Turcotte and Levine 2016; Violle *et al.* 2012).

While interspecific trait variation is often the most important source of trait variation when comparing between communities along strong environmental gradients (Jung *et al.* 2010; Siefert *et al.* 2015), its contribution to the overall trait variation depends strongly on the spatial scale at which the study is done and on the traits (Albert *et al.* 2011; Auger and Shipley 2013; Jung *et al.* 2010). In some cases, intraspecific trait variation contributes more to the total trait variation in a community than interspecific trait variation (de Bello *et al.* 2011; Messier *et al.* 2010; Siefert *et al.* 2015). Furthermore, inter- and intraspecific trait variation can occur both within a single local community and between local communities (Supplementary Table S1). As a result, intraspecific trait variation can be further decomposed into variability within communities (ITV_{within}) and among communities (ITV_{among}) as formalized in Lepš *et al.* (2011) and de Bello *et al.* (2011). ITV_{within} measures trait variation between individuals of the same species growing in the same community (Albert 2015; de Bello *et al.* 2011; Siefert *et al.* 2015), while ITV_{among} measures the spread of trait values between individuals of the same species growing in different communities. Several studies have now quantified these components of intraspecific variation under different conditions, including nitrogen and water addition (Lü *et al.* 2018), short- or long-term management (Volf *et al.* 2016), elevation gradients (Kichenin *et al.* 2013) and sandy grassland restoration (Zuo *et al.* 2017). As a meta-analysis, Siefert *et al.* (2015) reported that ITV_{within} accounted for 25% of the total trait variation within communities and 32% of the total trait variation among communities on average worldwide. However, the fact that a trait displays substantial intraspecific variation does not necessarily mean that such intraspecific trait variation is an important determinant of ecosystem processes. It remains unclear about how interspecific and intraspecific sources of variability, both within and among local communities drives ecosystem functions (e.g. NPP).

Plant height is generally considered important for light acquisition and competition (Bjorkman *et al.* 2018; Westoby 1998), and thus has an important impact on aboveground net primary production (ANPP). On the one hand, in light-limited habitats, all individuals, especially shaded individuals under reduced light would invest a large amount of energy into supporting tissue (e.g. via stem elongation) to reach as much light as possible, resulting in increasing height of different species (i.e. 'shade-avoidance syndrome'; Roscher *et al.* 2015). Thus, intraspecific trait variation in plant height within a community (ITV_{within}) may increase the utilization efficiency of light resources, ultimately increasing productivity by increasing niche partitioning and decreasing niche overlap (i.e. complementary effect) (Fahey *et al.* 2015; Gough *et al.* 2019). On the other hand, intraspecific variation in height among communities (ITV_{among}) and average fixed height (CWM_{fixed}) may also benefit productivity because communities consisting of taller individuals can access light more easily and synthesize more photosynthetic compounds (i.e. intraspecific and interspecific 'selection effect', respectively; Liu *et al.* 2017). These points suggest that both the community-weighted mean values of height and its levels of intraspecific trait variation could affect variation in aboveground net primary productivity but what is the relative importance of each? No study to date has considered both together and, since previous research has focused mostly on community-weighted means, it is possible that ecologists are missing an important intraspecific trait effect.

Experimental removal is a useful approach not only to investigate the influences of nonrandom loss of species or functional groups on ecosystem functions (Díaz *et al.* 2003; Kardol *et al.* 2018; Liu *et al.* 2015), but also to explore how plant functional trait variation mediate the change of ANPP in response to biodiversity loss. Compared with sampling on natural communities, removal leads to greater variation in not only productivity, but also functional diversity (Díaz *et al.* 2003; e.g. changes in community composition and species traits, including inter- and intraspecific variation). Thus, removal created a functional diversity–productivity pattern along a functional group richness gradient. Controlled experiments could also create that pattern, however, removal can more realistically mimic natural community composition with less changes of external variables (Díaz *et al.* 2003).

For example, nitrogen addition would result in significant changes in various abiotic factors, e.g. soil N enrichment and acidification (Zhang *et al.* 2020). In a previous study, we found that average fixed plant height caused by functional group identity is a powerful functional trait predictor for productivity in an alpine meadow (Liu *et al.* 2015). However, we did not assess the role of intraspecific variability of plant height in biomass production. Here, using data from this 4-year removal experiment, in which we manipulated the number and identity of different functional groups, we quantify the relative contributions of interspecific (TV_{inter} and CWM_{fixed} , Supplementary Table S1) and intraspecific trait variation (ITV_{within} and ITV_{among}) in plant height in determining primary productivity. Specifically, we test the following hypotheses: (i) productivity increases with increasing levels of intraspecific trait variation (including ITV_{within} and ITV_{among}), when the community has the same types of species and has species with the same average fixed height (i.e. besides interspecific variation); (ii) the combination of intraspecific variability and interspecific variability explains more variation in productivity than either of these effects alone.

MATERIALS AND METHODS

Study site

Our study site was located in the eastern part of the Tibetan Plateau (35°58' N, 101°53' E) at approximately 3500 m a.s.l. The average annual precipitation is 620 mm, which is mainly concentrated in the summer. Mean annual temperature is 1.2 °C, and monthly temperature ranges from −10.7 to 11.7 °C. The alpine meadow is rich in species diversity, having more than 30 species within a 50 cm × 50 cm subplot (Liu *et al.* 2017), and is dominated by perennial herbaceous species of the families Poaceae, Cyperaceae, Asteraceae and Fabaceae, such as *Elymus nutans*, *Kobresia myosuroides*, *Stipa aliena*, *Ligularia virgaurea*, *Saussurea pulchra* and *Thermopsis lanceolata*. The soil is typical alpine meadow soil (Genetic Soil Classification of China) with a depth of 80 cm (Liu *et al.* 2015), and is classified as Cambosols (Chinese Soil Taxonomy) (Shi *et al.* 2006).

Experimental design and data sampling

In June 2011, we established a functional group removal experiment in a 50 m × 50 m fenced area,

with yak grazing permitted from September to May. Seventy-five 1 m diameter circular plots were arranged regularly, separated by three meters from adjacent edges. All 54 species found in the study site were classified into four groups (hereafter functional groups because they differ functionally) based on their physical, reproductive and dispersal attributes: Poaceae and Cyperaceae (abbreviated as 'A'), Asteraceae (B), Fabaceae (C) and Others (D), which have been described in Table A1 in Liu *et al.* (2015). All possible combinations of the four taxonomic groups consisted of $2^4 - 1 = 15$ treatments (Treatment: ABCD, ABC, ABD, BCD, ACD, AB, AC, AD, BC, BD, CD, A, B, C, D), which were assigned randomly to plots, with five replicates for each treatment. These plots were maintained by removing the aboveground biomass of the nonfocal functional groups of species twice a year (in June and July, respectively). For example, the 'A' treatment (only species of Poaceae and Cyperaceae) was maintained by removing species belonging to the Asteraceae (B), Fabaceae (C) and Others (D).

We recorded species richness and each species' abundance (i.e. number of ramets) in a circular subplot of 50 cm diameter in the center of each plot in August (the peaking growing season) from 2012 to 2014 annually. All the aboveground parts present in each subplot were harvested using scissors at the soil surface, dried at 65 °C for 48 h and then weighed to 0.1 mg to estimate productivity (measured as annual aboveground biomass production). We also randomly selected and recorded the maximum height (including reproductive structures) of up to five individuals per species within each subplot in 2012, and up to 10 individuals per species in 2013 and 2014 for a total of 15 536 individuals' heights across 75 plots.

Calculating ITV

By using the variance partitioning method proposed by de Bello *et al.* (2011), we partitioned the total variability in height within a specific community into abundance-weighted interspecific (TV_{inter}) and intraspecific variability (ITV_{within}):

$$TV_{inter} = \frac{\sum_{i=1}^S a_i (x_i - \text{community-weighted mean})^2}{\sum_{i=1}^S a_i} \quad (1)$$

$$\text{Community-weighted mean} = \frac{\sum_{i=1}^S a_i x_i}{\sum_{i=1}^S a_i} \quad (2)$$

$$ITV_{within} = \frac{\sum_{i=1}^S a_i \frac{1}{N_{ind}} \sum_{j=1}^{N_{ind}} (x_{ji} - x_i)^2}{\sum_{i=1}^S a_i} \quad (3)$$

$$\text{Total variability} = TV_{inter} + ITV_{within} \quad (4)$$

where S is the number of sampled species in a subplot (community), a_i is the abundance of the i th species in the subplot and x_i is the average height of the i th species in the given community. The community-weighted mean of height is the mean of species height weighted by their relative abundance in a subplot. x_{ji} is the height value of the i th species at the individual level, and N_{ind} is the number of sampling individuals of the i th species. TV_{inter} , also called the community-weighted variance (Shipley 2010), represents the difference between the height of a given species in a community and the average height of all individuals in that community.

We also calculated the community-weighted mean caused by species turnover alone (CWM_{fixed}) and by ITV_{among} alone following Lepš *et al.* (2011). CWM_{fixed} indicates the community expected average height based on its constituent individuals. It is affected only by species turnover, which can be calculated as:

$$CWM_{fixed} = \frac{\sum_{i=1}^S a_i x_{fixed}}{\sum_{i=1}^S a_i} \quad (5)$$

where x_{fixed} is the fixed height average of the i th species over all sampling communities. ITV_{among} in each plot is the difference between community-weighted mean and CWM_{fixed} :

$$ITV_{among} = \text{community-weighted mean} - CWM_{fixed} \quad (6)$$

A positive ITV_{among} indicates that the community average height in a subplot is taller than expected (CWM_{fixed}), while a negative ITV_{among} means lower.

Statistical analysis

Our hypotheses concerned the relationship between community productivity and four predictor variables: TV_{inter} , ITV_{within} , ITV_{among} and CWM_{fixed} . However, community productivity could potentially be affected directly by the treatment manipulations and/or by biodiversity changes induced by these treatments (the number of functional groups, species richness, Shannon's evenness index, Simpson's diversity index and phylogenetic diversity), as shown in Liu *et al.* (2015). If so, then correlations between community productivity and our four predictor variables could

be spurious and reflect the common effects of the treatment manipulations or the biodiversity changes. We therefore tested our hypotheses in two steps.

First, we regressed community productivity in each of the subplots on the categorical treatment manipulation or on each of the measured biodiversity changes, in order to determine how best to control for such possible spurious patterns. Since we had no *a priori* reason to assume linearity, these regressions were done using generalized additive mixed models via the *gam* function of the *mgcv* library of R (Wood 2017), in which the predictor variables were added as fixed smoothed terms via penalized thin plate regression splines with both random intercepts and slopes over years. We used AIC (Akaike information criterion) statistics (see below) to choose the best of these variables as a covariate to serve as our ‘null’ model for comparison. We found that the categorical treatment variable itself, rather than the number of functional groups, species richness, Shannon’s index, Simpson’s index or phylogenetic diversity, was the best single explanatory variable for community productivity. Since the ΔAIC_c (AIC corrected for small sample sizes) for all of these biodiversity indices were >54.658 relative to the treatment variable, ‘Treatment’ defined the ‘null’ model (Supplementary Table S2).

Second, we also conducted model selection by regressing community productivity on the treatment factor (which we use as the ‘null’ model) plus each possible combination of the four predictor variables (TV_{inter} , ITV_{within} , ITV_{among} and CWM_{fixed}). A series of generalized additive mixed models with year as random intercepts and slopes were performed. Spearman’s correlation tests were performed using the *cor.test* function in the *stats* package to avoid including strong correlation indices in any model if Spearman’s $\rho > 0.5$ (Supplementary Table S3). We also tested the influences of the trait variabilities (total variability, TV_{inter} , ITV_{within} , community-weighted mean, CWM_{fixed} and ITV_{among}) on productivity after controlling for Treatment in 2012, 2013 and 2014, respectively, using the same approach used for data across all the years combined. We calculated information-theoretic Akaike’s information criterion corrected for small samples sizes (AIC_c), the change in AIC_c relative to the model with lowest AIC (i.e. ΔAIC_c). Following Burnham and Anderson (2010), the model with the lowest AIC_c has the most support, models with $\Delta AIC_c > 3$ having considerably less

support and models with $\Delta AIC_c > 7$ having essentially no support.

Furthermore, we used piecewise structural equation modeling (SEM) to test how the presence of four functional groups affected plant inter- and intraspecific variability indices (i.e. TV_{inter} , ITV_{within} , ITV_{among} and CWM_{fixed}), and then influenced community productivity (see an initial causal model in Supplementary Fig. S1). For example, ‘presence of A’ consisted of all the treatments that included A (i.e. A, AB, AC, AD, ABC, ABD, ACD and ABCD). Standard path coefficients (β), corresponding significance (P values) for each path and global goodness of fits of the final model were evaluated using *psem* function in piecewiseSEM package (Lefcheck 2016), which based on a d-sep approach (Shipley 2016). All statistical analyses were conducted in R 3.6.1 (R Core Team 2019).

RESULTS

Across 3 years, intraspecific trait variation among communities (ITV_{among}) was a significantly positive predictor of productivity (Estimate \pm SE = 1.346 ± 0.322 , $P < 0.05$) after controlling for the effects of Treatment and CWM_{fixed} , while ITV_{within} did not account for a significant proportion of the remaining variance (Estimate \pm SE = -0.030 ± 0.037 , $P = 0.408$) after controlling for the effects of Treatment, CWM_{fixed} and ITV_{among} (Fig. 1). During the study period, and after controlling for the Treatment effect, productivity was significantly and positively related to ITV_{among} except in 2014 (Supplementary Fig. S2). In contrast, the effect of ITV_{within} on productivity ranged from no significant effect to a positive effect after controlling for the Treatment effect from 2012 to 2014 (Supplementary Fig. S3). Productivity was significantly and positively related to both community-weighted mean and CWM_{fixed} in each year (Supplementary Fig. S2), while the effect of total variation and TV_{inter} on productivity weakened from 2012 to 2014 (Supplementary Fig. S3).

The best model, accounting for 82.6% of the variance in productivity, involved the treatment and linear functions of $CWM_{fixed} + ITV_{among}$ (Table 1; Supplementary Table S2). Experimentally changing the types of species in the community (the treatment) affected subsequent productivity (Supplementary Table S2). While the treatment accounted for 71.6% of the variance in productivity, the addition of CWM_{fixed} to the

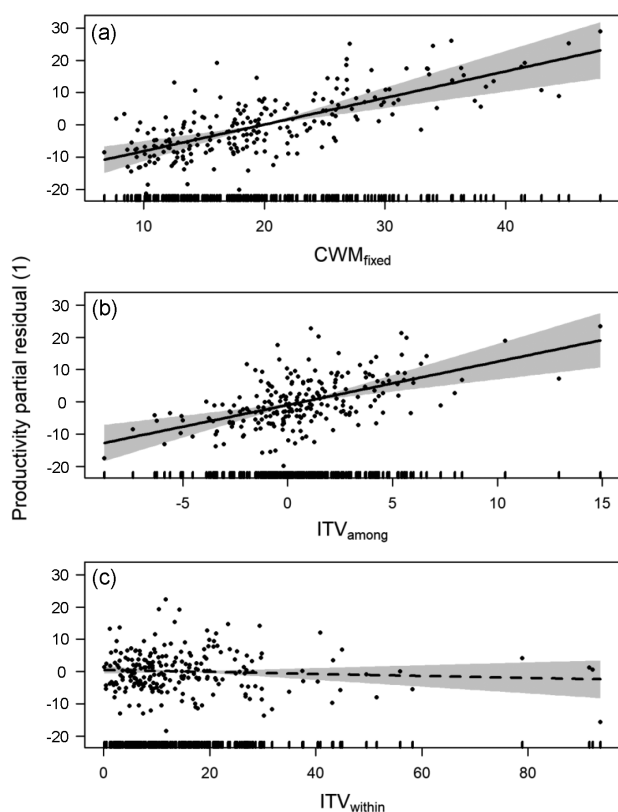


Figure 1: Partial residual plots (i.e. deviations of aboveground biomass production after controlling for other variables) as a function of the three variables identified in the two best-supported generalized additive mixed models used to predict variation in productivity: fixed community-weighted mean (CWM_{fixed} , Estimate \pm SE = 0.799 ± 0.158), intraspecific trait variability among communities (ITV_{among} , Estimate \pm SE = 1.346 ± 0.322) and intraspecific trait variability within communities (ITV_{within} , Estimate \pm SE = -0.030 ± 0.037). Solid lines showed variables having significant effects after controlling the other variables, and dashed lines showing no significant effect. Number in the brackets of the y-axis showed effective degrees of freedom (edf) for the model terms, and the edf equal 1 indicated the model penalized the smooth term to a simple linear relationship.

treatment accounted for an additional 3.5% of variance while adding ITV_{among} to the treatment accounted for an additional 9.1%. Adding both to the treatment resulted in an additional 11% of explained variance in productivity rather than an additional 3.5% + 9.1% since CWM_{fixed} and ITV_{among} shared some common variance (Spearman's $\rho = 0.234$, Supplementary Table S3). Each of these variables was significant predictors of productivity ($P < 0.05$). The second-best model ($\Delta AIC_c = 1.819$) contained these same variables plus a linear function of ITV_{within} , accounting for almost the same proportion of the variance in productivity.

All other models had ΔAIC_c values of >20.610 and could be essentially excluded from consideration. CWM_{fixed} was a significantly positive predictor of productivity (Estimate \pm SE = 0.799 ± 0.158 , $P < 0.05$, Fig. 1) after controlling for Treatment and ITV_{among} ($P < 0.05$). TV_{inter} did not have a significant effect on productivity after controlling for Treatment (Table 1).

The final piecewise SEM explained 79% of the variation in community productivity, which fitted the data adequately (Fisher's $C = 4.49$, $df = 2$, $P = 0.106$, Fig. 2). The presence of the functional group Poaceae and Cyperaceae (A , $\beta = 0.632$, $P < 0.001$), Asteraceae (B , $\beta = -0.160$, $P < 0.001$) and Others (D , $\beta = -0.225$, $P < 0.001$) significantly affect CWM_{fixed} , while the presence of functional group Poaceae and Cyperaceae (A , $\beta = -0.272$, $P = 0.004$) and Others (D , $\beta = 0.179$, $P = 0.005$) significantly affect ITV_{among} . From this final piecewise SEM, while our treatment (i.e. the presence of four functional group) had direct effect on productivity, it also had indirect effect on productivity via plant traits variability (including intraspecific variability). The results of the final piecewise SEM (Fig. 2) and generalized additive mixed model (Fig. 1) were similar, further confirming CWM_{fixed} ($\beta = 0.309$, $P < 0.001$) and ITV_{among} ($\beta = 0.303$, $P < 0.001$) were significantly positive predictors of productivity after controlling for treatment.

DISCUSSION

In recent years, ecologists have endeavored to incorporate functional traits in studies of community ecology. Intraspecific trait variability, which until recently has been largely overshadowed by interspecific trait variability, is receiving increasing interest (Albert *et al.* 2011; Bolnick *et al.* 2011; Siefert *et al.* 2015; Turcotte and Levine 2016; Violle *et al.* 2012). However, until now, most studies have focused on assessing the relative extent of intraspecific trait variability in functional traits (e.g. leaf nitrogen and phosphorus content, height, shoot biomass) compared with interspecific variation under different environmental conditions (Kichenin *et al.* 2013; Lepš *et al.* 2011; Lü *et al.* 2018; Siefert *et al.* 2015; Volf *et al.* 2016), leaving their effects on ecosystem functions largely unknown. In this paper, we partitioned total variability in plant height within each of 75 manipulated communities into two additive parts to assess their relative importance for explaining the

Table 1: The results of two best-supported models and models with four single trait variability indices

Model	df	AIC _c	ΔAIC _c	wAIC _c	R ² _{adj}
~CWM _{fixed} + ITV _{among} + Treatment	20	1550.424	0	0.713	0.826
~CWM _{fixed} + ITV _{among} + ITV _{within} + Treatment	22	1552.242	1.819	0.287	0.825
~ITV _{among} + Treatment	21	1573.853	23.429	<0.001	0.807
~CWM _{fixed} + Treatment	19	1610.265	59.841	<0.001	0.751
~TV _{inter} + Treatment	20	1622.146	71.723	<0.001	0.742
~Treatment	18	1648.390	97.966	<0.001	0.716
~ITV _{within} + Treatment	20	1650.199	99.775	<0.001	0.719

This table comes from the full table shown in [Supplementary Table S2](#), by performing 12 generalized additive mixed models (setting ‘Treatment’ as the ‘null’ model) for productivity as a function of nonlinear terms, i.e. interspecific variability (TV_{inter}), intraspecific variability with community (ITV_{within}), species turnover (CWM_{fixed}) and intraspecific variability among community (ITV_{among}). The horizontal axis is degree of freedom (df), corrected information-theoretic Akaike’s information criterion for small samples sizes (AIC_c), changes in AIC_c relative to the top-ranked model (ΔAIC_c), AIC_c weight (wAIC_c = model probability) and the variance explained by generalized additive mixed models (R²_{adj}, using *gam* function). For performing generalized additive mixed models, we set ‘year’ as random intercepts and slopes. Variable highlighted in bold shows a significant effect ($P < 0.05$). The model with the lowest AIC_c has the most support, models with ΔAIC_c > 3 have relatively little support and models with ΔAIC_c > 7 have essentially no support.

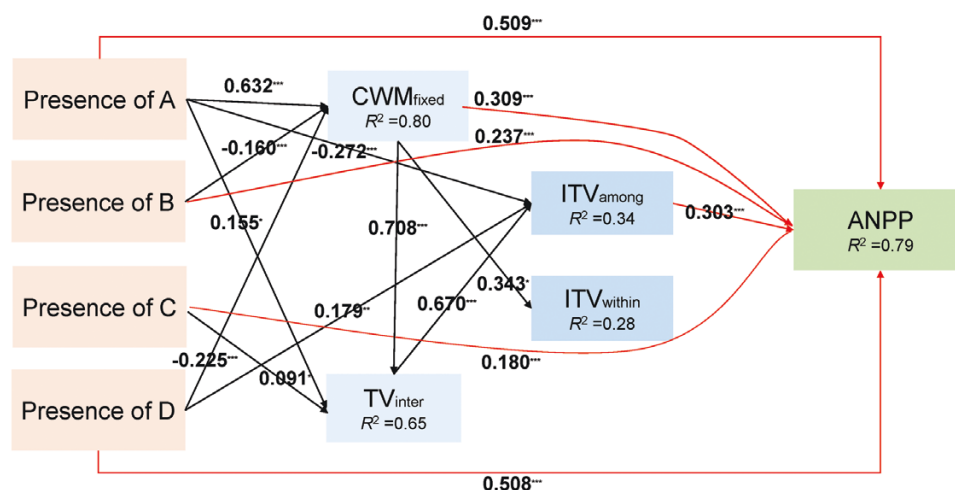


Figure 2: The results of the final piecewise SEM. The final model adequately fit the data: Fisher’s $C = 4.49$, $df = 2$, $P = 0.106$. Red arrows represent significant pathways to explain AN, and black arrows represent significant pathways to explain trait variability indices, respectively. Paths without sufficient statistical evidence are not shown. Numbers on or cross arrows are standardized path coefficients, and asterisks indicate statistical significance (*** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$). R² represents the proportion of variance explained by predictive variables in the model.

variation of productivity in response to functional group removal. This allows us to answer the two questions posed in this paper. First, community productivity does increase with increasing levels of intraspecific trait variation between communities (ITV_{among}) but there is must less evidence for an effect of intraspecific trait variation within a community (ITV_{within}). Second, the combination of intraspecific variability and interspecific variability explains

more variation in productivity than either of these effects alone.

Fixed community-weighted means (CWM_{fixed}) have been widely adopted to examine the functional diversity–community productivity relationship, with traits averaged over a range of environmental conditions (e.g. [Liu et al. 2015](#)), or extracted from a broad trait database ([Cornelissen et al. 2003](#); [Geng et al. 2017](#); [Kleyer et al. 2008](#); [Lepš et al. 2011](#)). The fixed community-weighted mean only

reflects species' average trait values irrespective of the environment (Lepš *et al.* 2011; Siefert *et al.* 2015). In our study site, species from different functional groups possess different typical heights (Fig. 2; Liu *et al.* 2015). Hence, we expected that differences between the experimental functional group removal treatments would lead to different impacts on light acquisition and competition of the remaining plants, and thus community productivity (Bjorkman *et al.* 2018; Westoby 1998). As found in other studies (Chanteloup and Bonis 2013; Fu *et al.* 2014), our results showed that after controlling for these experimental differences, increasing fixed community-weighted mean height (CWM_{fixed}) was associated with increasing productivity, with an increase of 1 cm in CWM_{fixed} of height increased productivity by 0.799 ± 0.158 g/subplot (i.e. 0.196 m^2). The positive relationship between productivity and fixed community-weighted mean height can be explained by the 'selection effect'. That is, communities dominated by taller species will tend to have higher biomass productivities. This is expected both because greater height usually results in greater aboveground biomass in these herbaceous communities and because taller individuals can more easily access light in competition, allowing them to synthesize photosynthetic compounds and then convert them to even more biomass (Anten and Hirose 2001; Falster and Westoby 2003).

More interestingly, the best model and SEM showed that intraspecific variation in height among communities having the same types of species (treatment) and having species with the same average fixed height (i.e. CWM_{fixed}), also resulted in higher productivity, since ITV_{among} was just as important a predictor as the CWM_{fixed} heights. However, the presence of different functional groups affected ANPP through different indirect pathways, i.e. via CWM_{fixed} and/or ITV_{among} (Fig. 2), suggesting ANPP variation mainly caused by selecting higher species and/or species who could grow higher. An increase in the difference between the intraspecific height of a species among subplots relative to its average height (ITV_{among}) of 1 cm increased the productivity by 1.346 ± 0.322 g/subplot (i.e. 0.196 m^2). The occurrence of a positive effect of intraspecific variability in plant height on productivity may reflect a 'shade-avoidance syndrome'. That is, all individuals, especially shaded individuals would invest a large amount of energy into stem elongation, resulting in increasing height of different species (Roscher *et al.* 2015). This intraspecific selection is presumably

some combination of genetic selection and phenotypic plasticity although we cannot separate the two sources in our study. The effect of ITV_{among} on productivity ranged from significantly positive to nonexistent after controlling for the Treatment effect from 2012 to 2014, which might suggest that the possibility of higher productivity caused by selecting taller individuals of the same species had been used up over the first 3 years.

We found that TV_{inter} (i.e. height variation among species within a community) was not included in the two best models, and ITV_{within} (i.e. height variation within species within a community) showed no significant effects on productivity although it was included in the second-best model. Increased productivity with ITV_{within} and TV_{inter} may result from structural complexity (e.g. canopy rugosity, Gough *et al.* 2019), which led to increased light acquirement and light use efficiency via greater space filling and higher occupy of light environment. However, from 2012 to 2014, the effect of ITV_{within} on productivity ranged from no significant effect to a positive effect, and the effect of TV_{inter} varied from significantly positive to nonexistent after controlling for the Treatment effect. This may suggest that the positive effect of intraspecific height difference on productivity became increasingly important over time. Thus, it would also be important to study the response of other traits that plastically respond to light intensity, and how this phenotypical plasticity contributing to ecosystem functioning.

Although both intraspecific variability and interspecific variability positively contributed to productivity, the combination of them explained more variation in productivity than either of these effects alone in our study. This suggests that both selection effect and a 'shade-avoidance syndrome' could incur higher CWM_{fixed} or ITV_{among} , and even niche differentiation induced structural complexity that could cause higher ITV_{within} , may simultaneously operate to regulate productivity in this study.

In conclusion, this study shows that the additional explanatory power of intra- and interspecific trait variability in height are comparable in magnitude. It provides new evidence that intraspecific trait variability in plant height should not be ignored when predicting productivity. Future studies considering more than one trait to quantify intraspecific trade-offs among life-history constraints between traits may largely broaden our understanding of the importance of intraspecific trait variability in maintaining ecosystem functions. Simultaneously, disentangling and quantifying relative

importance of genetic and environmental sources of intraspecific trait variability may help us understand evolutionary and ecological responses of species and communities to climate change.

Supplementary Material

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

Table S1: List of the abbreviations of trait variability metrics used in the analyses, and the study.

Table S2: Phase I shows the results of generalized additive mixed models between productivity and functional groups removal treatment (Treatment), the number of functional groups, species richness, Shannon's evenness index, Simpson index, phylogenetic diversity in the year of 2012–14 (year as random effects, i.e. both random intercept and random slope).

Table S3: Spearman's correlation matrix for raw input variables.

Figure S1: Initial causal model for piecewise structural equation modelling (SEM) exploring the effects the presence of functional group Poaceae and Cyperaceae (A), Asteraceae (B), Fabaceae (C) and Others (D), fixed community-weighted mean (CWM_{fixed}), interspecific trait variation within a community (TV_{inter}), intraspecific trait variability among communities (ITV_{among}) and intraspecific trait variability within communities (ITV_{within}) on community net primary productivity (ANPP) in the removal experiment from 2012 to 2014. Figure S2: Partial residual plots of trait variabilities among communities (Specific averages (community-weighted mean), species turnover (CWM_{fixed}) and intraspecific variability (ITV_{among})) in the generalized additive models to predict variation in productivity after controlling for Treatment difference in 2012, 2013 and 2014, respectively. Figure S3: Partial residual plots of trait variabilities within communities (total variation, interspecific variability (TV_{inter}) and intraspecific variability (ITV_{within})) in the generalized additive models to predict variation in productivity after controlling for Treatment differences in 2012, 2013 and 2014, respectively.

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Authors' Contributions

S.Z. conceived and designed the study. L.Z., X.L., B.S. and S.Z. analyzed the data and wrote the manuscript. All authors approved the final manuscript.

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