



Species with moderate intraspecific trait variability are locally abundant within an environmentally heterogeneous subtropical forest

Guochun Shen^{1,4} · En-Rong Yan^{1,2} · Avi Bar-Massada³ · Jian Zhang¹ · Heming Liu¹ · Xihua Wang¹ · Mingshan Xu¹

Received: 8 May 2018 / Accepted: 11 June 2019 / Published online: 18 June 2019
© Springer-Verlag GmbH Germany, part of Springer Nature 2019

Abstract

Species with large intraspecific trait variability (ITV) have larger niche breadth than species with low ITV and thus are expected to be more abundant at the local scale. However, whether the positive ITV–abundance relationship holds in heterogeneous local environments remains uncertain. Using an individual-based trait dataset encompassing three leaf traits (leaf area, specific leaf area, and leaf dry mass content) of 20,248 individuals across 80 species in an environmentally heterogeneous subtropical forest in eastern China, ITV for each trait of each species was estimated by rarefaction. Resource-based niche breadth and marginality (the absolute distance between the mean resource states used by a species and the mean plot-wise resource states) were estimated simultaneously by the K–S method and the outlying mean index, respectively. Species with moderate ITV were often locally abundant, while species with large or small ITV were locally rare. This unimodal relationship between ITV and species abundance persisted when traits were analyzed separately and for all tree size classes. There was also a hump-backed relationship between niche breadth and marginality, and ITV was positively associated with niche breadth. The combined results suggest either a trade-off between the benefit from expanding niche breadth to adapt to multiple habitats and the disadvantage of reducing competitive ability, or a scarcity of favorable resources. Our results do not support the traditional thought that ITV positively correlates with species abundance in heterogeneous local environments. Instead, our study suggests that moderate—rather than large—intraspecific trait variability increases species abundance at local scales.

Keywords Commonness and rarity · Trait-based ecology · Niche breadth and marginality · Unimodal relationship

Communicated by Jonathan A. Myers.

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s00442-019-04437-6>) contains supplementary material, which is available to authorized users.

✉ En-Rong Yan
eryan@des.ecnu.edu.cn

- ¹ Zhejiang Tiantong Forest Ecosystem National Observation and Research Station, Putuo Station for Island Ecosystem Research, School of Ecological and Environmental Sciences, East China Normal University, Shanghai 200241, China
- ² Institute of Eco-Chongming (IEC), 3663 N. Zhongshan Rd., Shanghai 200062, China
- ³ Department of Biology and Environment, University of Haifa at Oranim, 36006 Kiryat Tivon, Israel
- ⁴ Shanghai Institute of Pollution Control and Ecological Security, 1515 North Zhongshan Rd. (No. 2), Shanghai 200092, China

Introduction

Natural communities tend to be composed of a few common species and many rare ones (McGill et al. 2007). Understanding this universal pattern has long been a central focus in community ecology (Preston 1948) and many related hypotheses have been proposed (MacArthur 1957; Preston 1962; May 1973; Hubbell 2001; Harte et al. 2008). However, what causes a given species to be common or rare is still debated (Kunin and Gaston 1993; Umaña et al. 2015) and understanding the mechanisms behind this pattern is essential for the conservation of rare species and the control of invasive species (Hubbell and Foster 1986).

Understanding intraspecific trait variability (ITV) is a promising avenue for exploring the specific mechanisms behind species abundance patterns (Violle et al. 2012). The magnitude of ITV is comparable to interspecific variation in plant traits (Albert et al. 2010a, b; Jung et al. 2010; Messier et al. 2010) and is commonly assumed to be positively

related to species niche breadth (Svanback and Bolnick 2007; Clark 2010; Bolnick et al. 2011; Hart et al. 2016). Thus, species with large ITV can tolerate a diverse array of resource states (Brown 1984) and consequently, may become abundant in heterogeneous environments. This positive relationship between species ITV and abundance has been proposed for a long time (Gaston et al. 1997), though whether it holds in heterogeneous local environments remains unclear.

The uncertainty about the positive relationship between ITV and abundance is driven by the fact that local abundance is influenced not only by niche breadth, but also the total amount of any given resource state available to a species (Marsden and Whiffin 2003). This means that a broad niche, which might be manifested by large ITV, does not necessarily lead to high abundance in heterogeneous local environments. For example, species with large geographic ranges are considered to have a broader niche, but many of them are neither dominant nor abundant in a local community with heterogeneous environments (Boulangeat et al. 2012). A large niche breadth for a given species merely suggests that it is more likely to colonize and persist in various abiotic environments; it does not guarantee that it can establish and persist in habitats in which the availability of favorable resources is limited.

The possible effects of resource availability on local species abundance can be partially inferred from the patterns of species niche breadth and marginality (the absolute distance between the mean resource states used by a species and the mean plot-wise resource states) (Dolédec et al. 2000). Specifically, if resource availability has no significant effect on local species abundance, species with large niche breadths—irrespective of their marginality—can occupy more resource states and are more likely to be abundant in a local community. Thereby no relationship between niche breadth and marginality is expected. On the other hand, if resource availability strongly affects local abundance, species with small niche breadth might be more limited by the scarcity of favorable resources and thereby may have large niche marginality and low abundance. Under this case, if resource availability impacts species abundance significantly enough, species with small niche breadth might have large niche marginality, thus resulting in a negative relationship between species niche breadth and marginality.

Therefore, the relationships between species ITV and abundance in heterogeneous local environments depend on the assumption of two key relationships. The first is the relationship between ITV and niche breadth; the second is between niche breadth and marginality. Surprisingly, almost no studies have simultaneously examined these two relationships with respect to the relationship between ITV and local abundance, possibly because of the difficulty in collecting detailed data on ITV for an entire local community and environmental data at a fine spatial scale. Here, we used an

individual-based trait dataset for all 20,248 individuals of 80 woody plant species that inhabit a 5-ha subtropical forest, coupled with data on the abiotic environment, to quantify and model the relationship between species ITV and abundance, and to verify the above two relationships.

Materials and methods

Site description

This study was conducted in an evergreen broad-leaved forest at the Tiantong National Forest Park (29°48.817'N, 121°47.116'E) in Zhejiang Province, East China. This region has a typical subtropical monsoon climate with a hot, humid summer and a drier, cold winter. Annual mean air temperature is 16.2 °C and the lowest temperature is −8.8 °C (few cases). The warmest and coldest months are July and January with 28.1 °C and 4.2 °C monthly mean temperatures, respectively. Mean annual precipitation is 1374.7 mm, falling mostly between May and August (Yan et al. 2018). In 2010, a 20-ha forest plot was established in the core area of the park. All freestanding individuals with a diameter at breast height (DBH) \geq 1 cm in the plot were tagged, identified, measured, and mapped. The topography of the plot was mapped before the plant survey. Four topographical variables (mean elevation, mean convexity, mean slope, and mean aspect) were calculated for 20 \times 20 m quadrats encompassing the entire plot, using methods described in Harms et al. (2001). In 2011, soil nutrients (total C, total N, and total P) and soil pH values of the whole 20-ha plot were sampled and analyzed using standard protocol (Zhang et al. 2012).

Trait plot and species abundance

A 5-ha trait plot was established within the 20-ha plot. It comprised 125 adjacent 20 \times 20 m subplots in a roughly 220 \times 220 m region (Fig. S1). The abiotic environment in the 5-ha trait plot was very heterogeneous and this variation in abiotic conditions has significant impact on the spatial distributions of most measured leaf traits in the plot (Yan et al. 2018). The trait plot contained 20,248 individuals (DBH \geq 1 cm) belonging to 108 tree species. The abundance of each species was determined by counting the total number of individuals (DBH \geq 1 cm) in the 5-ha plot.

Trait measurements of individual trees

For each one of 20,248 individuals in the 5-ha trait plot, we measured three functional leaf traits: leaf area (LA), specific leaf area (SLA), and leaf dry mass content (LDMC). Specifically, we randomly sampled 20 mature and healthy leaves from three canopy branches in different orientations

from each individual and aggregated them into a single value for each trait. We scanned these leaves using a leaf area meter (LI-3100C, Li-Cor, USA) to determine LA (cm²) and weighed them immediately to quantify leaf wet mass (g). Finally, we dried leaf samples in an oven for 48 h at 75 °C and weighed them to obtain leaf dry mass (g). We calculated LDMC as the ratio between leaf dry mass and leaf wet mass, and SLA as the ratio of LA to leaf dry mass. Although these traits do not represent the full spectrum of plant function, they are robust indicators of some leading dimensions of plant ecological strategies, such as light capture (LA) and leaf economics spectrum (SLA and LDMC) (Westoby et al. 2002). Other functional traits such as seed mass and wood density would also be informative, but are difficult and expensive to collect.

Estimation of intraspecific trait variability

Because of the variation in species abundance, rarefaction is commonly used to generate comparable estimates of ITV across species. All traits were scaled to fit the range from 0 to 1. Specifically, out of 108 available species, 80 species with five or more individuals were selected. Then we randomly sampled five individuals without replacement and calculated the variance of trait values among them. The procedure was repeated 999 times to generate an index of mean trait variation for each trait and species. To rule out the effect of including species with relatively low abundance in the analysis, we repeated all analyses using a subset of 29 species which had at least 100 individuals. The results of both analyses were qualitatively similar (Figs. S3, S4), and therefore in the following sections we only present results that are based on the analysis of 80 species. In order to test whether a similar relationship between ITV and species abundance exists across different DBH size classes, we divided the entire tree in the 5-ha plot into three size groups: small trees ($1 \leq \text{DBH} < 3$ cm), medium trees ($3 \leq \text{DBH} < 10$ cm), and large trees ($\text{DBH} \geq 10$ cm). Again, we used rarefaction to calculate the mean variance of each trait for each species in each size group.

Estimation of species niche breadth and marginality

For each species, we estimated realized niche breadth (hereafter called niche breadth for simplicity) and marginality based on the interpolated soil (total C, total N, total P, and pH value) and topography (mean elevation, mean convexity, mean slope, and mean aspect) characteristics (hereafter called habitat for simplicity) at the location of each individual in the 5-ha plot. Although topography characteristics are not directly consumed by tree species, they can largely reflect spatial distributions of other unobserved resources in the 5-ha plot, and thus may help to accurately quantify

species niche breadth and marginality. Specifically, all environmental variables were centered and scaled with zero mean and one standard error. To avoid possible collinearity among environmental variables, estimations of niche breadth and marginality were based on principal components of the eight variables. We quantified the niche breadth of each species using the K–S method (Potts et al. 2004), which reflects the degree of available resource space utilized by a species. Specifically, given a species and the habitat occupied by each individual, we calculated the cumulative sample distribution $P(x)$; the proportion of individuals whose habitat value is less than or equal to x . Meanwhile, $P'(x)$ represented the available habitat space and was calculated by a random sample of 1000 points in the 5-ha plot. Niche breadth is then defined as twice the area between the curve formed by the pairs of points (P, P') and either the P or P' axis. We chose this method mainly because it can fully utilize individual-based community data and high-resolution environment data (John et al. 2007). By comparing $P(x)$ and $P'(x)$, the K–S method estimated species niche breadth by accounting for the availability of habitats. Species niche marginality (also called niche position) was quantified by using the outlying mean index (Dolédec et al. 2000), which calculates the absolute distance between the mean habitat conditions used by all individuals of a species and the mean plot-wise habitat conditions. Species with high values of marginality have marginal niche and low density of available resources. Species with low values of marginality have non-marginal niche and can utilize habitats with high resource availability. For each soil and topography characteristic, we calculated niche breadth and marginality for each species. Mean niche breadth and mean marginality for a species were also defined as the arithmetic mean of all niche breadths and all marginalities of that species in all available habitats, respectively.

Verification of expected relationships among ITV, niche breadth, marginality, and species abundance

Quadratic regressions were used to quantify the relationship between mean ITV of all measured traits and niche breadth, niche breadth and marginality, and mean ITV and species abundance. We applied the same method to quantify the relationships between ITV of each measured trait and species abundance for all individuals and for each size group. Additionally, we used linear and quadratic equations to estimate the global relationship between intraspecific trait variability (ITV) and species abundance.

To quantify the relative strength and type of the relationships across species abundance, ITV, niche breadth, and marginality, we used a structural equation model (SEM). The initial SEM contained all possible correlations among these variables and was selected for each significant path based on the AIC of the model, as well as the P value of each

regression coefficient. We used a Chi-square test, the comparative fit index (CFI), the Tucker–Lewis index (TLI), the root mean square error of approximation (RMSEA), and the standardized root mean square residual (SRMR) to evaluate the goodness-of-fit of the model.

We conducted all analyses in R software (version 3.2.4) (R Core Team 2017). SEM parameters were estimated using the R package “lavaan” (Rosseeel 2012).

Results

As we expected, species with large ITV generally had a large habitat-based niche breadth in our studied plot (Fig. 1). We also found a significant convex relationship between niche

breadth and marginality (Fig. 2), which was inconsistent with our expectation. In addition, we observed a significant unimodal relationship between species abundance and ITV of each trait (Fig. 3). The same pattern persisted when mean ITV of three traits was analyzed (Fig. S3) for all three tree size classes (Fig. S4). Model comparison showed that the unimodal model for $\log(\text{ITV})$ and $\log(\text{abundance})$ (i.e., M2 in Table 1, $y = -0.67x^2 - 1.96x + 3.23 = -0.67(x + 1.46)^2 + 4.66$, $-2.67 \leq x \leq 0.97$, $\text{AIC} = 289.8$) was essential (c_2 , the coefficient of quadratic term ITV^2 was significantly negative and the x value of the maxima was within the range of x , implying a local maxima) and was superior (ANOVA test, $\Delta\text{AIC} = 5.8$, P value < 0.01 , $df = 78$) to the simple linear model M1 (Table 1).

Fig. 1 Relationship between natural log-transformed intraspecific trait variability (ITV) and species resource-based niche breadth. Each point is the observed ITV and niche breadth for one species in the 5-ha stem-mapped plot. The solid line is the quadratic regression line (slope = 0.003, P value < 0.01 ; intercept = 0.85, P value < 0.01 ; $R^2_{\text{adjusted}} = 0.123$). The grey area is the 95% confidence interval of the regression line

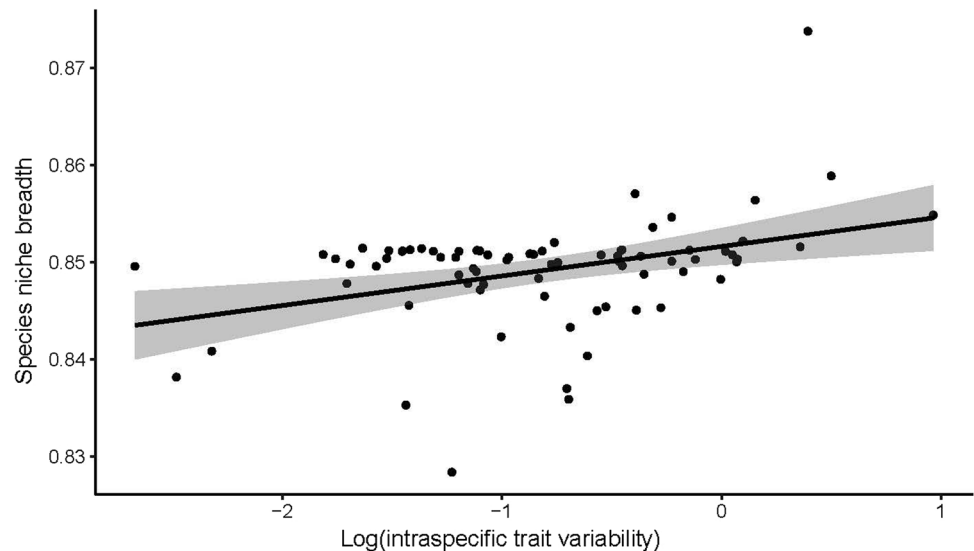
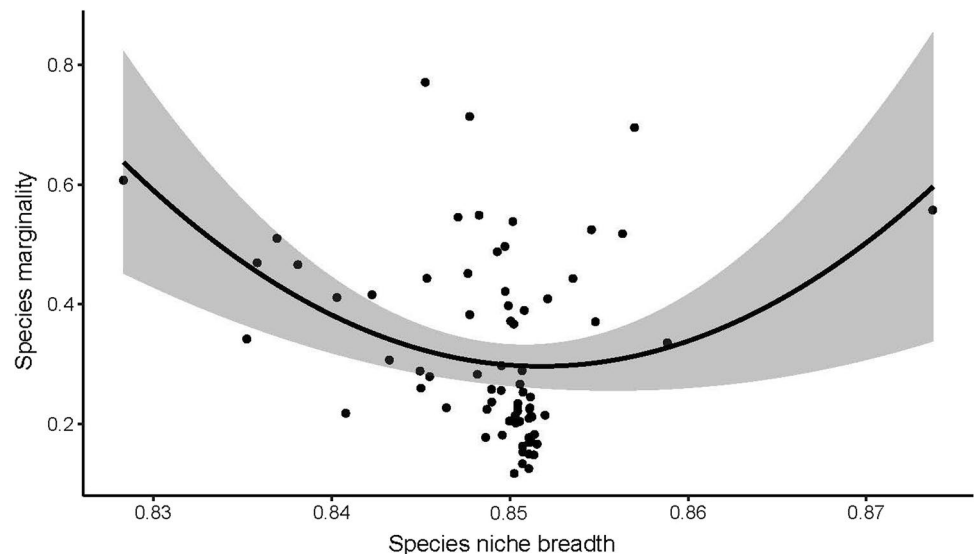


Fig. 2 Relationship between species mean niche breadth and marginality. Marginality is calculated as the absolute distance between the mean resource states used by a species and the mean plot-wise resource states. Each point is the observed niche breadth and marginality for one species in the 5-ha stem-mapped plot. The line is the quadratic regression line (coefficient of quadratic term: 0.49, P value < 0.01 ; $R^2_{\text{adjusted}} = 0.129$) with a 95% confidence interval



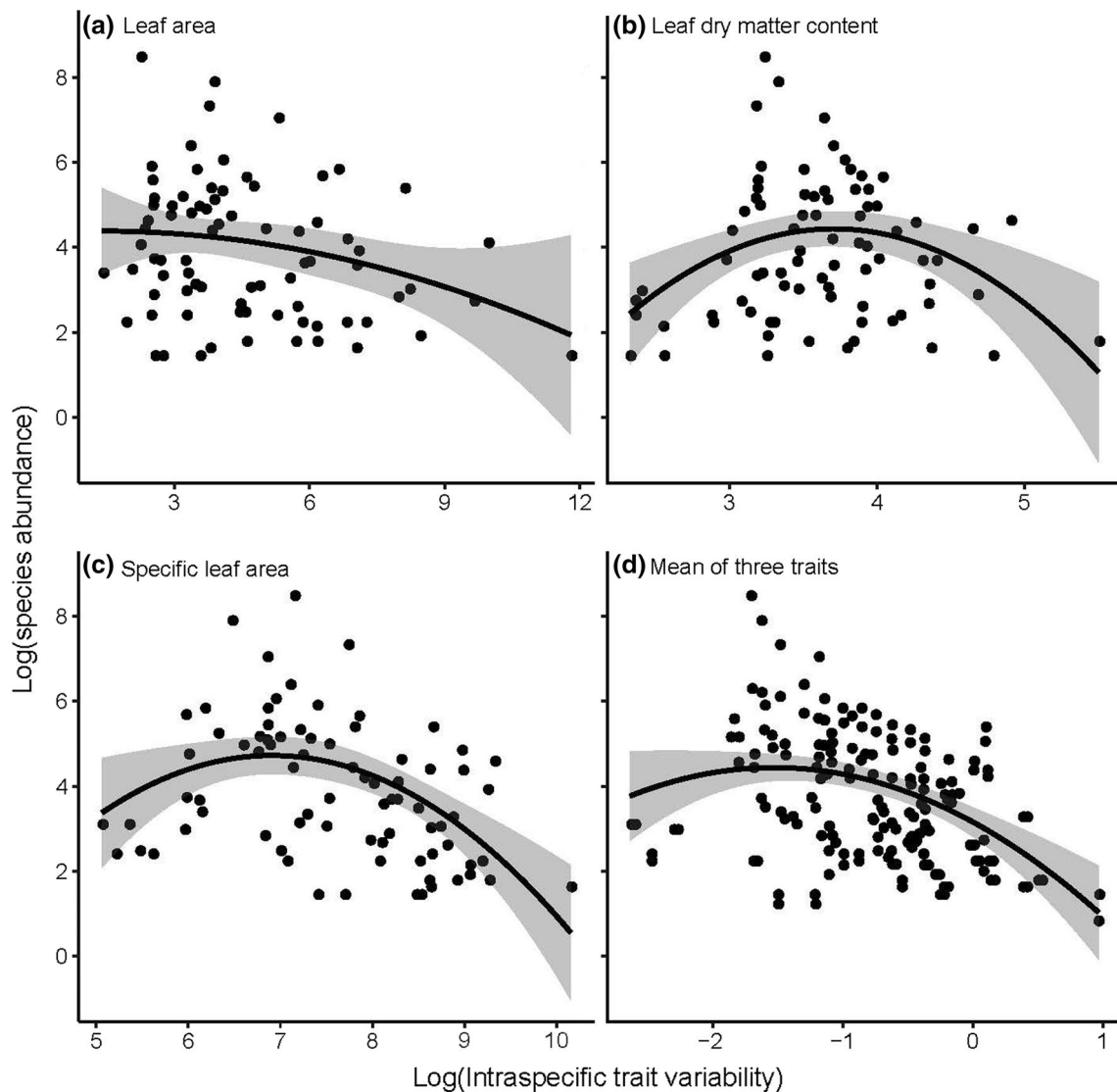


Fig. 3 Relationships between natural log-transformed intraspecific trait variability (ITV) of **a** leaf area (LA), **b** leaf dry matter content (LDMC), **c** specific leaf area (SLA), **d** mean ITV of the three traits and species abundance in the 5-ha stem-mapped plot. Each point is

the corresponding observed value for one species. Solid lines are the quadratic regression lines. The grey areas are the 95% confidence intervals of the regression lines

Table 1 Estimated parameters and goodness-of-fit of linear equation and quadratic equation to modal relationship between intraspecific trait variability (ITV, $-2.67 \leq \ln(\text{ITV}) \leq 0.97$) and species abundance in the 5-ha Tiantong stem-mapped plot

Name	Model	Parameter	Estimate	SE	<i>P</i>	AIC
M1	$\log(\text{Abundance}) = a_1 + b_1 \times \log(\text{ITV})$	a_1	3.43	0.27	<0.001	295.6
		b_1	-0.78	0.25	0.003	
M2	$\log(\text{Abundance}) = a_2 + b_2 \times \log(\text{ITV}) + c_2 \times \log(\text{ITV})^2$	a_2	3.23	0.27	<0.001	289.8
		b_2	-1.96	0.49	<0.001	
		c_2	-0.67	0.24	0.006	

The structural equation model successfully captured these relationships among species abundance, ITV, niche breadth,

and marginality (Fig. 4). Consistent with the independent analyses shown above, nonlinear relationships across ITV

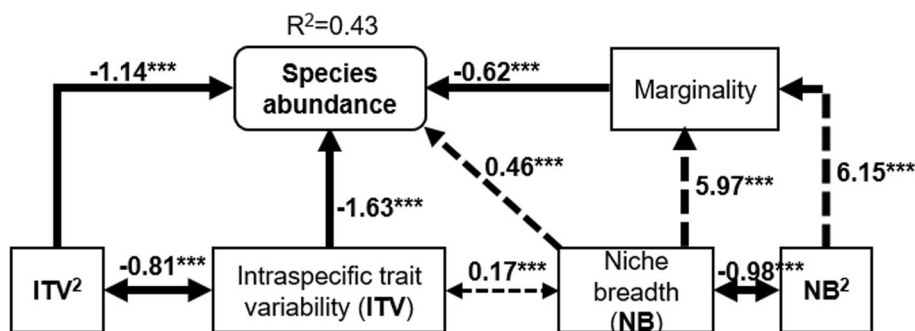


Fig. 4 The best-fitted structural equation model relating species abundance to intraspecific trait variability (ITV), square of ITV (ITV²), niche breadth (NB), square of NB (NB²), and marginality in heterogeneous local environments. All of these variables were log-transformed and standardized before analysis. The width of each path represents the strength of each positive (dashed line) or negative (solid

line) relationship. For each path the standardized regression coefficient and its significance level (*** P value ≤ 0.01 ; ** P value ≤ 0.05 ; * P value ≤ 0.1) are given. Non-significant (P value > 0.1) paths are not shown. R^2 is the adjusted R^2 of regression between species abundance and other variables

and species abundance, niche breadth, and marginality were superior to the simple linear relationship (the ITV² and NB² terms remained in the best-fitted SEM). Moreover, the SEM showed that species ITV positively correlated with niche breadth and indirectly and complexly linked with species niche marginality. ITV, together with niche breadth and marginality, explained 43% of the variation of species abundances in the studied plot.

Discussion

We found that tree species with moderate ITV were often locally abundant, and species with large or small ITV were locally rare in a topographically heterogeneous forest plot. This pattern is consistent with a few other studies (Cleavitt 2002; Heino et al. 2009; Dostál 2011; Siqueira et al. 2012) that find rare species do not have a higher level of environmental specialization than abundant species, but do not support expectations about the positive relationship between species ITV and abundance under heterogeneous local environments. This study extends the test of the relationship between ITV and local abundance from the seedling stage in homogeneous environments (Umaña et al. 2015) to the juvenile and adult stages in highly heterogeneous environments.

The observed convex relationship between niche breadth and marginality hints that other factors, other than resource availability, may simultaneously determine the relationship between ITV and local abundance. One possible factor not considered in our study is competition, which is often regarded as an important regulator of species abundance (Volterra 1928; Lotka 1932; Rabinowitz et al. 1984; McGill et al. 2006). According to the hypothesis of tolerance–dominance trade-offs between generalists and specialists (Wisheu 1998), a species cannot simultaneously occupy

and competitively dominate in all types of habitats (Boulangeat et al. 2012). If species with large ITV have large niche breadths, and if large niche breadths lead to low competitive ability (Violle et al. 2010), those species may have a large marginality and a low abundance in heterogeneous local environments. In other words, species with large ITV may have a trade-off with mean competitive ability, thus resulting in low local abundance (Boulangeat et al. 2012). To be abundant in heterogeneous local environment, species need to balance the benefit from being able to establish in many different habitats (due to their large niche breadth) and the disadvantage from reducing competitive ability by increasing ITV. This balance may eventually contribute to the convex relationship between niche breadth and marginality, as well as the unimodal relationship between ITV and abundance at the local scale.

The abundance of a species at the local scales also depends on the extent to which each habitat or resource type in a given heterogeneous environment is available to that species (Gregory and Gaston 2000). The resource availability hypothesis states that species with low ITV can finely adapt their traits to the available resources, and these resources are themselves more widely distributed in space or at a higher frequency than these resources utilized by other species (Marsden and Whiffin 2003). As a result, specialized species with low ITV could have more total available habitats to be utilized and thus higher overall abundance. However, species with too little ITV will be directly filtered out by most types of abiotic environments while species with too large ITV will be competitively driven away from the most suitable and common environments (Walker 2006). Therefore, our results emphasize that both niche breadth and marginality should be simultaneously considered to understand the unimodal relationship between species ITV and local abundance in natural communities.

We note that, in this study, niche breadths were measured by using Potts's method (2004), which have been used in other studies with similar data (John et al. 2007; Baldeck et al. 2013). However, when Dolédec et al.'s (2000) measure of niche breadth was used, we detected weak relationships of niche breadth with each of ITV (Fig. S5) and marginality (Fig. S6). These inconsistent patterns indicate that our results were sensitive to the selection of niche breadth measures. This is a common problem with method dependent results and the selection of methods often depends on the characters of collected data and methods (Wiegand et al. 2013). We chose Potts' method in this study mainly because our plant trait data are individual-based. In addition, spatial information of individuals and the high-resolution environmental maps can be fully utilized by using the Potts' measure. If we apply Dolédec's measure of niche breadth, our individual-based data should be transformed to quadrat-based data. Unavoidably, this approach results in information loss of individual locations and associated environment conditions; thus it may bias the estimation of niche breadth. Moreover, quadrat-based method will inevitably face another difficulty in the choice of quadrat sizes. Different quadrat sizes might lead to different estimations of niche breadth.

We acknowledge that other ecological processes such as dispersal ability, neighborhood crowding, random disturbance, and fecundity may also be important for local species abundance (Kunin and Gaston 1997; Rünk et al. 2009; Zambrano et al. 2017) and thus may contribute to the large variation among species with the same ITV (Fig. 3). Another potential limitation of our study is that all of the traits selected relate to light capture, yet most niche axes measured are essentially soil-related. This discrepancy may weaken our ability to find strong relationships among ITV, niche breadth, and marginality, although an abundance of tree species in heterogeneous environments will not only be affected by light, but also all other soil-related resources and conditions. Moreover, different total counts of individuals among species represent different upper-limits of trait sample sizes, thus the precision of ITV is generally lower for species with fewer individuals. This unbalanced precision of ITV among species can result in large ITV variation among species with low abundance and may contribute to the unimodal relationship between ITV and species abundance. Correction for these potential biases seems extremely difficult currently, because no general theoretical correction has been found for arbitrary probability distribution of trait values. Therefore, caution is needed in the interpretation of the unimodal patterns found in this study.

In summary, our study is among the first to empirically test how asymmetry in the magnitude of ITV links the abundance of tree species in an environmentally heterogeneous forest. We showed that locally abundant tree species were those species with moderate ITV. This pattern does not

support the common thought that ITV positively correlates with species abundance in locally heterogeneous environments. The hump-backed relationship between niche breadth and marginality, and the positive ITV–niche breadth relationship together shed light on our understanding of why species with moderate ITV are locally abundant. In addition, our study suggests that moderate—as opposed to large—intraspecific trait variability increases species abundance at local scales.

Acknowledgements We are grateful to Qun Song and Xiangcheng Mi for their constructive comments on the study. We also thank Min Guo, Qiang Zhong, Meng Kang, Yue Xu, Yilu Xu, Xiaodong Yang, Haixia Huang, Zhihao Zhang, Baowei Sun, Wenji Ma, Qingru Shi, Yantao Zhao, Liuli Zhou, Qingqing Zhang, Arshad Ali and many others for making this fantastic trait data available. Equipment used in this study was supported by ECNU Multifunctional Platform for Innovation (008).

Author contribution statement GS and ERY contributed equally to the study design, analyses, and manuscript drafting. ABM, JZ, HM, XW, and MX contributed substantially to revisions.

Funding This study was supported by the National Key Research and Development Program (2016YFC0503102 to G.C.S) and the National Natural Science Foundation of China (31870404 and 31470487 to G.S., and 31670438 and 31770467 to E.R.Y.).

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict interest.

References

- Albert CH, Thuiller W, Yoccoz NG, Douzet R, Aubert S, Lavorel S (2010a) A multi-trait approach reveals the structure and the relative importance of intra- vs. interspecific variability in plant traits. *Funct Ecol* 24:1192–1201. <https://doi.org/10.1007/s00442-017-4042-x>
- Albert CH, Thuiller W, Yoccoz NG, Soudant A, Boucher F, Saccone P, Lavorel S (2010b) Intraspecific functional variability: extent, structure, and sources of variation. *J Ecol* 98:604–613. <https://doi.org/10.1111/j.1365-2745.2010.01651.x>
- Baldeck CA, Kembel SW, Harms KE, Yavitt JB, John R, Turner BL, Chuyong GB, Kenfack D, Thomas DW, Madawala S, Gunatilleke N, Gunatilleke S, Bunyavejchewin S, Kiratiprayoon S, Yaacob A, Nur S, Mohd N, Valencia R, Navarrete H, Davies SJ, Hubbell SP, Dalling JW (2013) A taxonomic comparison of local habitat niches of tropical trees. *Oecologia* 173:1491–1498. <https://doi.org/10.1007/s00442-013-2709-5>
- Bolnick DI, Amarasekare P, Araújo MS, Bürger R, Levine JM, Novak M, Rudolf VW, Schreiber SJ, Urban MC, Vasseur D (2011) Why intraspecific trait variation matters in community ecology. *Trends Ecol Evol* 26:183–192. <https://doi.org/10.1016/j.tree.2011.01.009>
- Boulangeat I, Lavergne S, Es JV, Garraud L, Thuiller W (2012) Niche breadth, rarity and ecological characteristics within a regional flora spanning large environmental gradients. *J Biogeogr* 39:204–214. <https://doi.org/10.1111/j.1365-2699.2011.02581.x>

- Brown JH (1984) On the relationship between abundance and distribution of species. *Am Nat* 124:255–279. <https://doi.org/10.1086/284267>
- Clark JS (2010) Individuals and the variation needed for high species diversity in forest trees. *Science* 327:1129–1132. <https://doi.org/10.1126/science.1183506>
- Cleavitt NL (2002) Stress tolerance of rare and common moss species in relation to their occupied environments and asexual dispersal potential. *J Ecol* 90:785–795. <https://doi.org/10.1046/j.1365-2745.2002.00713.x>
- Dolédec S, Chessel D, Gimaret-Carpentier C (2000) Niche separation in community analysis: a new method. *Ecology* 81:2914–2927. <https://doi.org/10.2307/177351>
- Dostál P (2011) Plant competitive interactions and invasiveness: searching for the effects of phylogenetic relatedness and origin on competition intensity. *Am Nat* 177:655–667. <https://doi.org/10.1086/659060>
- Gaston KJ, Blackburn TM, Lawton JH (1997) Interspecific abundance range size relationships. An appraisal of mechanisms. *J Anim Ecol* 66:579–601. <https://doi.org/10.2307/5951>
- Gregory RD, Gaston KJ (2000) Explanations of commonness and rarity in British breeding birds: separating resource use and resource availability. *Oikos* 88:515–526. <https://doi.org/10.1034/j.1600-0706.2000.880307.x>
- Harms KE, Condit R, Hubbell SP, Foster RB (2001) Habitat associations of trees and shrubs in a 50-ha neotropical forest plot. *J Ecol* 89:947–959. <https://doi.org/10.1046/j.0022-0477.2001.00615.x>
- Hart SP, Schreiber SJ, Levine JM (2016) How variation between individuals affects species coexistence. *Ecol Lett* 19:825–838. <https://doi.org/10.1111/ele.12618>
- Harte J, Zillio T, Conlisk E, Smith A (2008) Maximum entropy and the state-variable approach to macroecology. *Ecology* 89:2700–2711. <https://doi.org/10.1890/07-1369.1>
- Heino J, Bini LM, Karjalainen SM, Mykrä H, Soininen J, Vieira LCG (2009) Geographical patterns of micro-organismal community structure: are diatoms ubiquitously distributed across boreal streams? *Oikos* 119:129–137. <https://doi.org/10.1111/j.1600-0706.2009.17778.x>
- Hubbell SP (2001) The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton
- Hubbell S, Foster R (1986) Commonness and rarity in a neotropical forest: implications for tropical tree conservation. In: Soule ME (ed) *Conservation biology: the science of scarcity and diversity*. Sinauer Associates Inc, Massachusetts, pp 205–231
- John R, Dalling JW, Harms KE, Yavitt JB, Stallard RF, Mirabello M, Hubbell SP, Valencia R, Navarrete H, Vallejo M, Foster RB (2007) Soil nutrients influence spatial distributions of tropical tree species. *Proc Natl Acad Sci USA* 104:864–869. <https://doi.org/10.1073/pnas.0604666104>
- Jung V, Violle C, Mondy C, Hoffmann L, Muller S (2010) Intraspecific variability and trait-based community assembly. *J Ecol* 98:1134–1140. <https://doi.org/10.1111/j.1365-2745.2010.01687.x>
- Kunin WE, Gaston KJ (1993) The biology of rarity: patterns, causes, and consequences. *Trends Ecol Evol* 8:298–301. [https://doi.org/10.1016/0169-5347\(93\)90259-R](https://doi.org/10.1016/0169-5347(93)90259-R)
- Kunin WE, Gaston KJ (1997) The biology of rarity: causes and consequences of rare-common differences. Springer, Surrey
- Lotka AJ (1932) The growth of mixed populations: two species competing for a common food supply. *J Wash Acad Sci* 22:461–469. <https://doi.org/10.1007/978-3-642-50151-7>
- MacArthur RH (1957) On the relative abundance of bird species. *Proc Nat Acad Sci USA* 43:293–295. <https://doi.org/10.1073/pnas.43.3.293>
- Marsden SJ, Whiffin M (2003) The relationship between population density, habitat position and habitat breadth within a neotropical forest bird community. *Ecography* 26:385–392. <https://doi.org/10.1034/j.1600-0587.2003.03465.x>
- May RM (1973) Patterns of species abundance and diversity. In: Cody M, Diamond J (eds) *Ecology and evolution of communities*. Belknap Press of Harvard University, Cambridge, pp 81–120
- McGill BJ, Enquist BJ, Weiher E, Westoby M (2006) Rebuilding community ecology from functional traits. *Trends Ecol Evol* 21:178–185. <https://doi.org/10.1016/j.tree.2006.02.002>
- McGill BJ, Etienne RS, Gray JS, Alonso D, Anderson MJ, Benecha HK, Dornelas M, Enquist BJ, Green JL, He FL (2007) Species abundance distributions: moving beyond single prediction theories to integration within an ecological framework. *Ecol Lett* 10:995–1015. <https://doi.org/10.1111/j.1461-0248.2007.01094.x>
- Messier J, McGill BJ, Lechowicz MJ (2010) How do traits vary across ecological scales? A case for trait-based ecology. *Ecol Lett* 13:838–848. <https://doi.org/10.1111/j.1461-0248.2010.01476.x>
- Potts MD, Davies SJ, Bossert WH, Tan S, Supardi MNN (2004) Habitat heterogeneity and niche structure of trees in two tropical rain forests. *Oecologia* 139:446–453. <https://doi.org/10.1007/s00442-004-1525-3>
- Preston FW (1948) The commonness, and rarity, of species. *Ecology* 29:254–283. <https://doi.org/10.2307/1930989>
- Preston FW (1962) The canonical distribution of commonness and rarity: part I. *Ecology* 43:185–215. <https://doi.org/10.2307/1931976>
- R Core Team (2017) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>. Accessed 6 Mar 2017
- Rabinowitz D, Rapp JK, Dixon PM (1984) Competitive abilities of sparse grass species: means of persistence or cause of abundance. *Ecology* 65:1144–1154. <https://doi.org/10.2307/1938322>
- Rossee Y (2012) Lavaan: an R package for structural equation modeling. *J Stat Softw* 48:1–36. <https://doi.org/10.18637/jss.v048.i02>
- Rünk K, Moora M, Zobel M (2009) Do different competitive abilities of three fern species explain their different regional abundances? *J Veg Sci* 15:351–356. <https://doi.org/10.1111/j.1654-1103.2004.tb02271.x>
- Siqueira T, Bini LM, Roque FO, Marques Couceiro SR, Trivinho-Strixino S, Cottenie K (2012) Common and rare species respond to similar niche processes in macroinvertebrate metacommunities. *Ecography* 35:183–192. <https://doi.org/10.1111/j.1600-0587.2011.06875.x>
- Svanback R, Bolnick DI (2007) Intraspecific competition drives increased resource use diversity within a natural population. *Proc R Soc B Biol Sci* 274:839–844. <https://doi.org/10.1098/rspb.2006.0198>
- Umaña MN, Zhang C, Cao M, Lin L, Swenson NG (2015) Commonness, rarity, and intraspecific variation in traits and performance in tropical tree seedlings. *Ecol Lett* 18:1329–1337. <https://doi.org/10.1111/ele.12527>
- Violle C, Pu Z, Jiang L (2010) Experimental demonstration of the importance of competition under disturbance. *Proc Nat Acad Sci USA* 107:12925–12929. <https://doi.org/10.1073/pnas.1000699107>
- Violle C, Enquist BJ, McGill BJ, Jiang L, Albert CH, Hulshof C, Jung V, Messier J (2012) The return of the variance: intraspecific variability in community ecology. *Trends Ecol Evol* 27:244–252. <https://doi.org/10.1016/j.tree.2011.11.014>
- Volterra V (1928) Variations and fluctuations of the number of individuals in animal species living together. *ICES J Mar Sci* 3:3–51. <https://doi.org/10.1093/icesjms/3.1.3>
- Walker JS (2006) Resource use and rarity among frugivorous birds in a tropical rain forest on Sulawesi. *Biol Conserv* 130:60–69. <https://doi.org/10.1016/j.biocon.2005.12.002>
- Westoby M, Falster DS, Moles AT, Vesk PA, Wright IJ (2002) Plant ecological strategies: some leading dimensions of variation between species. *Annu Rev Ecol Syst* 33:125–159. <https://doi.org/10.1146/annurev.ecolsys.33.010802.150452>

- Wiegand T, He F, Hubbell SP (2013) A systematic comparison of summary characteristics for quantifying point patterns in ecology. *Ecography* 36:92–103. <https://doi.org/10.1111/j.1600-0587.2012.07361.x>
- Wisheu IC (1998) How organisms partition habitats: different types of community organization can produce identical patterns. *Oikos* 83:246–258. <https://doi.org/10.2307/3546836>
- Yan ER, Zhou LL, Chen HYH, Wang XH, Liu XY (2018) Linking intraspecific trait variability and spatial patterns of subtropical trees. *Oecologia* 186:793–803. <https://doi.org/10.1007/s00442-017-4042-x>
- Zambrano J, Marchand P, Swenson NG (2017) Local neighbourhood and regional climatic contexts interact to explain tree performance. *Proc R Soc B Biol Sci* 284(1855):20170523. <https://doi.org/10.1098/rspb.2017.0523>
- Zhang N, Wang X, Zheng Z, Ma Z, Yang Q, Fang X, Xie YB (2012) Spatial heterogeneity of soil properties and its relationships with terrain factors in a broadleaved forest in Tiantong of Zhejiang Province, East China. *Chin J Appl Ecol* 23:2361–2369