

THE CONTRIBUTION OF INTRASPECIFIC TRAIT VARIABILITY TO PLANT COMMUNITY ASSEMBLY PATTERNS ON THE NICHE-NEUTRAL CONTINUUM

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Abstract

Many trait-based plant investigations have neglected the intraspecific trait variations. A lot of ecologists consider that this is unreasonable, because intraspecific variation significantly affects various ecological dynamics. However, it is not feasible to record the traits of each plant individually at every community site. Therefore, the aim of this study was to determine in which circumstances it is most important to account for intraspecific trait variations. We conducted analyses using a trait-based niche-neutral continuum model integrating inter- and intraspecific variance. Then we tested the model through three popular community pattern indexes generated from four kinds of community assembly processes. The results showed that it was more important to consider intraspecific variations in plant communities with large niche overlaps. In such cases, including intraspecific variation increases the number of species and strongly affects the community's abundance structure. In contrast, when there is strong niche differentiation, the contribution of plant intraspecific variation could be neglected. In addition, the species richness and rank-abundance curve were insensitive to the magnitude of intraspecific variation, but plant trait distribution increased exponentially when intraspecific variation was included. Our results will be useful when designing field studies, to determine which data are most informative for various community types.

Key words: Niche and neutral theory, Spatially explicit model, Plant richness, Trait-abundance distribution, Abundance rank.

Introduction

Uncovering the mechanism of species' coexistence has always challenged ecologists. Currently, there are two prevailing paradigms to explain species' coexistence; the deterministic (niche) theory, and stochastic (neutral) theory. Deterministic theory explains community diversity based on niche differentiation and environmental filtering processes (Tilman & Downing, 1994; Webb *et al.*, 2002), while neutral theory regards community assembly as a random sample process. The latter assumes that species have no difference in their demographic attributes, such as birth, death, dispersal, and speciation probability (Hubbell, 1997, 2001). Although data from multi-species communities fits the neutral theory better than the niche theory, the two theories are debated by many ecologists (McGill, 2003; Chase, 2005; Dornelas *et al.*, 2006; Clark, 2009, 2010). To tackle the limitations of both theories, unified theoretical frameworks integrating niche and neutral hypotheses have been developed (Chase & Leibold, 2003; Tilman, 2004; Alonso *et al.*, 2006; Adler *et al.*, 2007). One such framework is the niche-neutral continuum proposed by Gravel *et al.* (2006); this model has become widely accepted in the field of community ecology.

Plant functional traits such as specific leaf area, height, seed mass, and leaf nitrogen content directly or indirectly determine species' performance and their types of interactions. These traits may generate competitive hierarchies (environmental filtering) and simultaneously promote species coexistence (niche partitioning) (Maire *et al.*, 2012; Adler *et al.*, 2013), and so measuring these traits is useful to unravel some aspects of community ecology (McGill *et al.*, 2006). Hence, many plant ecologists

analyze phenotypic trait dispersion patterns to distinguish stochastic and deterministic processes (HilleRisLambers *et al.*, 2012; Hulshof *et al.*, 2013). Various established statistical tools such as the fourth-corner (Legendre *et al.*, 1997; Dray & Legendre, 2008) and RLQ methods (R, L and Q respectively represent three tables: environmental characteristics, species distribution across samples, and species traits) (Doledec *et al.*, 1996; Brind'Amour *et al.*, 2011), or a recent method that combines the two (Dray *et al.*, 2014), can be used to assess the distribution of plant traits along an environmental gradient. These existing trait-based approaches represent important advances. However, the issue with most of the trait-based approaches is that they are not explicitly related to community dynamics. It is important to assess community dynamics to predict how biodiversity will respond to global climate change (Jabot, 2010; Webb *et al.*, 2010). Adler *et al.* (2013) have described some of the limitations of phenomenological approaches; for example, such studies cannot explain why there is greater plant richness in some communities than in others. Their analyses also combined species functional traits with recognized coexistence mechanisms such as spatial heterogeneity, resource partitioning, natural enemies, and temporal heterogeneity. However, functional traits are not usually considered in the unified niche-neutral assembly rule but Jabot (2010). In this study, therefore, we have combined plant functional traits with the niche-neutral continuum.

Most previous studies have considered plant species on a mean trait level, rather than distinguishing each individual (Jabot, 2010; Maire *et al.*, 2012; Adler *et al.*, 2013). This is based on the assumption that traits show more variability between than within species (McGill *et al.*, 2006). However, there is now mounting evidence challenging this assumption. The values of plant traits are

variable depending on genetic and environmental factors. Interspecific variance is not always greater than intraspecific variance (Messier *et al.*, 2010; Albert *et al.*, 2011), and even slight intraspecific variation may have a significant ecological effect. Intraspecific variations can allow species to establish successfully (Forsman *et al.*, 2012), directly affect nutrient cycles (Crutsinger *et al.*, 2009), buffer population fluctuations caused by disease (Garrett *et al.*, 2009), and release species from extinction (Gonzalez-Suarez & Revilla, 2013). Therefore, it is unwise to omit intraspecific variations from plant community analyses. However, it is not feasible to measure trait values for every individual at every community site, because of the time and costs involved. Also, the effect of intraspecific variations depends on the community; for example, some grasslands may not be significantly affected by intraspecific variation. Thus, whether to include plant intraspecific variation is case-dependent.

Motivated by both of these problems, we first established a trait-based niche-neutral continuum in which the intraspecific trait variation was considered. Four types of plant community assembly processes were represented on the niche-neutral continuum: completely neutral and niche cases at either end of the continuum, somewhere in between and randomly transited continuum (the niche degree randomly moves between two ends of the continuum as the time going). We explored the effect of including intraspecific variability in analyses of these four kinds of plant communities. Our study addressed two main questions: (1) when does intraspecific trait variability matter most on the niche-neutral continuum; and (2) what are the effects of changes in the magnitude of the intraspecific variation?

Material and Method

Trait-based niche-neutral continuum: In order to generate the community dynamic by using plant functional trait, we involve trait parameters into Gravel's niche-neutral continuum (Gravel *et al.*, 2006). The habitat is assumed as a two dimensional ($n \times n$) lattice with wrap-around boundaries. Each lattice cell has one certain habitat type, and as a whole, the habitat is spatially autocorrelated but temporally constant (generation process can be seen in Appendix). All plant individuals interact with each other on this lattice. In details, at each time step, we randomly pick certain proportion d of plants to die. Because the "zero-sum dynamic" hypothesis here, those empty cells caused by death will be re-occupied by immigrants from a species pool with probability m or by recruits of neighbor plants (eight nearest-neighbors) with probability $1-m$. Our species pool's framework is generated by Hubbell's neutral sample formula (Hubbell, 2001). The distinction is that plants in the metacommunity are not only labeled with species type but also possess trait values on species and individual levels. They are respectively chosen from two kinds of initial probability distribution (see Appendix for details).

At location x , the chosen new organism will be

individual i with probability $R(i, x) = \lambda(i, x) / \sum_{j=1}^{N_{nei}} \lambda(j, x) \mathbf{E}$ where $\lambda(i, x)$ is the surviving rate of plant i at location x . N_{nei} is the total number of neighbors. The surviving rate also has a Gaussian form like many previous ecologists (Gravel *et al.*, 2006; Ai *et al.*, 2012).

$$\lambda(i, x) = \exp\left\{-\frac{[h_x - \mu(T_m)]^2}{2\sigma(T_i)^2}\right\} \mathbf{E}$$

where h_x is the habitat type at x position. Because the competitive ability of each plant depends both on environment and functional trait values, plant's optimal position on environment gradient μ and niche width σ are trait related (Jabot, 2010). Let the trait range among $[0, 1]$. μ has something to do with species level trait T_m while σ depends on the individual level trait T_i (a certain species' T_m equals the mean of its belonging individuals' T_i). That is, all the individuals within one species have the same optimal position on environment gradient because they are family. But each one also personally possesses different niche width. On the other hand, to control the degree of niche overlap in our community system, it is necessary for us to identify a parameter well reflecting the degree of niche differentiation which is called niche degree here. Violle *et al.* (2012) once inferred the ratio $\Delta\mu / \sigma$ (d / σ in their paper) can be regarded as the degree of limiting similarity. The smaller $\Delta\mu / \sigma$ is, the more niche overlaps will be. Here, we follow this and hence as the niche degree variable ascends, $\Delta\mu$ is demanded to increase meanwhile σ should decrease. The detail forms about μ and σ are as follows:

(i) Data regression of plant trait vs performance often presents a negative correlation (Webb *et al.*, 2010). For example, a plant with high water use efficiency (large trait value) may favor xeric environment (small environment value) and performance better but the ones with low efficiency behave oppositely. So here, we utilize a negative linear function (the positive linear function is also appropriate like for resource-acquisitive trait) $\mu(T_m) = -slope \cdot T_m + a_1 \cdot slope + a_2 \mathbf{E}$ where $slope$ is the line's slope and a_1, a_2 are parameters which will be decided later. We can see that $\mu(T_m)$ is a decreasing function of T_m and $\Delta\mu = |\mu(T_{m1}) - \mu(T_{m2})| = |-slope \cdot (T_{m1} - T_{m2})|$ will rise as $slope$ value increase. Let N be the maxim habitat value. We fix the position of $slope=0$ at the middle of the environment gradient axis so that $a_1 = N/2$ (Fig. 1a). All the lines' intersection point is $(0.5, N/2)$, then $-slope/2 + a_1 \cdot slope + N/2 = N/2 \Rightarrow a_1 = 1/2$. Thus, the final form of $\mu(T_m)$ is $\mu(T_m) = -slope \cdot T_m + 2/N \cdot slope + 1/2$. From above functional properties, we know how the $slope$ value controls the plant niche overlap of our system (Fig. 1b and c). And when niche completely overlaps (purely neutral case $slope=0$), all plant traits tend to be regarded as the same.

(ii) Also according to former assumptions, we let the $\sigma(T_i)$ to be a decreasing function of $slope$

$\sigma = \sigma_0 + (T_i - T_m) - b \cdot slope$, where σ_0 is the original niche width. Parameter b is used as a limitation to the change effect of $slope$. Here we set $\sigma_0 = 2.5$ and $b = 1 / N$.
 When without considering plant intraspecific variance

$$R(i, x) = \frac{\lambda(i, x) Rab(i)}{\sum_{j=1}^{S_m} \lambda(j, x) Rab(j)}, \lambda(i, x) = \exp \left\{ -\frac{[h - \mu(T_m)]^2}{2\sigma^2} \right\}$$

where $Rab(i)$ is the relative abundance of species i . Here $\lambda(i, x)$ is the surviving rate of species i rather than individual i at location x . S_m is the total number of plant species.

Finally, our simulation is performed under the Matlab R2014a. Total plant individuals J_m in species pool is assumed as 100000 and $\theta = 20$. Prior to implementation, the lattice should be initiated. Individuals are one-by-one selected to fill empty cells and filtering rules follow above local dynamic processes. To determine the equilibrium time of community evolution, all simulations are performed first until a fixed time steps ensuring the majority of plant species reached stable. Once this has

happened, we begin to simulate our system under parameter ranges. The habitat spatial autocorrelation is set as 0.01, 1, 2 and niche degree $slope$ changes among {0, 10, 50, 150, 254}. Finally, we totally analyze ten levels of plant intra variability ratio $CV_{intra}/CV_{inter} = \{0.07, 0.5, 0.56, 0.6, 0.66, 0.72, 0.79, 0.9, 1.2, 1.8\}$. The formulas throughout our context are edited by the MathType 6. All the meaning and values of parameters occurred in our simulation are put in Table 1.

Randomly transited niche-neutral continuum: Recently, Fisher and Mehta have mentioned that there exist transitions between neutral and niche phase depending on the changed environment. It likes the water diagram translation among gas, liquid and solid phase as temperature varying (Fisher & Mehta, 2014). Therefore, in a plant community suffering environment fluctuations, the species assembly type may not be kept constant. So here, we consider a randomly transited continuum. The niche degree point will randomly move between the two ends of our niche-neutral continuum. For the sake of brevity, the varying process of our niche degree parameter $slope$ is assumed as a one-dimensional random walk process.

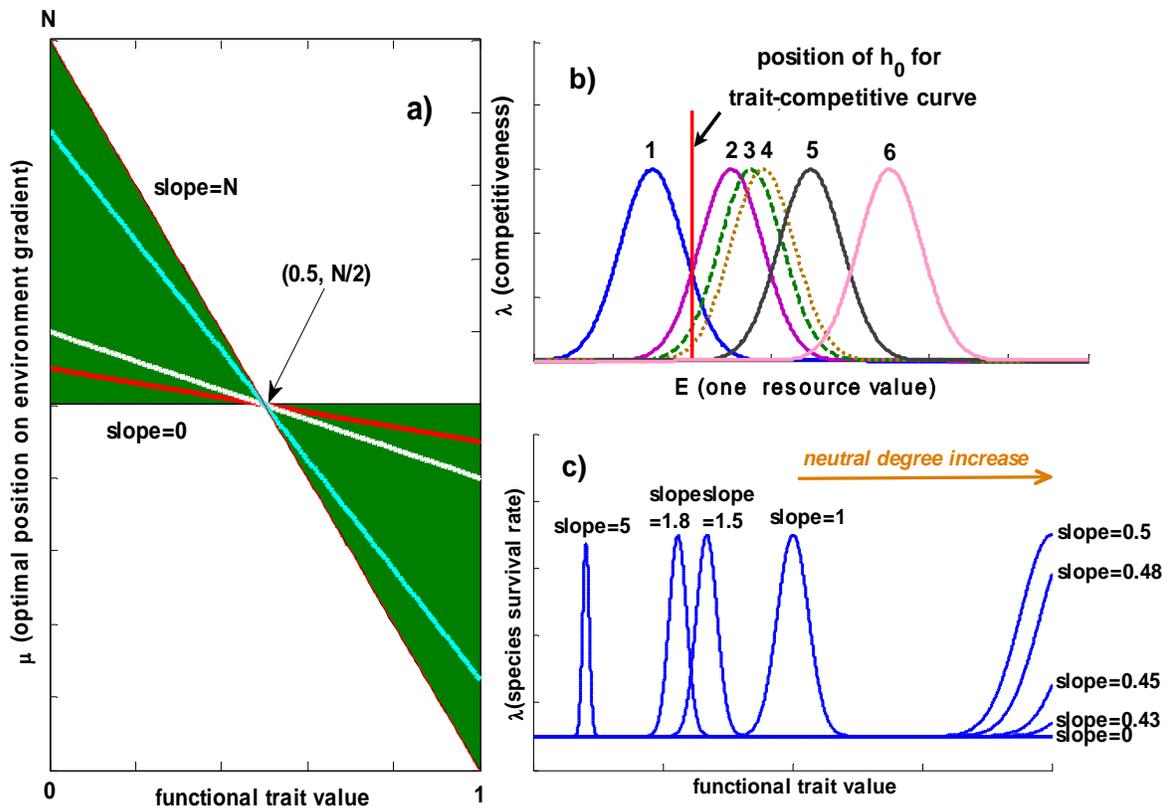


Fig. 1. Species optimal environmental position vs trait value and schematic illustration of species filtering by environment and trait values. a) Lines are optimal environmental position function $\mu(T_m) = -slope \cdot T_m + 2 / N \cdot slope + 1 / 2$ with different $slope$ values, where T_m is the species level trait variable. Green area is the part swept by lines whose $slope$ vary from 0 to N . b) The niche overlap on environmental gradient. Species' competitive inequality is represented by the survival rate. At a certain habitat type h_0 (the position of red line), we observe c) how niche degree variance generates species' survival rate difference. When slope tends to zero, the survival rate gradually becomes a flate line in trait space.

Table 1. Identifications of the parameters used in this paper.

Parameters	Meanings	Values
J_m	Total number of individuals in the species pool	100000
$v=\theta/(\theta+j-1)$	Probability to generate a new species	$\theta=20$
K	Total number of habitat recursive algorithm	7
n	Size of our lattice	$2^k \times 2^k$
w	Autocorrelation coefficient of habitat	{0.01,1,2}
N	Maximum number of habitat types	254
d	Death rate of plants	0.02
m	Probability of choosing offspring from species pool	0.1
$slope$	Degree of niche differentiation	{0,10,50,150,254}
μ	Optimal position on environmental gradient	—
σ	Niche width	—
CV_{intra}/CV_{inter}	Intraspecific variability ratio	{ 0.07, 0.5, 0.56, 0.6, 0.66, 0.72, 0.79, 0.9, 1.2, 1.8 }

Results

Our goal was to explore how intraspecific variations contribute to different community assembly processes. To achieve this goal, we first conducted two preliminary studies. First, we chose appropriate pattern indexes. In most previous investigations, researchers counted the species number and identified measures about how differently abundant for each species within the same community because they were quite informative and played a very important role in conservation ecology. Simultaneously, many researchers collected more data by including the taxonomic or phylogenetic attributes of species within a community. In this study, we considered three frequently-used pattern indexes: species-related indexes (species richness, rank abundance curve, and species abundance distribution), plant trait related index (trait distribution), and the rank–trait relationship (Cornwell & Ackerly, 2010). Then, we quantified the distance between these pattern indexes with and without including intraspecific variation. For species richness, the minus value of species number was regarded as its distance, while the area between two lines represented the distance for the rank–abundance curve. Because there were some statistical measurements for quantifying the difference between two distributions, we used Jensen–Shannon divergence (JSD) to estimate trait abundance distribution’s variation. The formula is given by

$$JSD(P, Q) = \frac{1}{2} [KL(P \square \frac{1}{2}(P + Q)) + KL(Q \square \frac{1}{2}(P + Q))],$$

where KL was the Kullback-Leibler divergence $KL(P \square Q) = \int dx P(x) \ln [P(x) / Q(x)]$ (Fisher & Mehta, 2014).

Effect of intraspecific variation on species-level pattern indexes: First, when there was slight niche

partitioning ($slope=0, 10, 50$; Fig. 2), the number of species was greatly increased when intraspecific variation was included. When there was strong niche differentiation ($slope=150, 254$), there was little or no effect of including intraspecific variation, thus, it could be omitted. Each curve remained approximately the same, regardless of a slight shake. The magnitude of intraspecific variation did not affect plant richness. Therefore, incorporating intraspecific variation could increase the number of species, but a greater magnitude of intraspecific variation did not have a stronger effect. Based these results, we concluded that it is more important to include intraspecific differences when counting species richness in plant communities with greater niche overlaps than in plant communities with strong niche differentiation.

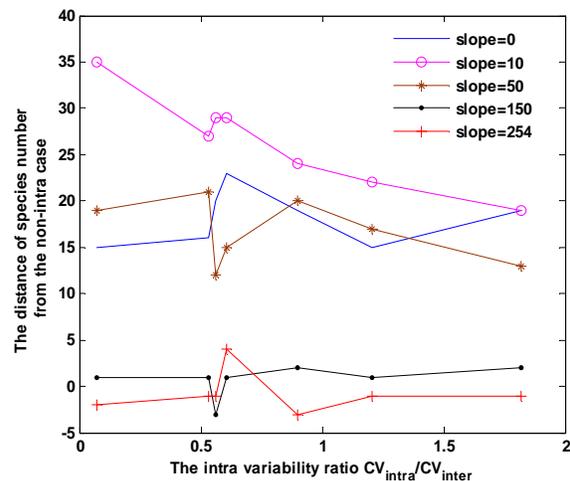


Fig. 2. The distance (quantified by the number minus) of species richness from non-intra case reacts on the intraspecific variability gradient. Lines with different colors correspond to different positions on the niche-neutral continuum, namely various slope values: purely neutral ($slope=0$), mixed occasion ($slope=\{10,50,150\}$) and completely niche ($slope=254$). The spatial autocorrelation coefficient of habitat $w=1$.

Another common measurement of pattern is the rank–abundance curve. Figure 3 shows the effect of intraspecific variation on this index for the non-changed niche–neutral system and the randomly transited continuum. In Fig. 3, the blue line representing no intraspecific variation was strongly reshaped by the introduction of the intraspecific variation factor (two panels on upper left corner; $slope=0$, 10; Fig. 3). In contrast, in the upper right corner ($slope=50$, 254), all the rank abundance curves were located closely together. The shapes of the lines became less skewed when the intraspecific variation factor was introduced. In effect, adding the intraspecific variation factor decreased the number of rare species and decreased the rarity of the plant community. However, these trends differed on the randomly transited niche–neutral continuum. The strongest influence was when there was a medium initial niche degree ($slope=10$, 50). In purely neutral or niche cases ($slope=0$, 254), the contribution of intraspecific variation could be neglected. To determine whether this was because of special habitat constructions, we quantified the distance between rank–abundance curves with and without intraspecific variation under three different habitat structures ($w=0$ random habitat, $w=1$ medium clustering habitat, and $w=2$ clustering habitat; Fig. 4). The distance was represented by the integrated area between the two lines. Whether it was the standard niche–neutral model or the randomly moved continuum, the lattice autocorrelation gradient only enhanced the contribution of intraspecific variation.

Effects on trait-level pattern indexes: The trait distribution curve, as a statistical distribution, describes the frequency of occurrence within local community for each category of plant trait. For a given habitat structure ($w=1$), Fig. 5 shows the index for a given habitat structure ($w=1$) under three degrees of niche partitioning on the niche–neutral continuum. When there was weak niche partitioning ($slope=0$, 10), species in local community had similar trait values; therefore, they selected mainly by relative abundance rather than trait values. As such, the trait distribution derived from the species pool was over-converged, relative to the purely niche case ($slope=254$). Only one or two abundant species remained when intraspecific variation was neglected. However, introduction of intraspecific variation caused the strong neutral curve (first two panels in the second and third row; Fig. 5) to become over-dispersed. As the CV_{intra}/CV_{inter} increased, that is, the intraspecific variation became larger than interspecific variation (last row $CV_{intra}/CV_{inter}=1.8$), all the curves became the same shape. Therefore, under strong intra variance, plant trait distribution was not appropriate for detecting community assemblages when there was strong niche partitioning.

To quantify the size of the contribution of plant intraspecific variation, we used Jensen–Shannon divergence to measure the distance of trait distribution with and without intraspecific variation (Fig. 6). In all three kinds of spatial autocorrelations (Fig. 6a, b, and c), the distance of trait distribution decreased as the degree of niche partitioning increased. Thus, the stronger the niche overlap, the greater

the contribution of intraspecific variation. In particular, when $slope=0$ (purely neutral case), even a small amount of intraspecific variation resulted in a large difference in community assemblage estimates, compared with the case when intraspecific variation was omitted. Focusing on the blue lines in Fig. 6, as the $slope$ changed from 0 to 254, the initial, almost flat line changed to an exponentially increasing curve. This rapid upward trend means that when there is strong niche partitioning, the contribution of plant intraspecific variation will increase as its magnitude increases. In addition, the blue lines lay within the two red lines that corresponded to the randomly transited case with initial $slope=0$ and 254. This means that the trend for intraspecific variation to have a greater effect on communities with great niche overlaps increases with environmental fluctuations.

Impact on species rank–trait relationship: Plant functional traits are important parameters when considering species presence, but can also explain species abundance and rarity (Cornwell & Ackerly, 2010). We plotted pairs of abundance rank and plant trait values (Fig. 7). Within each panel, the x -axis was relative abundance rank; that is, points on the left represented dominant plants, and those of the right represented rare species. All of the blue dots evenly filled the whole quadrant in panels of the first row and first column. However, when we made individuals distinguishable within the community of $slope=10$, 254 (the middle figures in second to last rows), the dots showed different clustering patterns. In the niche–neutral mixed case ($slope=10$), plants with medium trait values were chosen as common species, but rare species always had medium trait values. In the complete niche case ($slope=254$), all plants had medium trait values. To some extent, including intraspecific variation could help to analyze trait distribution when detecting assemblages. Also, the contribution of intraspecific variation could not be neglected on the randomly moved niche–neutral continuum the contribution of intra also should not be neglected (last column, Fig. 7).

Discussion

Recently, there has been growing debate about the relative contributions of intra- and interspecific variation to plant community assemblage patterns. These variations are essential yet understudied drivers of biodiversity. While researchers cannot measure plant trait values for a huge number of individuals at every site because of time and financial constraints. The aim of this study was to evaluate whether the intraspecific difference could be safely ignored for any plant community assemblage process. To address this question, we simulated community assemblages on a trait-based niche–neutral continuum, and conducted analyses including or omitting intraspecific variation. Our results showed that intraspecific trait variation makes the largest contribution when there is weak niche partitioning. The size of the contribution remains the same on the magnitude gradient of intraspecific variability. We have illustrated this by analyzing various pattern indexes.

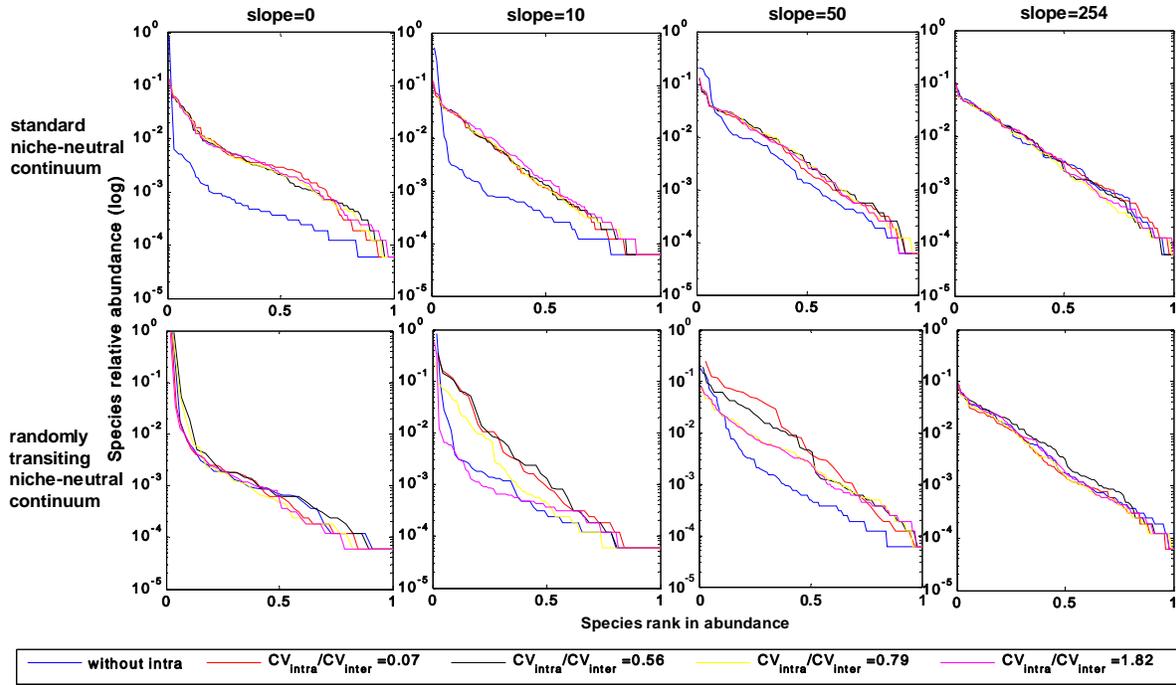


Fig. 3. The log transformed species rank-abundance curve. Because the outcome species number of different local community may not be the same, we use the relative rank (the rank divided by total species number) to instead. There are four columns corresponding to four different niche degree values: *slope*=0, 10, 50, 254. The figures in first row are non-changed niche-neutral continuum while the second row represents our randomly transited case under the four initial slope values. Five curves with different colors are the rank-abundance lines from community without intra factor and under four intra magnitude level $CV_{intra}/CV_{inter}=0.07, 0.56, 0.79, 1.52$. The spatial autocorrelation coefficient of habitat $w=1$.

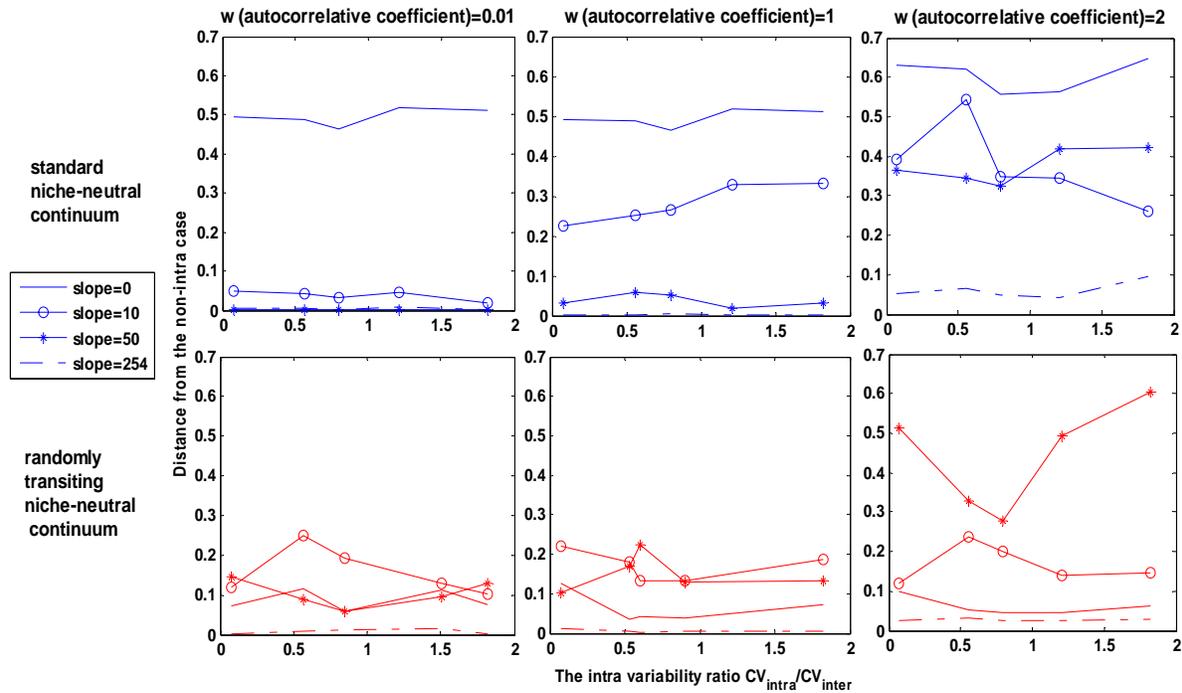


Fig. 4. The distance of rank-abundance curve from its non-intra case plotted against the intra variability ratio CV_{intra}/CV_{inter} . It is quantified by the area between two lines. The first row is non-changed niche-neutral continuum while the bottom row is for our randomly transited case. Three columns are under three levels of spatial autocorrelation ($w=0$ randomly habitat, $w=1$ medium clustering habitat and $w=2$ clustering habitat). Different curves within each panel correspond to four kinds of niche degrees.

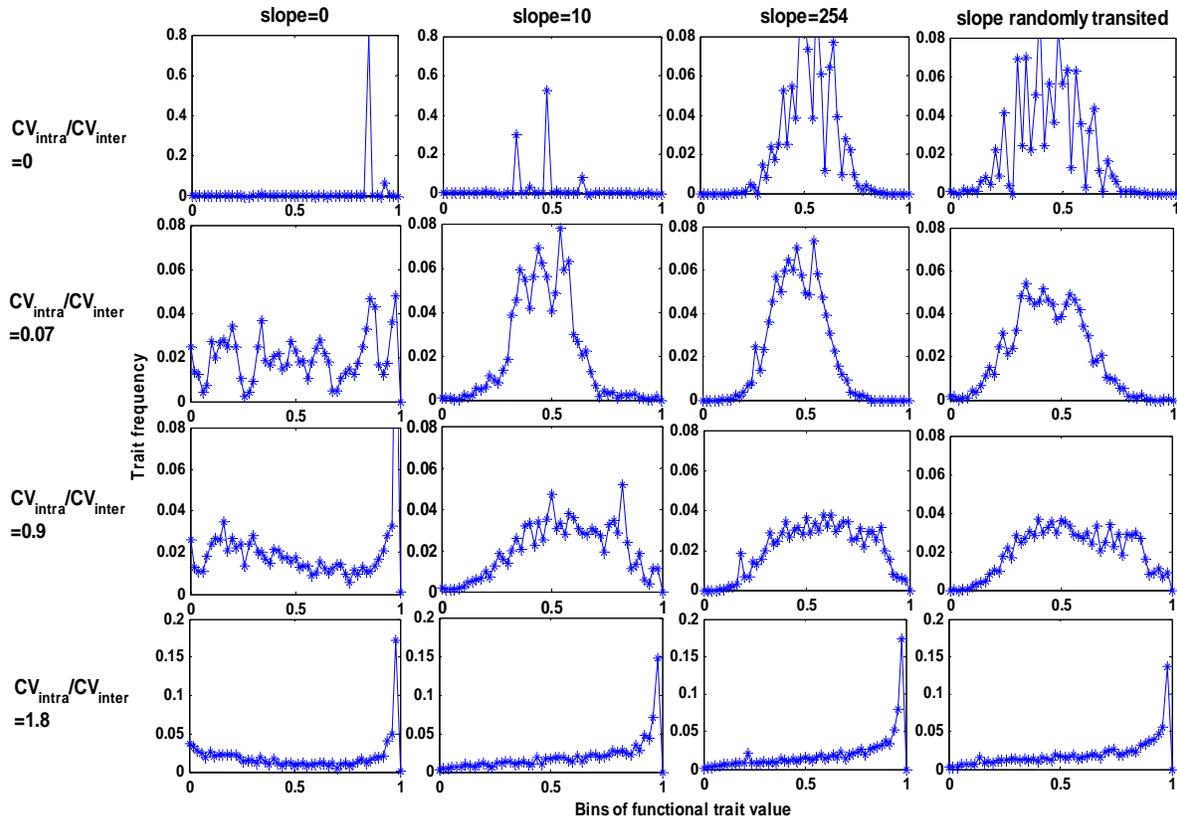


Fig. 5. Species trait distribution graph. The first three columns correspond to three neutral degree values ($slope=0,10,254$) and the last column represents randomly transitioned continuum whose initial slope is 254. Each row is given a intra variability ratio CV_{inter}/CV_{intra} . They are 0, 0.07, 0.8, 1.8. The spatial autocorrelation coefficient of habitat $w=1$.

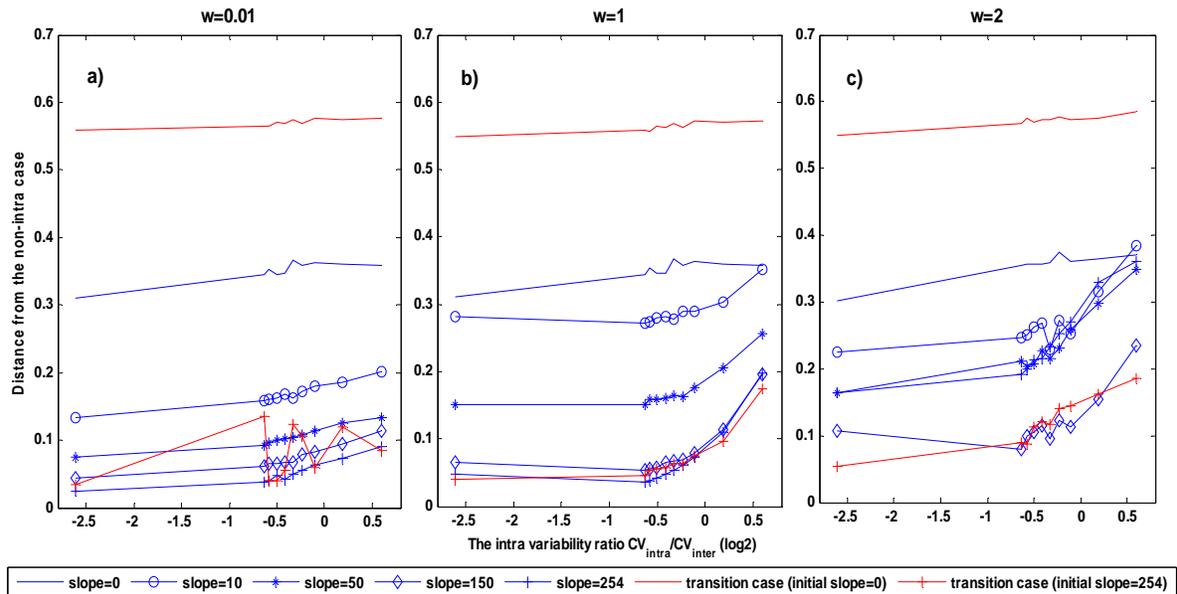


Fig. 6. The distance of species trait distribution from its non-intra case plotted against the \log_2 transformed intra variability ratio CV_{intra}/CV_{inter} . It is quantified by the Jensen-Shannon divergence (JSD). There are three levels of spatial autocorrelation: a) $w=0$ randomly habitat, b) $w=1$ medium clustering habitat and c) $w=2$ clustering habitat. Blue curves are non-changed niche-neutral continuum under four $slope$ values 0, 10, 50, 150, 254 while two red lines correspond to the randomly transitioned case whose initial slopes are 0 and 254.

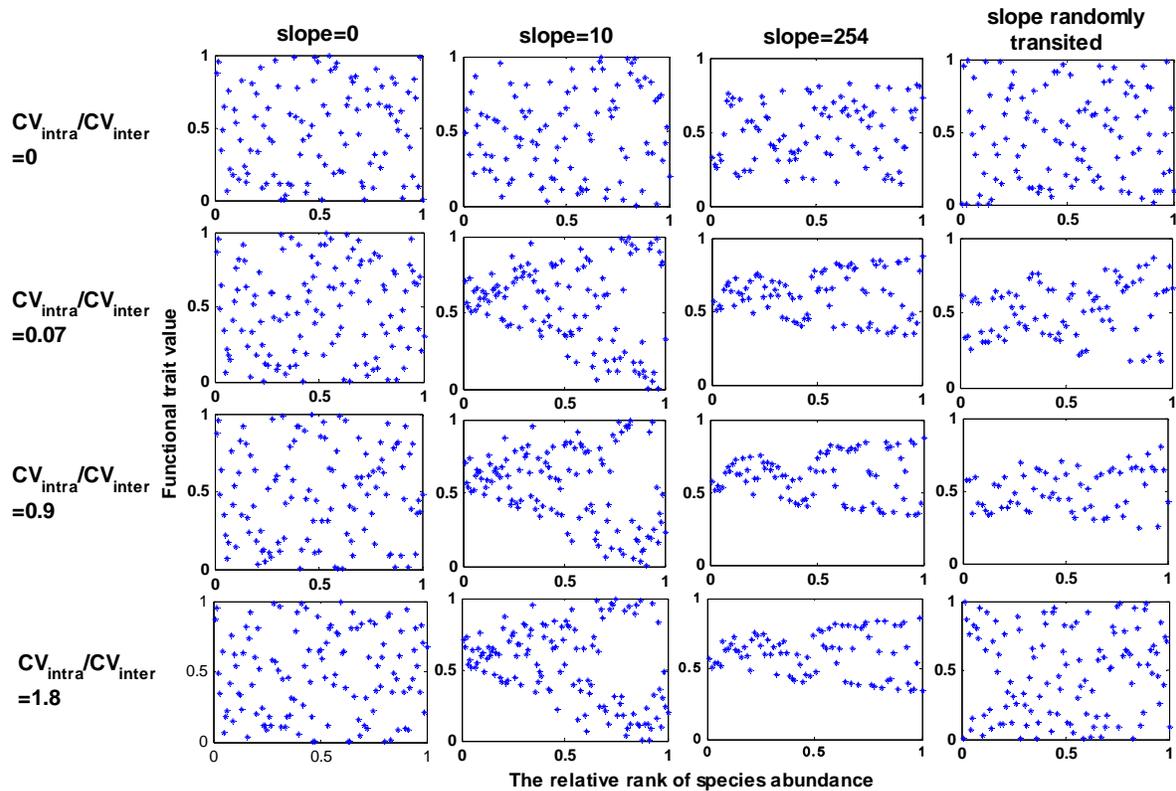


Fig. 7. The species rank-trait relationship. The first three columns correspond to three niche degree values ($slope=0, 10, 254$) and the last column is the slope randomly transitioned case whose initial slope is 254. Each row is given a intra variability ratio CV_{inter}/CV_{intra} . They are 0, 0.07, 0.8, 1.8. The spatial autocorrelation coefficient of habitat $w=1$.

In terms of species-related pattern indexes, we first selected species richness and rank–abundance, because they not only indicate the composition of the local community, but also provide a visual representation of species' abundance structure (Magurran, 2004; Magurran & McGill, 2011). Violle *et al.* (2011) noted that incorporating intraspecific variation can result in higher local diversity, but our analyses suggested that this is case-dependent. When there is weak niche partitioning, including plant intraspecific variation strongly increases the number of coexisting species. When there is strong niche partitioning, including plant intraspecific variation results in almost no change, or even the loss of a few species. Plants within the same species have the same optimal environmental position but their niche width is different caused by intraspecific trait variations. Some organisms have a wide range of habitat preferences, which reduces niche overlaps both at the species and individual levels. The main reason for the outcome dependence is the different alter speed on species and individual levels. When there is weak niche partitioning, differences in niche width release more competitive exclusion among species than among individuals, so that intraspecific competition exceeds interspecific competition, which is generally regarded as the condition that promotes species coexistence (Chesson & Kuang, 2008). However, when there is strong niche partitioning, species occupy separate positions. In this case, species coexistence has reached the maximum, so that the competition-releasing effect of niche-width variation has been ignored. Another result is the contribution of intraspecific variation to

community abundance structure (rank–abundance curve); that is, plant rarity. Also in slight niche partition community, intraspecific difference could matter most. Part of rare species' abundance recover, namely less rare species. The plant abundance structure becomes more uniform. In addition, many studies have emphasized the role of habitat structure in ecological dynamics (Kallimanis *et al.*, 2005; Elkin & Possingham, 2008; Altermatt & Holyoak, 2012; Rybicki & Hanski, 2013). To eliminate interference from habitat structure, we implemented our models with other spatial autocorrelation coefficients. This made the trend slightly stronger.

In many plant trait-based studies, trait distribution has been used as a tool to address ecological questions (McGill *et al.*, 2006; Webb *et al.*, 2010; Adler *et al.*, 2013). Our results show that when plant niches overlap, all species are regarded to have almost the same trait value, and so species are mainly filtered by random samplings according to their relative abundance. Finally, only the dominant species in the pool are heavily selected, leading to the convergence of trait distribution. However, including an intraspecific variation factor modifies the shape of the curve; the divergence is greater with large-scale intraspecific variability (when it is greater than interspecific variability). In that case, the trait distribution curve cannot reveal community assemblages. Studies that consider individual heterogeneity usually include intraspecific variation, but seldom consider the effects of the magnitude of intraspecific variation (Bolnick *et al.*, 2011; Violle *et al.*, 2012; Adler *et al.*, 2013), except for the study of De Laender *et al.*, (2014). We can draw some quantitative

conclusions from the Jensen–Shannon divergence. First, in a purely neutral community, the contribution of intraspecific variation remains the same, regardless of its magnitude. However, in a more niche-differentiated community, the contribution of intraspecific variability becomes exponentially larger as the magnitude of the intraspecific variation increases. This is even more conspicuous in a higher clustering habitat or a fluctuating environment.

Species presence mainly depends on its trait values, but trait values can also affect species' dominance (Cornwell & Ackerly, 2010). We explored this relationship in our model. When intraspecific variation was not considered, there was almost no difference in the outcomes of the rank–trait curve based on different processes. However, there were differences when intraspecific variation was included. Weak niche partitioning makes the system select species with middle trait values as the dominant species. The species with large or small trait values are selected as rare plant species. When niches are completely separate or in a fluctuating environment, there is no clear relationship between species rank and species traits. This phenomenon mainly results from Jensen's Inequality, which states that if $f(t)$ is a concave (convex) function of variable trait t , the average of $\overline{f(t)}$ will be smaller (larger) than the function's evaluation of the mean trait value $f(\bar{t})$ (Bolnick *et al.*, 2011). In our analyses, plant survival was a continuous nonlinear function of trait value (Fig. 1c). When the niche degree was around 10, there was a bulge in the shape of the line around the middle position on the plant trait axis. Therefore, according to the Jensen's Inequality, intraspecific variation increases the survival rate of species with middle trait values. Those species at either end of the plant trait axis have a low competitive ability, which causes them to be rare.

We have established a trait-based niche–neutral continuum model and obtained how plant intraspecific variation alters community assemblage pattern indexes. These findings will be useful for future field data collection. For the sake of brevity, our model considers plant traits in one dimension. In future analyses, the model may be extended to include multiple traits, because plants have many traits (Jabot, 2010; Webb *et al.*, 2010; Albert *et al.*, 2011; Bolnick *et al.*, 2011) and they are not independent of each other (Laughlin, 2014). In fact, it is easy to extend our system to a two-dimensional trait space if the traits have a certain relationship, for example, a trade-off. In that cause, the plant trait axis is the ratio of the two traits. All of the possible combinations would be represented in the range of $[0, \infty]$. For higher dimensional plant traits, more multivariate methods and careful choices of plant trait space should be required in future studies.

Appendix

The algorithms for generating species pool and habitat design in our paper

Species pool: The generation algorithm of species pool follows Hubbell's neutral sample formula (Hubbell, 2001). The difference is trait-based test. Therefore, when a new plant occurs, it will be assigned with a species level trait value which is randomly chosen from a uniform distribution. On the other hand, each plant organism also processes a personal individual level trait.

It is gotten from a beta distribution. This distribution presents a wide range of $[0, 1]$. And its majority sample values gather around one certain point, which better follows ecological rules: most individuals among one species share similar attributes. In order to well control the degree of intraspecific over interspecific trait variability and see what happens for community dynamic along the magnitude gradient, we introduce a variability ratio CV_{intra}/CV_{inter} (where CV_{intra} quantifies the trait difference between species while CV_{inter} is the intraspecific variability). Like DeLaender *et al.* (2014), it is represented by the 95th–05th inter-percentile distance. Let

$$CV_{inter} = \frac{v_{95} - v_{05}}{v_m},$$

where v_{95} is the position when cumulative probability equals 0.95 and v_{05} is for 0.05 (Fig. 8a). v_m is the median trait (here is the expected value of distribution). Thus, index CV_{inter} describes the distance between 95th and 05th percentile to median trait value. Similarly,

$$CV_{intra} = \frac{v_{j,95} - v_{j,05}}{v_{j,m}}.$$

Without any prior knowledge on the trait distribution source, we here suppose species level trait value to follow a uniform distribution on $[0, 1]$. Then the ones on individual level follows a beta distribution $Beta(a,b)$ whose expectation $a/(a+b)$ equals their species level trait value (Fig. 8b). By doing so, each trait value on species level can be controlled as the average of all individuals among its population. Because the CV_{inter} of uniform distribution on $[0, 1]$ can be easily calculated as 0.9, after giving an intraspecific variability level CV_{intra} , the generating process are performed as follows:

step1: set the species number $sp=1$, individual number $j=1$ and calculate the “species generator” $v=\theta/(\theta+j-1)$

step2: draw a random number x from uniform distribution. If $x < v$, $s=s+1$, $j=j+1$ and label the species.

step3: get a random number T_m from uniform distribution of $[0, 1]$ as the individual's species level trait value.

step4: If $x \geq v$, label the species as an abundance-related specimen from the previously generated species collection. T_m is the chosen species' trait and set $j=j+1$.

step5: obtain our beta distribution whose expectation is T_m and the distance between 95th and 05th percentile is CV_{intra} . Draw a random T_j from this beta distribution and label it as the individual level trait.

step6: if $j > J_m$, simulation stop otherwise turn to step1. In short, with a “species generator” $v=\theta/(\theta+j-1)$, a plant collection of J_m individuals belonging to S_m species is developed. This configuration will be fixed in our paper.

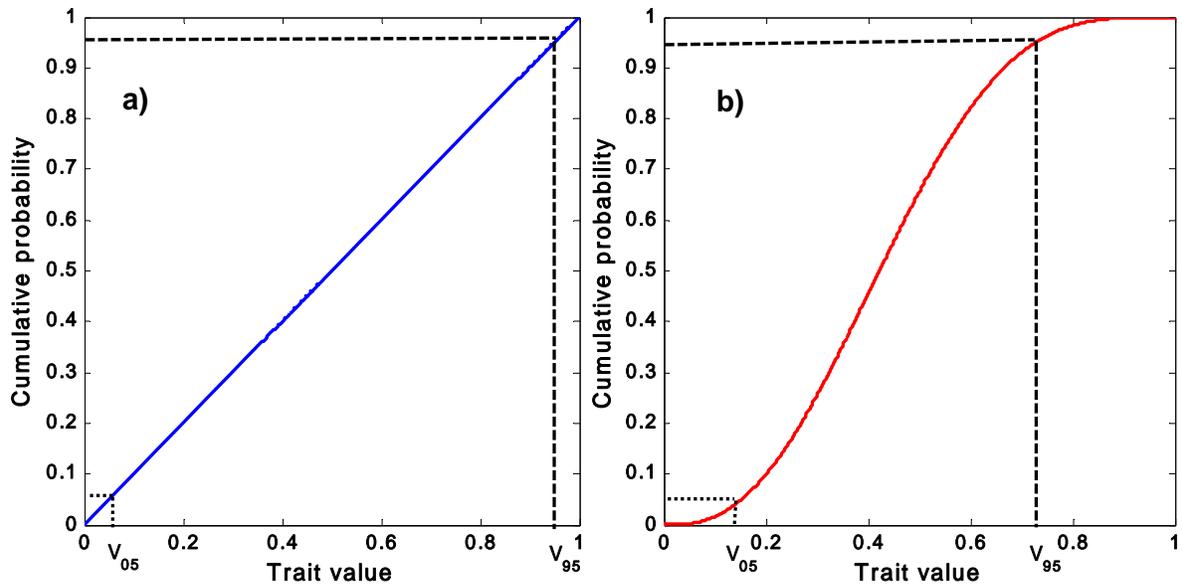


Fig. 8: The cumulative probability curves: a) for the species level trait distribution (uniform distribution); b) for the individual level trait distribution ($\text{beta}(3,4)$). Dotted lines respectively directs the 95th and 05th inter-percentile positions.

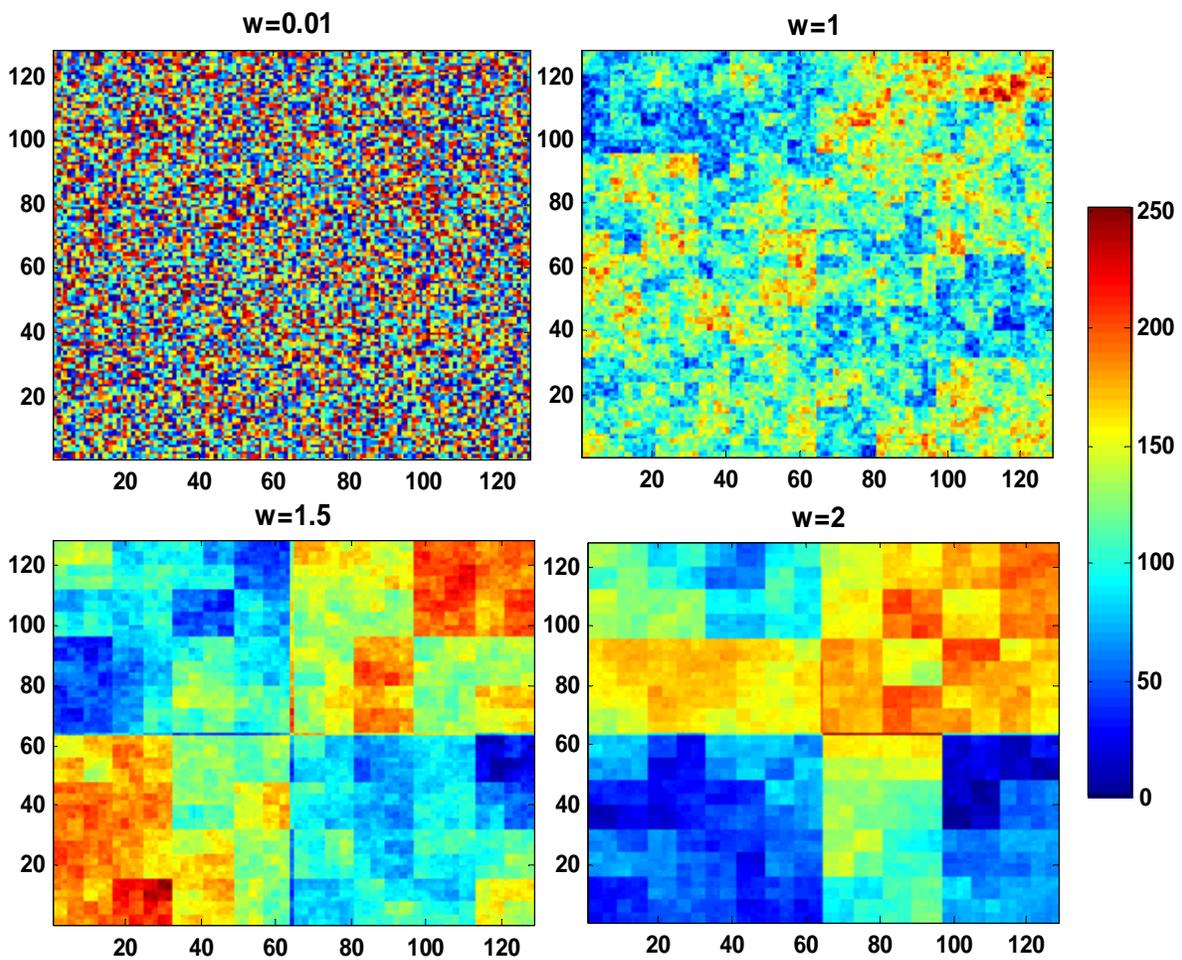


Fig. 9: The spatially auto-correlative gradients of habitat ($w=0.01, 1, 1.5, 2$). Different colors correspond to different habitat types. The habitat type range is $[0, 254]$ and lattice size is 128×128 .

Habitat design: We design a simple yet robustly realistic landscape which is heterogeneous and spatially autocorrelated (Rybicki & Hanski, 2013). The habitat matrix is generated through a recursive quadtree subdivision algorithm: recursively dividing the lattice into four rectangles until single cells. For convenience, we set size of the lattice as $2^k \times 2^k$ where K is the total number of recursion. So the number of total recursive steps is K . Let $H(i, j)$ be the habitat type on the (i, j) position. Initially, the lattice is divided to four parts $A_{1,1}, A_{2,2}, A_{3,2}, A_{4,4}$ and four random values from uniform distribution of $[0, 1]$ $X_{1,1}, X_{2,2}, X_{3,2}, X_{4,4}$ were selected to assign the cells in respective four parts. Then at the second step, each sub-lattice is continually broken down into four sections and new chosen random numbers for cells are weighted-summed to their previous cell values. So, in any recursive level k , we divide the lattice into four parts $A_{1,k}, A_{2,k}, A_{3,k}, A_{4,k}$, uniformly choose four values $X_{1,k}, X_{2,k}, X_{3,k}, X_{4,k}$ from $[0,1]$ and get the weighted accumulation. Finally, when K steps are finished, the $H(i, j)$ is

$$H(i, j) = \frac{1}{W} \sum_{k=1}^{4K} [(i, j) \in A_k] X_k w^{\lceil k/4 \rceil}, \text{ where } W = \sum_{k=1}^K w_k, (w_k = w^{-k}).$$

Overall, the single parameter $w > 0$ is used to control the scale of spatial autocorrelation. A large w corresponds to the high spatial autocorrelation while for extremely small w , the habitat is randomly positioned (Fig. 9).

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