

Habitat hotspots of common and rare tropical species along climatic and edaphic gradients

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Summary

1. Understanding coexistence in high biodiversity ecosystems requires knowledge of how rare and common species share the multidimensional environmental space. Climatic and edaphic conditions can provide a plethora of habitats, supporting different compositional and structural communities where species can adapt and differentiate.

2. We used a large data set consisting of 580 tropical tree species sampled in 163 25 × 25 m quadrats along an altitudinal gradient covering an area of 160 km² of tropical rain forest in Jianfengling reserve (Hainan Island, China). For each plot, the data include tree species and abundance, altitude and six soil properties from which a two dimensional environmental space was constructed.

3. With this extensive data set, we tested the hypothesis that different combination of environmental factors can generate multiple hotspots on three axes of diversity: species richness, Shannon-equivalent species richness and habitat preference, a measure of evenness in the distribution of individuals across an environmental gradient.

4. We found that humid and cool areas with more nitrogen availability were occupied by richer and more diverse communities of wide range species. Rare (in terms of number of individuals) and range-restricted species instead, tended to prefer minor habitats, generally warmer with high potassium, calcium, magnesium and, in particular, phosphorous. As a result, wide and range-restricted species were segregated across the environmental space.

5. *Synthesis.* Our findings indicate rare species tend to occur more frequently where common species are less abundant. A clear pattern of species richness and diversity was driven by a combination of several environmental factors (soil properties and climate). The complexity of the environment not only explains the different species distribution along each habitat, but also determines the relative abundance of each species in the entire community. Although some habitats have low species richness and diversity, they are highly preferred by rare species; therefore, biodiversity conservation efforts should consider protecting these fragile ecosystems.

Key-words: climatic gradient, common and rare species, determinants of plant community diversity and structure, elevation, habitat differentiation, habitat preference, multiple hotspots, range-restricted species, soil properties, species interaction

Introduction

The coexistence of a large number of common and rare species in tropical forests is a result of physiological adaptation to biotic and environmental conditions, evolutionary history and geographic constraints (Janzen 1970; Ashton 1989; Wright 2002; Hawkins *et al.* 2003; Colwell, Rahbek & Gotelli 2004; Leigh *et al.* 2004; McCain & Grytnes 2010).

Understanding the distribution and the interactions of a large variety of species across space could greatly improve our knowledge about species responses to habitat selection and climate change, and how communities are structured in tropical forests (Lenoir *et al.* 2008; Volkov *et al.* 2009; Lennon *et al.* 2011; Condit *et al.* 2013).

Currently, the challenge lies in revealing the heterogeneous responses of diverse species to multidimensional environmental gradients (Condit *et al.* 2005; Guisan & Thuiller 2005). The study of species distribution can highlight the importance

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of environmental factors in structuring plant communities because species respond to the environment in many different ways (Jones, Tuomisto & Olivas 2008; Baldeck *et al.* 2013).

However, at intermediate spatial scales ($\sim 100 \text{ km}^2$), a comprehensive and representative assessment of stem and biomass density patterns along multidimensional environmental axes are scant for a large number of species (Condit *et al.* 2013). For rare species, which contribute largely to the diversity of these forests, their entire niche might never be captured from observations. Nevertheless, tropical forests offer the possibility to investigate species rarity more systematically. Study the distribution of a large number of common and rare species may show if rare species tend to occur more frequently where common species are less abundant (Prendergast *et al.* 1993).

Different combinations of environmental conditions support different species compositions at different spatial scales. Therefore, a wide spectrum of environmental variables must be used to address questions about species restriction (Wright *et al.* 2011; Baldeck *et al.* 2013). For example, soil nutrients and hydrological conditions have long been recognized as key factors in regulating species composition at both local (John *et al.* 2007; Baldeck *et al.* 2013) and regional scales (Swaine 1996; Potts *et al.* 2002; John *et al.* 2007; Toledo *et al.* 2012). However, results from a single large forest plots (25–50 ha), where all individuals above a certain size are mapped, are spatially limited, because, for example, hydrological processes act in these forests at larger scales (Detto *et al.* 2013) and climate does not vary on such short distances. Large biogeographic studies instead are often based on the presence/absence data only and suffers of data-deficient species, although considerable improvements have been recently made using a spatial-phylogenetic statistical framework (Jetz & Freckleton 2015). Therefore, altitudinal gradients are well-suited for investigating species distribution and diversity patterns (Körner 2000; Lenoir *et al.* 2008). Within relatively small geographic areas, $\sim 100 \text{ km}^2$, mountains span a broad range of environmental variability, in climate (e.g. temperature and radiation), edaphic and hydrological conditions (e.g. soil nutrients and water availability) and disturbances (e.g. typhoon and landslides).

Several hypotheses had been proposed regarding how species occupy this compound environmental space. Colwell, Rahbek & Gotelli (2004) proposed that if species were confined to altitude zones due to dispersal or chance alone, the ranges of species would tend to overlap in the centre of the domain, a phenomenon known as the mid-domain effect (MDE). On the other hand, if species were confined to altitude zones in response to climate and other environmental factors, species can differentiate habitat preference and possibly display multiple distribution hotspots (Lomolino 2001; McCain & Grytnes 2010). It is a phenomenon which has been reported globally, along the latitudinal gradients, but less along the altitudinal gradients (Stevens 1992; Myers *et al.* 2000; Jump, Mátyás & Peñuelas 2009; McCain & Grytnes 2010). Clearly, the presence of multiple species distribution hotspots implies that some groups of species are range restricted with similar habitat association.

In this study, we test for the presence of hotspots in tropical woody plants, defined as regions on a multidimensional environment that rank significantly high on one or more of three axes of diversity: species richness, equivalent richness (in Shannon sense) and habitat preference. The latter is the equivalent number of species which have high preference on a particular habitat.

Three mutual exclusive null hypotheses were formulated to test the presence of hotspots: (i) the structure of the multidimensional habitat has no effect on species distribution; (ii) species distribution are influenced only by habitat geometrical constraints (MDE); (iii) given the association between species richness and the habitat, Shannon diversity is independent on habitat structure. We further investigate whether rare and common species display different distribution pattern across the environments. Here, rarity defines species with small population size and restricted range of habitats, which are the first and third axes proposed by Rabinowitz (1981) – the second axis is whether the species has small geographic range.

The large census data set from the tropical forest reserve in Jianfengling, Hainan Island, China, provides an ideal setting for studying species responses to environmental variation. It is a tropical ecosystem with high species richness distributed along steep gradients in altitude and soil properties (Fig. 1). The data set included 580 species of woody plants with diameter (at breast height) larger than 1 cm identified in 163 plots ($25 \times 25 \text{ m}$) ranging from 259 to 1131 m above sea level (Fig. S1 in Supporting Information). The ecosystem spans from lowland to mountain tropical rain forests across an area of 160 km^2 .

A multidimensional environment was constructed by six soil properties of resource availability and altitude as climatic factor. From this analysis, significant patterns and hotspots in species richness, diversity and habitat preference emerged. Statistical tests, based on Monte Carlo randomizations, rejected all the above null models with confidence, indicating

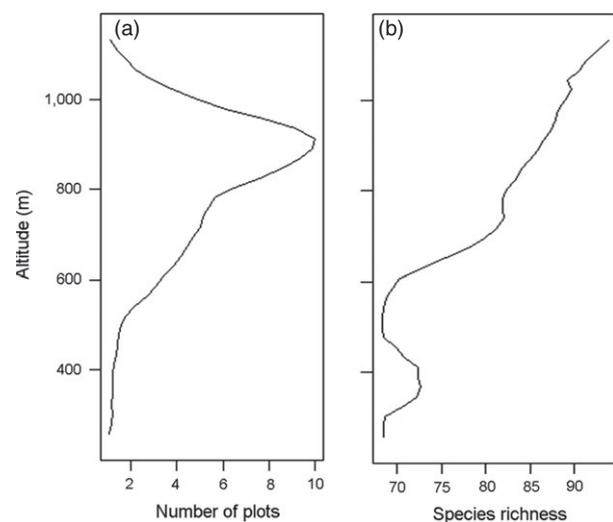


Fig. 1. Variation of (a) sampling stratification and (b) species richness with elevation obtained using a kernel density estimator.

a strong role of environmental heterogeneity in structuring communities. We further show that rare and range-restricted species were segregated from common and wide range species on the multidimensional environment.

This work constitutes an important step towards understanding how environmental heterogeneity shape the co-occurrence and distributions of common and rare species at intermediate spatial scales (~100 km²), and the potential impacts of habitat and climate changes on plant species and community structures in the tropics.

Materials and methods

STUDY SITE AND DATA SET

The study site is located in the Jianfengling forest reserve (JFR), south-west Hainan Island, China (latitude and longitude ranges: 18°23'–18°50' N and 108°36'–109°05' E, altitude range: 0 to 1412 m). JFR comprises 472 km² tropical rain forests. It has a tropical monsoon climate with the wet season from May to October and the dry season from November to April. The annual rainfall ranges from 1000 to 3600 mm. The annual average temperature is 24.5 °C with the coldest and warmest monthly average temperature being 19.4 and 27.3 °C, respectively. The total number of wild plant species in JFR is 2287 (Xu *et al.* 2012). Mountain rain forest and lowland rain forest are the two dominant vegetation types in JFR.

A total of 163 plots (25 × 25 m) were established from August 2007 to June 2009 in the middle of the reserve, with altitude ranging from 259 to 1135 m (Fig. S1, doi:10.5061/dryad.f0ph9). These plots were established on a 1 × 1 km grid, covering approximately 160 km² of the reserve. Each of the plots data set includes the following: altitude, soil properties and species identification of each free-standing stem with DBH ≥ 1.0 cm (species nomenclature followed the Flora of China). Soil properties were measured from five surface soil samples (0–30 cm) collected in each plot and combined. These properties included the following: dry season mass water content, exchangeable calcium content, exchangeable magnesium content, alkali-hydrolysable nitrogen content, available phosphorus content and available potassium content. The latter three soil indices represent nutrients in forms which are biologically available to plants.

Four main climate variables vary dramatically along the altitude gradients, including annual rainfall, annual rain days, annual average temperature and annual sunshine days (Fig. S2). Using several meteorological stations located at different altitudes, we found that following relationships with altitude *H* (expressed in metres):

$$\begin{aligned}
 P &= 1276.4 \times e^{0.009H}, \text{ where } P \text{ is annual rainfall} \\
 D &= 65.4 + 37.1 \times \log(H), \text{ where } D \text{ is annual rain days} \\
 T &= 25.0 - 0.006H, \text{ where } T \text{ is mean annual temperature, and} \\
 Sun &= 2398 - 0.97H, \text{ where } Sun \text{ is annual sunshine days (Jiang \& Lu 1991). Area decreases with altitude (Fig. S2). Soil properties were correlated with altitude (Fig. S3).}
 \end{aligned}$$

KERNEL METHODS FOR ESTIMATING SPECIES DISTRIBUTIONS, RICHNESS, DIVERSITY AND HABITAT PREFERENCE ALONG MULTIDIMENSIONAL HABITATS

The environmental space was defined as the first and second ordination axes (PC₁ and PC₂) of the principal components analysis of altitude and the six soil properties. The cumulative proportion of

variance explained by the PC₁ and PC₂ was 70% of the total variance.

In contrast to many biogeographic studies, where only information about the presence/absence is available, our data set provided information on species abundance. However, since environmental space is not equally sampled, observed abundances may not correctly represent the actual distribution of species on the entire range of the environmental conditions, resulting in potentially biased cells within the environmental space (Warren, Glor & Turelli 2008; Itoh *et al.* 2010; Broennimann *et al.* 2012). Therefore, a conditional kernel density estimator, called Nadaraya–Watson estimator, was applied to determine the expected value of a particular variable in each cell of a 2-dimensional habitat $x = (PC_1, PC_2)$ as:

$$E[y|x] = Y(x) = \frac{\sum_{i=1}^m y_i K_w(x - x_i)}{\sum_{i=1}^m K_w(x - x_i)}, \tag{eqn 1}$$

where y_i can be, for example, number of individuals, number of species or available soil nutrient observed at plot i . K_w is a quadratic kernel function, called Epanechnikov, $K_w(x) = 1 - (x/w)^2$ for $x < w$, zero otherwise. The kernel width, w , was set to $2.78\sigma_x m^{-1/5}$ to optimize error and bias (Silverman 1986; De Haan 1999), where σ_x is the standard deviation of the environmental axis.

Using the Nadaraya–Watson kernel approach, three axes of diversity were computed and used for hypothesis test. Species richness is computed as follows:

$$S(x) = \frac{\sum_{i=1}^m s_i K_w(x - x_i)}{\sum_{i=1}^m K_w(x - x_i)}, \tag{eqn 2}$$

where s_i is the number of species in the plot i . Equivalent species richness is computed as follows:

$$S^H(x) = \frac{\sum_{i=1}^m s_i^H K(x - x_i)}{\sum_{i=1}^m K(x - x_i)}, \tag{eqn 3}$$

where $s_i^H = \prod_{j=1}^{s_i} p_{ij}^{-p_{ij}}$ is a Shannon-equivalent species richness or Hill number with $q = 1$, and p_{ij} is the proportion of species j in the plot i . Habitat preference is computed as follows:

$$Z(x) = \frac{\sum_{j=1}^s N_j(x)}{\sum_{i=1}^m n_{ji}}, \tag{eqn 4}$$

where $N_j(x)$ is the expected abundance of species j conditional on the habitat x , and n_{ji} is the number of stems of species j in the plot i . The expected abundance is computed as follows:

$$N_j(x) = \frac{\sum_{i=1}^m n_{ji} K_w(x - x_i)}{\sum_{i=1}^m K_w(x - x_i)}. \tag{eqn 5}$$

Similar to Shannon-equivalent richness, preference function is a measure of evenness in the distribution of individuals along an environmental gradient. Preference function can be high where many range-restricted species occupy the same habitat and low where the habitat is occupied by wide range species, because range-restricted species have highly peaked abundance distributions, indicating that they have strong preferences. Some examples of species abundance distributions are shown in supporting information (Fig. S4).

CORRELATION ACROSS THE ENVIRONMENTAL SPACE FOR SPECIES WITH DIFFERENT RANGE SIZES

Species range is often defined as the convex Hull of its distribution, which is the smallest convex polygon that covers the distribution (Laurie & Silander 2002). A species range size index h [0, 1] is computed as the area of convex Hull, formed by the points in the 2-D environmental space, corresponding to plots where the species was found, divided by the area of convex Hull of all sampled plots.

Let h_j be the range size index of a species j and define $N(x|h)$ as the expected abundance–habitat function for species of range size h :

$$N(x|h) = \frac{\sum_j N_j(x) K_w(h - h_j)}{\sum_j K_w(h - h_j)}. \quad \text{eqn 6}$$

The overlap between habitats of species with different range size is studied with the Pearson correlation matrix:

$$R(h, h') = \text{corr}[N(x|h), N(x|h')]. \quad \text{eqn 7}$$

Positive/negative correlations mean that species with range size h and h' prefer/do not prefer the same habitats.

RANDOMIZATION TESTS

Ecological and statistical significance were evaluated with randomization methods. Randomizations aim to exclude spurious results derived from random sampling errors, which are particularly severe for rare species, and highlight significant hotspots of the three diversity axes. Three null models were formulated as follows:

1 Species composition and richness are independent from their habitats. This model was evaluated by random permuting the locations of the plots without changing species composition or abundance. The test reveals any significant association of species richness, diversity and preference with the environmental space.

2 Species compositions and distributions are independent from habitat, but species maintain the altitudinal range size. This model was evaluated by randomizing each species distribution while preserving the altitudinal range. Because of geometrical constraints imposed by habitat boundaries, it clearly shows a mid-domain effect (MDE).

3 Given an association between species richness and their environments, diversity is independent from the habitats. For this model, the community matrix was randomized in a way that preserved the number of species in each plot. Hence, the trend between richness and habitat remains unchanged, while any pattern in species diversity and preference is randomly permuted.

For each model, the calculation was repeated 1000 times, in order to obtain robust expectations and quantiles to ensure that the null hypothesis can be accepted or rejected with high confidence. Hotspots were defined as regions of the environmental space where one or more diversity functions were higher than 95% confidence interval of the null model. All analyses were done in R 3.1.0.

Results

SPECIES RICHNESS, DIVERSITY AND HABITAT PREFERENCE PATTERNS ACROSS A MULTIDIMENSIONAL ENVIRONMENT

Average number of species per plot varied from 62 to 94 and was strongly correlated with altitude, $R^2 = 0.74$, P -value $< 4e-6$ (Fig. 1). The trend was not monotonic, with a secondary local maximum around 400 m altitude. Species spanned about three orders of magnitude in abundance (Fig. 2a). Species range size was correlated with species abundance, $R^2 = 0.46$, P -value $< 1e-15$, with most abundant species occupying almost every available habitat (Fig. 2b, c).

The contents of the six soil properties among the 163 plots varied markedly (Table S1). The exchangeable calcium content has a maximum variation of 3000-fold. In three soil chemical variables, with biologically available forms, alkali-hydrolysable nitrogen content varied less than both available phosphorus content and available potassium content. Magnesium, potassium and calcium were strongly correlated.

Figure 3 shows the distribution of altitude and soil properties on the PC_1 – PC_2 axes indicating that higher elevation habitats were wetter and had higher nitrogen content. Magnesium, calcium and potassium were more available at mid altitude (ca. 600–800 m), while phosphorus showed three hotspots, in high, middle and low elevation.

With respect to altitude and soil properties, the species distribution showed a significant trend within the environmental space. Higher elevation, nitrogen and water availability supported richer and more diverse communities (Figs 3a,b,c and 4a,b) and multiple hotspots of diversity emerged. Habitat randomization and MDE were rejected, because low richness or diversity occurred in high altitude range, while high richness and diversity occurred in low altitude range (Figs 3a and 4g,

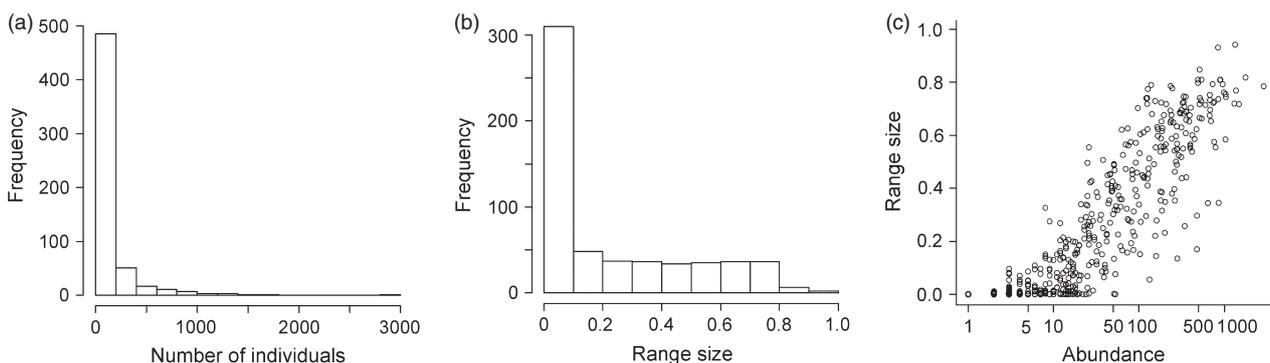


Fig. 2. (a) Histogram of species abundance distribution. (b) Histogram of species range size distribution. (c) Relationship between species abundance and range size distribution.

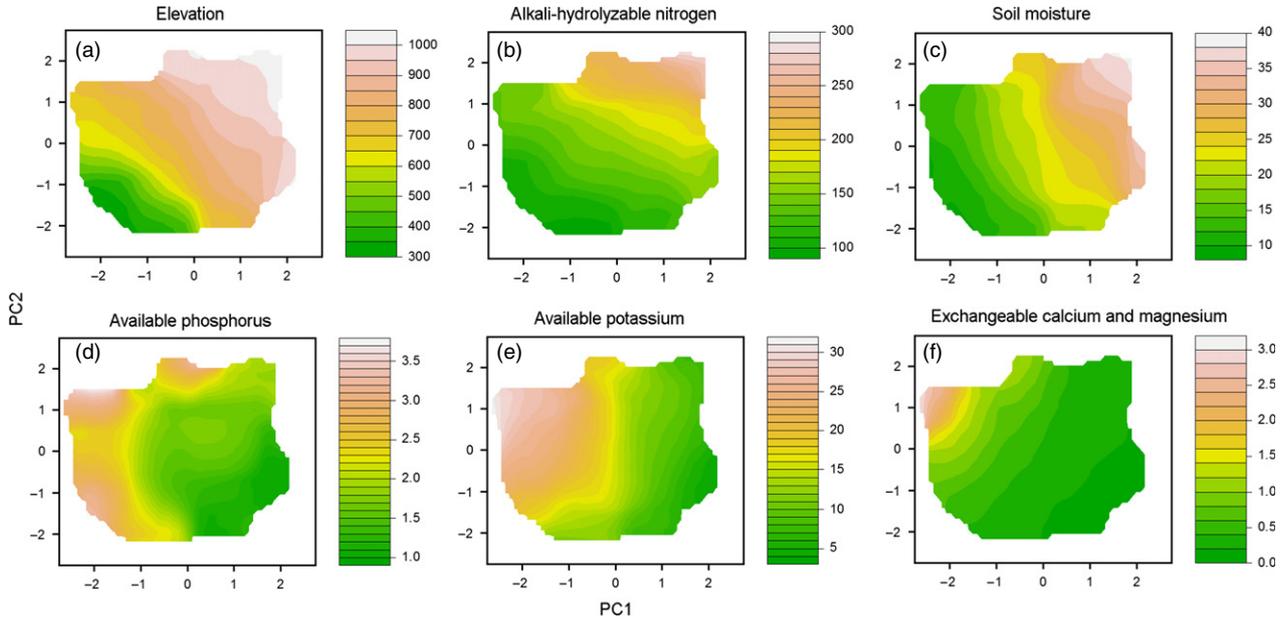


Fig. 3. Distribution of altitude and six soil properties along the first two principal components. Because exchangeable calcium and magnesium were highly correlated, only their sum is shown.

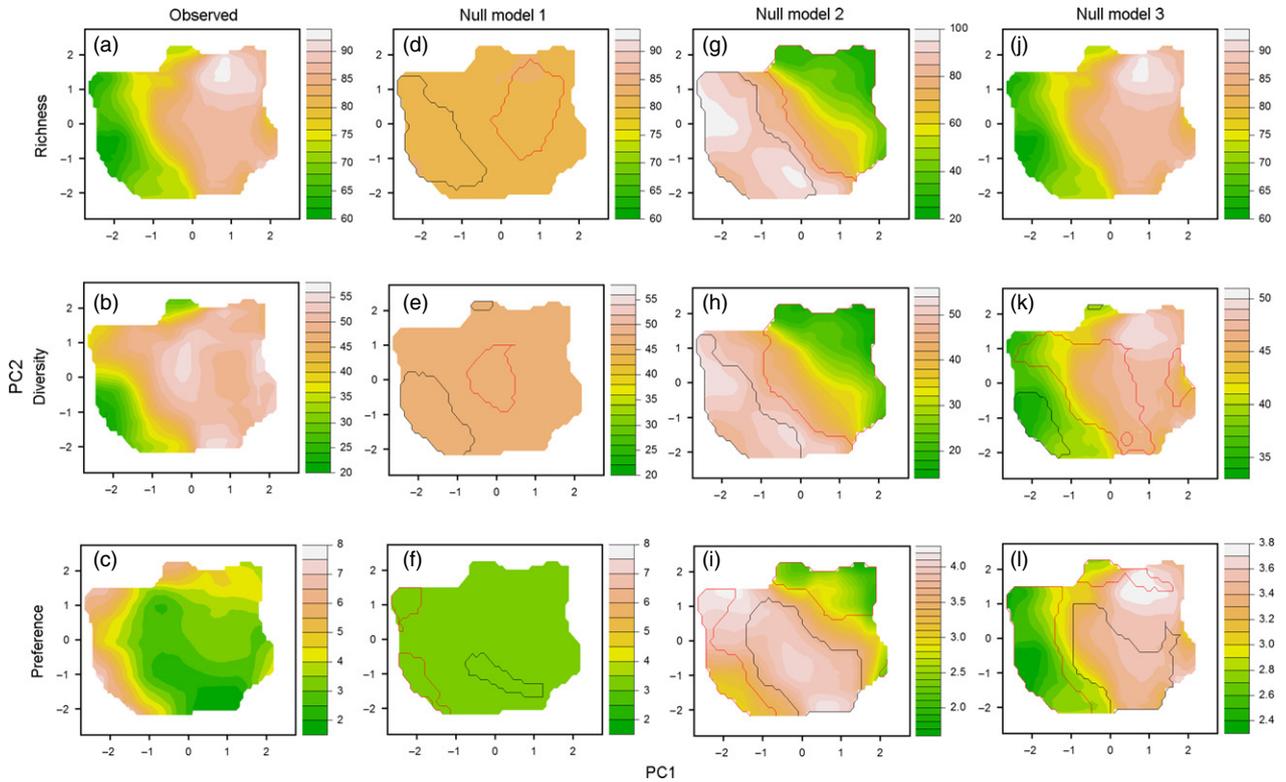


Fig. 4. (a–c) Species richness, Shannon-equivalent species richness and habitat preference distributions along the first two principal components. (d–f) Expectations of null model 1: random habitat association. (g–i) Expectations of null model 2: Mid-domain effect. (j–l) Expectations of null model 3: given richness–habitat association, diversity is independent on habitat. Contour lines are defined by the 95% confidence regions of 1000 randomizations with black (red) lines indicating lower (higher) than expected.

h). However, given the association between richness and habitat, some areas with less species had significant lower diversity than expected, while some areas with more species were more diverse than expected (Fig. 4k).

The habitat preference of species showed that the environment is not equally exploited and several hotspots appeared (Fig. 4c). These hotspots mainly occurred at the edge of the environmental space and significantly differed from the null

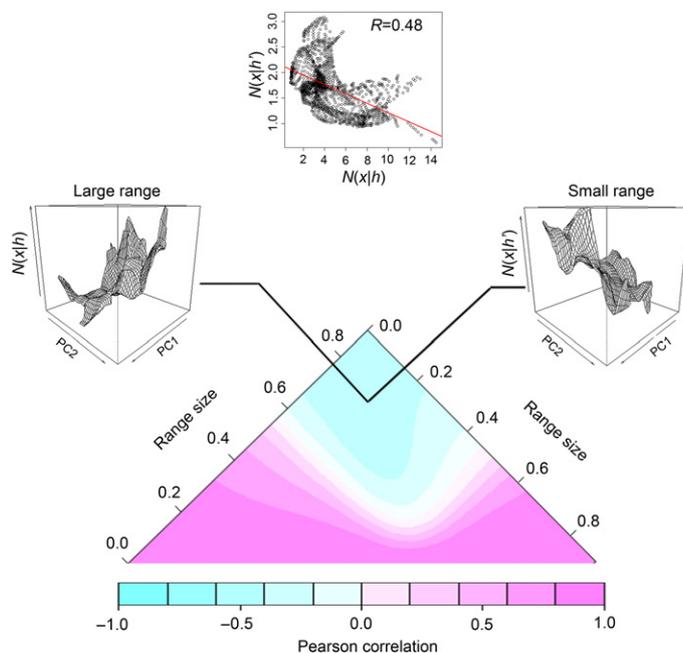


Fig. 5. Correlation matrix between species distributions along range sizes. Colours indicate Pearson coefficient of correlation. Range size is normalized from zero to one. As an example, the distributions of large ($h = 0.75$) and small range species ($h' = 0.15$) and their scatter plots are also shown.

model which randomizes the habitats (Fig. 4f) and the MDE (Fig. 4i), because hotspots were found in both high and low altitude ranges. Null model which randomizes species composition, preserving richness, revealed that these highly preferred habitats were less diverse than expected for a given number of species (Fig. 4l).

Interestingly, hotspots of habitat preference, richness and diversity did not overlap exactly (Figs 4a,b,c and S5), and these differences were significant (Fig. 4k,l), suggesting that different habitats support structurally different communities.

Further analyses on the species differentiation of habitat preference showed that large range species were negatively correlated with small range species (Fig. 5). Together with result from Fig. 4, we can infer that large range species tend to utilize dominant habitats, water and nitrogen rich, while rare species were restricted to marginal habitats. These marginal habitats were not necessarily low-quality habitats (Fig. 3). Further comparing areas with low species richness with each of the soil properties disclosed that these areas are high in phosphorous, calcium, magnesium and potassium (Fig. 3d–f) and this may explain why these habitats ranked high in preference. Phosphorus, in particular, seemed to be responsible for the preference hotspots which were identified in the analysis in Fig. 4c.

Discussion

HOTSPOTS AND THE DISTRIBUTION OF RARE AND ABUNDANT SPECIES

Environmental gradients have been long recognized as the critical primary factors shaping species distribution. Ample evidence has inferred the importance of altitude, climate and soil properties (Swaine 1996; Paoli, Curran & Zak 2006; Toledo *et al.* 2012; Condit *et al.* 2013), although less

literature has considered the species differentiation along multidimensional axes (Sklenár & Ramsay 2001; Wright *et al.* 2011; Condit *et al.* 2013). In our study, species richness increased with altitude, an uncommon but previously documented pattern, with plants along moderate altitudinal ranges (Grytnes 2003) and with other taxa, for example frogs and salamanders (Wake, Papenfuss & Lynch 1992). This pattern is associated with nitrogen and water availability, cooler temperature and lower radiation (Fig. S2). If we consider that the area–elevation curve decreases drastically with altitude (Fig. S2), the trend in species richness appears even more dramatic. Interestingly, areas with low richness and diversity along multidimensional environmental gradients were found to be preferred hotspots for rare species. This implies that other than dispersal or chance, species adopt different trade-off between environmental factors. This hypothesis is supported through several considerations.

Primarily, the preference hotspots were generally located in areas with high available phosphorous content (Fig. 3d), while species-rich communities were associated with greater nitrogen and water availability. This resulted in rare species to be confined to minor habitats, supporting previous reports that rare species are more aggregated than common species (Condit *et al.* 2000).

Secondly, this pattern was inconsistent with the prediction from MDE, an alternative hypothesis which reflects species influenced only by geometrical constraints (Colwell, Rahbek & Gotelli 2004). It cannot be excluded that MDE was still present, however, only in conjunction with other factors, and not as the main mechanism; though, testing this hypothesis with randomizations could prove more challenging.

Furthermore, rare and common species were negatively correlated and diversity was lower than expected in at least two hotspots. There was also a connection between species range size and habitat preference, which determines community

structure. This could be correlated to the strategies that different species adopt in order to utilize space and compete for resources. Explaining rarity of species in tropical forests remains an open question (Leigh *et al.* 2004) and, in particular, in determining the ecological dissimilarity of rare and common species. Here, we speculate that rare species tend to evade the strain of common species competition in their dominant areas, primarily, where some climatic and hydrological conditions are more favourable and nitrogen is more abundant, specializing in other resources. Species that have higher chance to survive in marginal environmental spaces are inevitably rare and persist because competition pressure is relatively low (Oberndorfer & Lundholm 2009; Lennon *et al.* 2011). This explanation is consistent with the hypothesis of niche differentiation, in that primary forests shelter a high number of rare species because they can provide more specialized microhabitats (Barlow *et al.* 2010); however, it also highlights the role of environmental heterogeneity in structuring communities.

IMPLICATIONS FOR CLIMATE CHANGE AND CONSERVATION

Range restrictions by multiple environmental factors indicate that species have optimum realized niches and are sensitive to habitat homogenization and climate changes (Dynesius & Jansson 2000; Olden *et al.* 2004). The more the range-restricted conditions for species, the less easy it becomes to disperse and adopt new habitats. This is especially apparent for rare species aggregated in marginal hotspots, which may not reside successfully in different habitats. If forced to migrate outside the optimum ranges, because of land use or climate changes, they are more susceptible to extinction (Midgley *et al.* 2002; Olden *et al.* 2004; Wilson *et al.* 2005; Colwell *et al.* 2008; Lenoir *et al.* 2008). Similarly, they cannot tolerate expansion of common species, which typically did not occupy and dominate these areas when climatic conditions were different. A 10% increase in precipitation is projected within this tropical region by the end of the century according to the RCP4.5 scenario of IPCC (Van Oldenborgh *et al.* 2013). Abundant species, which now live in higher elevations, may expand their range, attracted by the increase in water availability. Increasing precipitation and cloud cover will consequently reduce light availability, giving favour to higher elevation species which are more accustomed to lower light levels (Fig. S2).

Given these considerations, models that predict species distribution (Guisan & Thuiller 2005; Franklin *et al.* 2013; Storlie *et al.* 2013) should take into account multiple environmental gradients, combining soil properties and climate variables, as well as the interactions among habitat utilizers.

For conservation practices, our findings imply that, if limited by economic or social investments, efforts should be directed to protect habitat diversity. Unfortunately, these habitats, which host rare and range-restricted species (Schwartz 1999), do not frequently coincide with most species rich or diverse areas (Orme *et al.* 2005; Ceballos & Ehrlich 2006).

Naturally, we may not be able to conserve all species confined to minor habitats; however, we may improve the balance of resource limitation, considering different types of species distribution hotspots (Stork & Habel 2014) and projected habitat shifts (Jump, Mátyás & Peñuelas 2009). This study emphasizes the importance of habitat conservation diversity in tropical rain forests and the role of rare species in predicting biodiversity loss.

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Data accessibility

Xu, H. Data from: Habitat hotspots of common and rare tropical species along climatic and edaphic gradients. Dryad Digital Repository. doi:10.5061/dryad.f0ph9.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Summary statistics of six soil properties.

Figure S1. Geographic location of the 163 25 × 25 m plots in Jianfengling, Hainan Island, China.

Figure S2. Variation of four climate variables and forest area along altitude gradient.

Figure S3. Relationship between elevation and the first principal components of six soil properties ($R^2 = 0.27$, P -value < 1e-6).

Figure S4. Example of species density distribution in the 2-D domain (PC 1 and PC 2) defined by elevation and soil properties. (a), *Adinandra hainanensis* Hayata. (b), *Acronychia pedunculata* (Linnaeus) Miquel. (c), *Helicia reticulate* W. T. Wang. (d) *Benkara hainanensis* (Merrill) C. M. Taylor.

Figure S5. Total stem density distribution as function of the bidimensional environmental space. Stem density: individual per m².