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Soil resources and topography shape local tree community structure in tropical forests

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Both habitat filtering and dispersal limitation influence the compositional structure of forest communities, but previous studies examining the relative contributions of these processes with variation partitioning have primarily used topography to represent the influence of the environment. Here, we bring together data on both topography and soil resource variation within eight large (24–50 ha) tropical forest plots, and use variation partitioning to decompose community compositional variation into fractions explained by spatial, soil resource and topographic variables. Both soil resources and topography account for significant and approximately equal variation in tree community composition (9–34% and 5–29%, respectively), and all environmental variables together explain 13–39% of compositional variation within a plot. A large fraction of variation (19–37%) was spatially structured, yet unexplained by the environment, suggesting an important role for dispersal processes and unmeasured environmental variables. For the majority of sites, adding soil resource variables to topography nearly doubled the inferred role of habitat filtering, accounting for variation in compositional structure that would previously have been attributable to dispersal. Our results, illustrated using a new graphical depiction of community structure within these plots, demonstrate the importance of small-scale environmental variation in shaping local community structure in diverse tropical forests around the globe.

1. Introduction

A major challenge for community ecology is to understand the importance of niche-assembly processes in shaping community structure. This is of particular interest in species-rich communities such as tropical forests, because niche partitioning is thought to facilitate species coexistence and may, therefore, play an important role in biodiversity maintenance [1,2]. Evidence for the role of habitat partitioning among tropical forest tree species has been found from local to landscape scales, and comes from observed non-random associations between species distributions and environmental variables, and observations of species turnover along environmental gradients [3–10]. However, at local scales (less than 1 km^2), limited dispersal also plays an important role in determining species distributions, resulting in aggregated seedling and adult populations [11–13]. Disentangling the relative importance of niche and dispersal mechanisms to local community structure is problematic because both contribute to spatial correlation in species composition at this scale. Dispersal processes lead to spatially aggregated species distributions and, therefore, spatially structured communities. Additionally, habitat partitioning leads to spatial community structure owing to the high spatial correlation of environmental variables.

Despite substantial evidence for the importance of niche partitioning in structuring communities, surprisingly little is known about the relative influence of different environmental factors. At local scales, evidence for niche partitioning has been based mostly on topographic variation [4,5,7,14–17], as topography is relatively easily measured and acts as a useful proxy for habitat heterogeneity because it influences water availability and soil biogeochemical processes. However, recently created fine-scale soil resource maps for several tropical forest dynamics plots greatly enhance our ability to directly examine the effects of resource variation on tropical forest community structure. In a previous analysis using these soil maps for three neotropical forest plots, John *et al.* [10] found that *ca* 30–40% of tree species were non-randomly distributed with respect to soil nutrient variation. While these results indicate that soil resource variation influences the distributions of many individual species, the community-level effects of soil resource variation have not yet been examined extensively, nor has any study combined soil resource and topographic data to examine their relative contributions in shaping local species compositional variation.

Variation partitioning [18,19] via canonical redundancy analysis (RDA [20]) provides one way to assess the relative importance of habitat niche and dispersal-assembly processes, or of different sets of environmental variables on community structure. With variation partitioning, the total variation in community composition within a study area (an expression of the beta diversity of the area [21,22]) may be decomposed into fractions explained by different sets of variables (see fig. 1 in Legendre *et al*. [21]). To address the relative contribution of habitat niche and dispersal processes, the geographical coordinates of the sampling sites may be used to derive a set of spatial variables [23], and when paired with environmental variables, compositional variation may be partitioned into fractions explained by pure spatial variation, pure environmental variation, spatially structured environmental variation and the unexplained remainder [21]. The component of compositional variation that is explained by environmental variables (the pure environmental plus the spatially structured environmental component) is generally interpreted as resulting from species responses to measured environmental variation, whereas the component explained by pure spatial variation is thought to result from the influence of dispersal processes and species responses to unmeasured environmental variation [15,21,22].

Previous variation partitioning analyses of tropical forest community compositional variation have used topographic variables to estimate the contribution of the environment [15,17]. The addition of soil resource measurements to such analyses can reveal the importance of previously unmeasured environmental variation. If soil resources are relatively unimportant in shaping community structure or if soil resource variation strongly covaries with topography, then the proportion of variation explained by the environment would not greatly increase with the addition of soil resource variables. Alternatively, if soil resources exert an important influence on community structure beyond what can be explained by topography, then in the absence of information on soil resource variation, the contribution of the environment is underestimated and the contribution of dispersal processes is overestimated.

We combine data on both topography and soil resource variation for eight tropical forest plots to investigate the relative contributions of spatial and total topo-edaphic variation, as well as the relative contributions of topographic and soil resource variation, and the degree to which they are redundant with one another in explaining the community compositional variation of tropical forests. By assembling a more comprehensive battery of environmental variables, we may better resolve the relative contributions of environmental variation and dispersal processes to tropical forest community structure. To visualize compositional variation within a study site, we adapted a technique from landscape and regional mapping where an ordination of community composition is converted into a red-green-blue RGB image [24]. We use these 'beta diversity' maps to inform our interpretation of the variation partitioning results and illustrate that local habitat heterogeneity may be more important to tropical forest community structure than commonly thought.

2. Material and methods

(a) Study sites and environmental data

Our data come from eight long-term tropical forest dynamics plots of the Center for Tropical Forest Science (CTFS) network: Barro Colorado Island (BCI), Panama; Huai Kha Khaeng and Khao Chong, Thailand; Korup, Cameroon; La Planada, Colombia; Pasoh, Peninsular Malaysia; Sinharaja, Sri Lanka; and Yasuni, Ecuador. The forest plots range from 24 to 50 ha in size, span a number of biogeographic regions, and vary in soil fertility and precipitation regime—from continuously wet to seasonally dry. Within each plot, all free-standing trees larger than 1 cm dbh have been mapped, identified to species and measured for dbh according to a standard protocol [25]. Plot sizes and vegetation and soil characteristics are presented in table 1.

Topographic variables consisted of elevation, slope, convexity (the relative elevation of a quadrat with respect to its immediate neighbours), and aspect. Throughout each plot, elevation was recorded at the intersections of a 20×20 m grid and used to calculate topographic variables at the 20×20 m quadrat scale. Mean elevation was calculated as the mean of the elevation measurements at the four corners of a quadrat. Slope was calculated as the average slope of the four planes formed by connecting three corners of a quadrat at a time. Convexity was the elevation of a quadrat minus the average elevation of all immediate neighbour quadrats. Finally, aspect was the

Table 1. Study site characteristics. BCI, Barro Colorado Island.

study site	size (ha)	forest type	no. of species	elevation range (m)	soil order	soil variables used
BCI	50	semideciduous lowland moist	298	38	oxisol	Al, B, Ca, Cu, Fe, K, Mg, Mn, N-min., P, Zn, pH
Huai Kha Khaeng	50	seasonal dry evergreen	233	85	ultisol	Al, B, Ca, Cu, Fe, K, Mg, Mn, P, Zn, pH
Khao Chong	24	mixed evergreen	571	239	ultisol	Al, Ca, Fe, K, Mg, Mn, P, Zn, pH
Korup	50	lowland evergreen	452	95	oxisol/ ultisol	Al, Ca, Fe, K, Mg, Mn, P, Zn
La Planada	25	pluvial premontane	192	67	andisol	Al, Ca, Cu, Fe, K, Mg, Mn, N-min., P, pH
Pasoh	50	lowland mixed dipterocarp	790	24	ultisol/ entisol	Al, Ca, Cu, Fe, K, Mg, Mn, P
Sinharaja	25	mixed dipterocarp	199	145	ultisol	Al, Ca, Fe, K, P, pH
Yasuni	50	evergreen lowland wet	1088	32	ultisol	Al, Ca, Cu, Fe, K, Mg, Mn, N-min., P, Zn, pH

direction of the steepest slope of a quadrat, calculated in ArcMap v. 9.3 (www.esri.com).

Soil samples were collected throughout each plot, analysed, and the variables were kriged using comparable methods [10]. In each study site, soil samples were taken at the intersections of a 40 or 50 m grid across the study area, with additional samples taken near alternate grid points to estimate fine-scale variation in soil variables. The first 10 cm of topsoil was sampled, excluding the top organic horizon. Non-nitrogen elements were extracted with Mehlich-III solution and analysed on an atomic emission-inductively coupled plasma (AE-ICP, Perkin Elmer Inc., Massachusetts, USA), with the exception of phosphorus at the Yasuni study site, which was extracted with Bray extract solution and analysed by automated colorimetry on a Quickchem 8500 Flow Injection Analyzer (Hach Ltd., Loveland, CO, USA). For the three neotropical study sites (BCI, La Planada and Yasuni) an estimate of the *in situ* N-mineralization rate was taken at each sample location by measuring nitrogen before and after a 28 day incubation period. Nitrogen was extracted as NH_4^+ and NO_3^- with 2M KCl and analysed with an auto analyzer (OI FS 3000, OI Analytical, College Station, TX, USA). Sample values were kriged to obtain estimated concentrations of soil nutrients at the 20×20 m quadrat scale. The set of soil variables for each study site contained 6–12 variables, generally including Al, Ca, K, Mg, Mn, P and pH, but where available also included the N-mineralization rate, B, Cu, Fe and Zn (table 1).

(b) Partitioning beta diversity

Spatial patterns in community compositional variation were modelled with principal coordinates of neighbour matrices (PCNM) according to the methods described in Borcard & Legendre [23]. PCNM is a powerful technique that is able to model spatial structure in a dataset at any spatial scale that can be resolved by the sampling design (here, the 20×20 m spatial resolution) [15,23,26,27]. The method for calculating PCNM eigenfunctions [15] is briefly summarized as follows: a truncated geographical distance matrix was produced for all 20×20 m quadrats in a study site. In this matrix, neighbouring quadrats were determined using the queen criterion of contiguity (i.e. each quadrat has up to eight neighbours). The geographical distance between neighbours was retained, but the distances between all non-neighbour quadrats was replaced with a value of four times the distance between diagonally contiguous quadrats. A principal coordinates analysis was then performed on this truncated geographical distance matrix, and all eigenfunctions with positive eigenvalues were retained. These PCNM eigenfunctions made up the set of spatial variables used to model spatial structure in the community data.

We used canonical RDA [20] to partition the total compositional variation in a community into portions explained by spatial, soil and topographic variables at the 20×20 m scale. Throughout this study, we refer to the set of soil and topographic variables together as environmental variables. Prior to analysis, we expanded the set of environmental variables according to the method of Legendre *et al.* [15] to increase model flexibility, adding the squared and cubed values of each variable, with the exception of aspect. We included the sine and cosine of aspect as the only aspect variables. This created a set of 11 topographic variables and 18–36 soil variables for each study site. The proportion of variation explained by a set of variables is given as the adjusted R^2 of the explanatory variable set in the RDA, which is an unbiased estimator that corrects for the number of variables in the set [28].

For a more detailed look at the contributions of different variables, both the soil and topographic variable sets were separately subjected to forward selection to extract the important variables. In this forward selection procedure, new variables are added to the model in order of importance using two stopping criteria: each additional variable must be significant at the $\alpha = 0.05$ level, and the cumulative adjusted R^2 of the variable set may not exceed that of the adjusted R^2 of the full variable set [29]. The resulting cumulative adjusted R^2 values from the forward selection procedure were nearly identical to the adjusted R^2 values from the full variable sets, thus the adjusted R^2 values from the full variable sets were used represent the fraction of variation explained in the variation partitioning analysis. Variation partitioning with RDA was performed in the 'vegan' package [30] and forward selection was performed in the 'packfor' package [31] in the R statistical programming language (v. 2.13.0 [32]).

To check the robustness of our variation partitioning results to the type of canonical analysis used, we repeated the variation partitioning analysis with a distance-based RDA [33], based on square-root transformed Bray–Curtis distances among quadrats. Fractions of explained variation from the ordinary RDA were compared with those from the distance-based RDA. We also checked our results for robustness to plot size. Larger plots may be expected to have a higher beta diversity owing to the species–area relationship, and they may encompass greater environmental variation. For the five 50-ha plots, we compared the variation partitioning results with those obtained from their two 25-ha plot halves. Methodological details, results and discussion of these analyses are presented in the electronic supplementary material. The relative sizes of the variation fractions were found to be robust to the type of canonical analysis used and to differences in plot size; therefore, only the results of the ordinary RDA for original plot sizes are discussed here.

With all constrained ordination techniques, lack-of-fit of model to data occurs because ecological data are messy and do not perfectly match the species response model assumptions [34]. This lack-of-fit contributes to the unexplained portion of variation, and may be large (30–70% in simulated communities [34]), but the size depends on the dataset. Following the recommendations of Økland [34], we avoid comparing the fractions of variation explained among study sites, and focus on comparing the relative sizes of fractions of variation explained by different variable sets within a single study site.

(c) Beta diversity maps

To produce a map of community composition within a study site, we first calculated the Bray–Curtis distances among all 20 $\times$ 20 m quadrats within a study site, then this distance matrix was subjected to non-metric multi-dimensional scaling on three ordination axes. Each quadrat's position in three-dimensional ordination space was then translated into an RGB colour by assigning quadrat positions on ordination axes 1, 2 and 3 to intensities of red, green and blue, respectively [24]. We applied the same translation from axis position to colour intensity to all axes simultaneously, so that the variation shown by each of the colours is proportional to the variation explained by its respective axis. The red, green and blue components of each quadrat were combined to create RGB colours that were then mapped. This method of mapping community structure displays a greater portion of community variation than possible by displaying one species or ordination axis at a time.

3. Results

(a) Niche and dispersal assembly

Total explained variation from environmental and spatial variables together varied markedly among sites, ranging from 32 per cent at La Planada to 74 per cent at Korup and Sinharaja (table 2, refer to diagram of fractions in figure 1). Across study sites, nearly all the total explained variation was accounted for by the spatial variables, resulting in an effective lack of pure environmental variation. The proportion of variation explained by environmental variables also varied widely from site to site, from as little as 13 per cent at La Planada to as much as 39 per cent at Khao Chong (table 2). The proportion of variation explained by spatial variables alone (after controlling for the effect of environmental variation) ranged from 19 to 37%, similar in magnitude to the variation explained by environmental variables.

(b) Soil resource and topographic effects

The sets of soil and topographic variables each explained a statistically significant proportion of compositional variation

Table 2. Variation partitioning results for spatial, soil and topographic variables. Components are labelled with reference to figure 1: total = the proportion of variation explained by all spatial and environmental variables combined (a + b + c + d + e + f + g); space = the proportion explained by spatial variables (a + d + f + g); env. = the proportion explained by environmental variables (b + c + d + e + f + g); space|env. = the pure spatial component (a); space&env. = the spatially structured environmental component (d + f + g); env.|space = the pure environmental component (b + c + e); soil = the proportion explained by soil variables (b + d + e + g); topo. = the proportion explained by topographic variables (c + e + f + g); soil|topo. = the proportion explained by soil after accounting for topography (b + d); soil&topo = the topographically structured soil component (e + g); topo.|soil = the proportion explained by topography after accounting for soil (c + f).

study site	total	space	env.	space|env.	space&env.	env.|space	soil	topo.	soil|topo.	soil&topo.	topo.|soil
BCI	0.54	0.54	0.25	0.29	0.25	0.00	0.20	0.13	0.12	0.08	0.04
Huai Kha Khaeng	0.47	0.45	0.14	0.33	0.11	0.02	0.09	0.08	0.06	0.03	0.04
Khao Chong	0.61	0.57	0.39	0.22	0.35	0.03	0.34	0.17	0.22	0.12	0.05
Korup	0.74	0.74	0.38	0.36	0.38	0.00	0.30	0.28	0.10	0.19	0.09
La Planada	0.32	0.29	0.13	0.19	0.10	0.03	0.11	0.05	0.08	0.03	0.02
Pasoh	0.47	0.47	0.20	0.28	0.19	0.01	0.17	0.10	0.10	0.07	0.03
Sinharaja	0.74	0.73	0.37	0.37	0.36	0.01	0.20	0.29	0.08	0.12	0.17
Yasuni	0.50	0.49	0.22	0.28	0.21	0.01	0.17	0.11	0.11	0.06	0.05

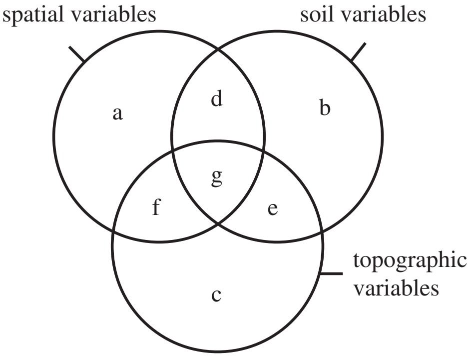

Figure 1. Diagram of variation fractions for a three-way variation partitioning of the variable sets used in this study. Letters correspond to those given for the variation fractions in table 2.

at every study site ($p < 0.001$). Soil variables explained more variation than topographic variables in seven of the eight study sites (table 2). Additionally, at six of the study sites (excepting Korup and Sinharaja), the amount of additional variation explained by soil resource variables after accounting for topographic variables was similar to the amount explained by topographic variables alone, thus effectively doubling the proportion of variation accounted for by the environment.

(c) Beta diversity maps

Maps of plot beta diversity are presented alongside site elevation maps in figure 2. In the beta diversity maps, quadrats of similar colour contain similar tree communities (lower Bray–Curtis dissimilarity), providing a visual interpretation of both the turnover between any two quadrats within a study site and the total variation in community composition. The maps for Korup and Sinharaja (figure 2*b*,*f*), where 74 per cent of the variation in community composition is explained by environmental and spatial variables, clearly show far more spatial structure than the La Planada map (figure 2*e*), where only 32 per cent of variation is explained. These maps also reveal community responses to specific environmental features, such as the stream bed running east to west across the Pasoh study site (figure 2*c*) and the swamp located near the centre of the Barro Colorado Island study site (figure 2*a*; cf. fig. 1 in Harms *et al*. [4]).

4. Discussion

The interpretation of the relative roles of niche and dispersal processes is complicated by the fact that the purely spatial fraction of compositional variation is attributed to the effects of dispersal-assembly and species responses to unmeasured environmental variation. Our analysis demonstrates the importance of previously unmeasured environmental variation in shaping community structure in tropical forests: the inclusion of soil resource data in the analysis nearly doubled the proportion of variation explained by environmental variables compared with topography alone at most sites. Although the soil and topographic variables covary, neither the effect of soil nor the effect of topography was entirely nested within the other, indicating that both soil resources and topography have important and independent effects on community structure in a wide variety of tropical forest communities.

There is certainly still important unmeasured environmental variation (i.e. light, soil moisture and drainage) that contributes to the community structure of these forests. Some variables, such as soil moisture and drainage, which exhibit spatial variation over larger spatial scales (hundreds of meters), may contribute to the portion of variation that is spatially structured yet unexplained by our environmental variable set. Other important unmeasured environmental variables may exhibit spatial structure that is not captured by the 20×20 m resolution of our study design, such as light availability, which may vary dramatically over distances less than 20 m [35]. Species responses to such environmental variables may contribute to the unexplained portion of compositional variation, along with stochasticity in species distributions and model lack-of-fit [22,34]. However, our data for any one study site are among the most complete environmental datasets for any tropical forest community. The large proportion of community variation that is spatially structured and remains unaccounted for by either soil or topographic variables suggests an important role for dispersal-assembly alongside habitat niche processes in shaping community structure in these forests.

The spatial resolution of our analysis is also expected to affect the balance between the proportion of variation explained by environmental and pure spatial variation [15], and thus the inferred relative importance of habitat niche and dispersal-assembly processes. As the spatial resolution of the analysis decreases (or quadrat size becomes larger), smaller scale dispersal effects and environmental heterogeneity are smoothed over, causing the explanatory power of the environment to increase [15]. For this analysis, we chose the 20×20 m resolution because this quadrat size best represents soil resource variation as measured by our sampling scheme, and it is the scale at which elevation was measured. Therefore, the sizes of the fractions of compositional variation that are explained by environmental and pure spatial variation are specific to the 20×20 m resolution of our analysis.

The beta diversity maps we generated help inform the interpretation of our variation partitioning results. From these maps one can see that the topographic signature on community structure is strong at many of the sites even though the set of topographic variables always accounts for less than 30 per cent of compositional variation (figure 2 and table 2). The variable selection procedure identified slope as the most important topographic variable at the BCI study site, explaining 3.4 per cent of compositional variation (see the electronic supplementary material, table S4), yet this effect can be discerned from the RGB map (figure 2*a*; cf. fig. 1 in Harms *et al*. [4]). The four most important topographic variables from the variable selection procedure (elevation, convexity, slope and cosine of aspect) explain 9.6 per cent of the community variation at the Yasuni study site (see the electronic supplementary material, table S4), and there is a strong similarity between the beta diversity and topographic maps for this site (figure 2*d*). The strongest effect of any single environmental variable on community structure in our study is elevation at Sinharaja, explaining 14.7 per cent (see the electronic supplementary material, table S4), which coincides with sharply defined features of the community (figure 2*f*). Therefore, in the context of our analysis, a variable that explains 3 per cent of variation in community composition may have a discernible but subtle effect on community structure, whereas a variable that explains 15 per cent

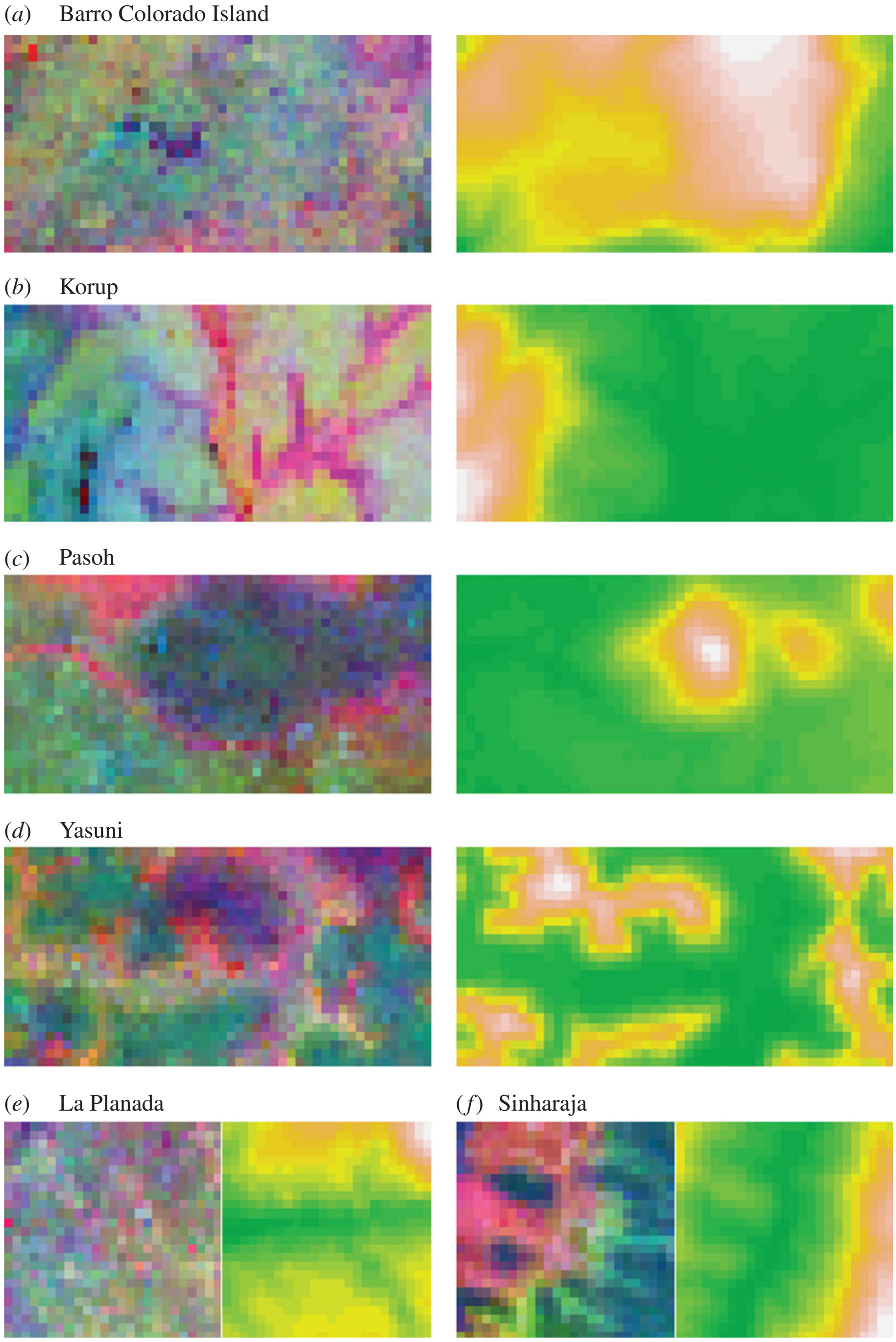

Figure 2. Beta diversity maps along with elevation maps for six of the eight study sites: (*a*) Barro Colorado Island, Panama; (*b*) Korup, Cameroon; (*c*) Pasoh, Penninsular Malaysia; (*d*) Yasuni, Ecuador; (*e*) La Planada, Colombia; and (*f*) Sinharaja, Sri Lanka. Beta diversity and elevation maps for Huai Kha Kheng and Khao Chong, Thailand are in the electronic supplementary material, figure S2. In elevation maps, the colour scheme moves from dark green (low elevation) to white (high elevation). The colours of the community map have no absolute meaning—only the colour differences between locations within the same study site are meaningful.

may have a very strong effect. The fact that environmental factors that appear to be quite ecologically important may account for less than 5 per cent of compositional variation in an RDA is unsurprising when one considers the great deal of random noise in ecological data and the lack-of-fit of model to data inherent in constrained ordination techniques [34].

We found that the proportion of community compositional variation explained by the environment greatly increased with the addition of soil resource variables to the environmental variable set relative to topographic variables alone. The inclusion of a more comprehensive set of environmental variables in our variation partitioning analysis shifts our understanding of the relative importance of habitat filtering and dispersal processes towards greater importance of habitat filtering. Additionally, maps of beta diversity plotted as an RGB image indicate that environmental factors that account for a small proportion (less than 5%) of compositional variation may nonetheless produce an important signal in community structure. For these reasons, we argue that the role of habitat filtering may have been underappreciated in the past.

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Appendix S1. Methods for checking robustness of results to canonical analysis and plot size

Distance-based RDA

For the distance-based RDA (Legendre & Anderson 1999), principal coordinate analysis was performed on the square-root transformed Bray-Curtis distance matrix. Bray-Curtis distances were square-root transformed to allow distance relationships to be fully represented in Euclidian space (i.e., eliminate negative eigenvalues; Legendre & Legendre 1998). The principal coordinates were then submitted to variation partitioning with RDA. Thus, the Euclidian distances among quadrats preserved by RDA are equal to the square-root of the Bray-Curtis distance.

The variation partitioning results for the distance-based RDA using square-root transformed Bray-Curtis distances are presented in Table S1. For comparison, the variation explained by each of the two variation partitioning methods (distance-based RDA and plain RDA) are plotted in Fig. S1. In general, the magnitude of the explained variation fraction was larger when based on the plain RDA than when based on the distance-based RDA. However, the results were highly correlated between the two methods (Fig. S1). Based on these results, we conclude that the relative sizes of our explained variation fractions were robust to the method used to calculate them. Our results also highlight the fact that the proportion of variation found to be explained by a set of explanatory variables depends heavily on the method of canonical analysis chosen.

Plot size

To test for the robustness of our results to plot size, we split each of the five 50-ha plots in half and recalculated the variation partitioning results for each of the 25-ha halves. The variation partitioning results for both halves of the 50-ha plots are presented in Table S2. In general, the proportion of variation explained by the environment was slightly greater, and the proportion of variation explained by spatial variables was slightly smaller, for the 25-ha subsections than for the entire 50-ha plots. However, these differences were very small (1-3% of the total variation, comparing the average value for the two 25-ha subplots to the value from the 50-ha plot). This difference is usually less than the differences among variation fractions within the same plot, or among the same variation fraction at different plots. Therefore, these effects do not change the overall interpretation of our results, in terms of the relative importance of different sets of variables. However, it is worth noting that in our analysis we found a slight tendency toward greater spatial variation and less environmental variation with larger plot size within the same plot. More extreme differences in plot size may result in larger biases that need to be factored into variation partitioning analyses.

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Tables and Figures

Table S1. Variation partitioning results for spatial, soil, and topographic variables from a distance-based RDA using square-root transformed Bray-Curtis distances among subplots. Components are referred to with reference to Fig. 1: total = the proportion of variation explained by all spatial and environmental variables combined (a+b+c+d+e+f+g); space = the proportion explained by spatial variables (a+d+f+g); env. = the proportion explained by environmental variables (b+c+d+e+f+g); space|env. = the pure spatial component (a); space&env. = the spatially structured environmental component (d+f+g); env.|space = the pure environmental component (b+c+e); soil = the proportion explained by soil variables (b+d+e+g); topo. = the proportion explained by topographic variables (c+e+f+g); soil|topo. = the proportion explained by soil after accounting for topography (b+d); soil&topo = the topographically structured soil component (e+g); topo.|soil = the proportion explained by topography after accounting for soil (c+f).

study site	total	space	env.	space|env.	space&env.	env.|space	soil	topo.	soil|topo.	soil&topo.	topo.|soil
BCI	0.26	0.26	0.13	0.13	0.13	0.00	0.11	0.07	0.06	0.05	0.02
Huai Kha Khaeng	0.23	0.22	0.09	0.13	0.09	0.00	0.07	0.06	0.03	0.04	0.02
Khao Chong	0.31	0.30	0.18	0.13	0.18	0.00	0.15	0.10	0.08	0.06	0.04
Korup	0.41	0.41	0.22	0.20	0.21	0.01	0.17	0.17	0.05	0.12	0.05
La Planada	0.17	0.16	0.08	0.09	0.07	0.01	0.06	0.04	0.04	0.02	0.02
Pasoh	0.22	0.21	0.10	0.12	0.10	0.00	0.08	0.05	0.04	0.04	0.02
Sinharaja	0.47	0.46	0.26	0.21	0.25	0.01	0.15	0.21	0.05	0.10	0.11
Yasuni	0.20	0.20	0.10	0.10	0.10	0.00	0.07	0.06	0.04	0.03	0.03

Table S2. Variation partitioning results for spatial, soil, and topographic variables from the two 25-ha subplots created by halving each of the five 50-ha plots. Components are referred to with reference to Fig. 1: total = the proportion of variation explained by all spatial and environmental variables combined (a+b+c+d+e+f+g); space = the proportion explained by spatial variables (a+d+f+g); env. = the proportion explained by environmental variables (b+c+d+e+f+g); space|env. = the pure spatial component (a); space&env. = the spatially structured environmental component (d+f+g); env.|space = the pure environmental component (b+c+e); soil = the proportion explained by soil variables (b+d+e+g); topo. = the proportion explained by topographic variables (c+e+f+g); soil|topo. = the proportion explained by soil after accounting for topography (b+d); soil&topo = the topographically structured soil component (e+g); topo.|soil = the proportion explained by topography after accounting for soil (c+f).

study site	total	space	env.	space|env.	space&env.	env.|space	soil	topo.	soil|topo.	soil&topo.	topo.|soil
BCI	0.54/0.49	0.55/0.49	0.27/0.28	0.27/0.21	0.28/0.28	0.00/0.00	0.22/0.24	0.16/0.16	0.11/0.12	0.11/0.13	0.05/0.04
Huai Kha Khaeng	0.44/0.50	0.37/0.48	0.18/0.16	0.25/0.34	0.12/0.14	0.06/0.02	0.15/0.11	0.09/0.11	0.10/0.06	0.05/0.05	0.03/0.05
Korup	0.73/0.70	0.72/0.68	0.42/0.37	0.31/0.33	0.41/0.35	0.01/0.01	0.26/0.27	0.31/0.25	0.11/0.12	0.15/0.15	0.16/0.10
Pasoh	0.47/0.45	0.46/0.44	0.24/0.21	0.23/0.24	0.23/0.20	0.01/0.01	0.21/0.18	0.11/0.11	0.13/0.10	0.08/0.07	0.03/0.04
Yasuni	0.47/0.49	0.46/0.48	0.26/0.27	0.21/0.22	0.25/0.26	0.01/0.01	0.21/0.22	0.13/0.15	0.14/0.13	0.08/0.10	0.05/0.05

Table S3. Forward selection results for the set of soil variables for each study site. Variables are listed in order of addition to the model, along with the cumulative adjusted R^2, giving the variation explained by the variable plus all previous variables.

(a) BCI

Rank	Variable	R^2adj. Cum	P-val
1	Cu	0.045	0.001
2	Mg	0.079	0.001
3	P	0.098	0.001
4	Al	0.113	0.001
5	Fe	0.130	0.001
6	Nmin.cu	0.139	0.001
7	pH	0.146	0.001
8	Cu.sq	0.152	0.001
9	Mg.sq	0.157	0.001
10	Nmin	0.162	0.001
11	K	0.165	0.001
12	K.sq	0.169	0.001
13	B	0.172	0.001
14	Mn	0.175	0.001
15	pH.cu	0.177	0.001
16	Mn.sq	0.180	0.002
17	Fe.sq	0.181	0.008
18	K.cu	0.183	0.006
19	Cu.cu	0.187	0.001
20	Mn.cu	0.188	0.005
21	Ca	0.190	0.003
22	Al.cu	0.192	0.004
23	Al.sq	0.193	0.005
24	Fe.cu	0.194	0.012
25	pH.sq	0.196	0.009
26	Nmin.sq	0.197	0.015
27	P.cu	0.198	0.035
28	B.sq	0.198	0.040
29	Mg.cu	0.199	0.040
30	B.cu	0.200	0.020
31	Zn	0.200	0.049

(b) Huai Kha Khaeng

Rank	Variable	R^2adj. Cum	P-val
1	K	0.019	0.001
2	Zn	0.030	0.001
3	Ca	0.038	0.001

4	P.sq	0.045	0.001
5	Ca.cu	0.049	0.001
6	pH	0.053	0.001
7	K.sq	0.057	0.002
8	Cu	0.060	0.001
9	Cu.sq	0.062	0.003
10	Cu.cu	0.066	0.010
11	Fe.cu	0.069	0.003
12	Mn.sq	0.072	0.002
13	Al	0.074	0.005
14	Al.sq	0.077	0.005
15	Zn.sq	0.080	0.011
16	Ca.sq	0.082	0.003
17	Al.cu	0.084	0.007
18	pH.cu	0.086	0.018
19	B	0.088	0.006
20	K.cu	0.089	0.026
21	B.sq	0.091	0.029
22	Mn	0.092	0.046

(c) Khao Chong

Rank	Variable	R^2adj. Cum	P-val
1	K	0.071	0.001
2	pH.cu	0.151	0.001
3	pH.sq	0.204	0.001
4	pH	0.230	0.001
5	Mn.sq	0.245	0.001
6	Mg.sq	0.268	0.001
7	Al.cu	0.276	0.001
8	P	0.284	0.001
9	Mg	0.291	0.001
10	Fe.cu	0.298	0.001
11	Fe	0.303	0.001
12	K.cu	0.309	0.001
13	Zn	0.313	0.001
14	Mn	0.317	0.002
15	K.sq	0.320	0.001
16	Mg.cu	0.323	0.002
17	Ca	0.325	0.009
18	Al	0.327	0.010
19	Al.sq	0.328	0.029

(d) Korup

Rank	Variable	R^2adj. Cum	P-val
1	Mn	0.124	0.001
2	P	0.165	0.001
3	K	0.190	0.001
4	Fe	0.203	0.001
5	Mn.sq	0.214	0.001
6	Fe.sq	0.223	0.001
7	K.sq	0.231	0.001
8	Ca	0.239	0.001
9	Zn	0.246	0.001
10	Al.cu	0.252	0.001
11	P.cu	0.256	0.001
12	Zn.sq	0.262	0.001
13	Zn.cu	0.266	0.001
14	Ca.sq	0.269	0.001
15	Ca.cu	0.274	0.001
16	Mg	0.277	0.001
17	Mg.sq	0.280	0.001
18	Mg.cu	0.286	0.001
19	K.cu	0.288	0.001
20	Fe.cu	0.290	0.001
21	Mn.cu	0.291	0.002
22	P.sq	0.292	0.015
23	Al	0.293	0.047
24	Al.sq	0.295	0.001

(e) La Planada

Rank	Variable	R^2adj. Cum	P-val
1	P	0.024	0.001
2	Fe	0.045	0.001
3	K	0.057	0.001
4	pH.cu	0.064	0.001
5	Cu.cu	0.070	0.001
6	Ca	0.073	0.001
7	Mg.sq	0.079	0.001
8	Mn	0.082	0.005
9	Mg	0.084	0.009
10	Al.sq	0.087	0.007
11	P.cu	0.089	0.006
12	Cu.sq	0.093	0.003
13	Cu	0.096	0.008
14	K.sq	0.098	0.011

15	K.cu	0.102	0.001

(f) Pasoh

Rank	Variable	R^2adj. Cum	P-val
1	Mn	0.051	0.001
2	P	0.084	0.001
3	Mn.sq	0.099	0.001
4	K.sq	0.112	0.001
5	Ca.cu	0.120	0.001
6	Fe	0.124	0.001
7	Cu	0.129	0.001
8	Ca	0.132	0.001
9	Cu.sq	0.135	0.001
10	K	0.138	0.001
11	Mn.cu	0.141	0.001
12	K.cu	0.143	0.001
13	Cu.cu	0.146	0.001
14	Al.cu	0.148	0.001
15	Al.sq	0.152	0.001
16	P.cu	0.154	0.001
17	Mg	0.156	0.001
18	Ca.sq	0.158	0.001
19	Mg.sq	0.160	0.001
20	P.sq	0.161	0.001
21	Fe.sq	0.162	0.001
22	Al	0.164	0.001
23	Fe.cu	0.165	0.001
24	Mg.cu	0.166	0.010

(g) Sinharaja

Rank	Variable	R^2adj. Cum	P-val
1	P	0.069	0.001
2	K	0.116	0.001
3	pH	0.132	0.001
4	Fe	0.145	0.001
5	Al	0.158	0.001
6	Fe.sq	0.164	0.004
7	K.cu	0.171	0.001
8	P.sq	0.177	0.001
9	K.sq	0.179	0.033

(h) Yasuni

Rank	Variable	R^2adj. Cum	P-val
1	pH	0.062	0.001
2	Fe	0.076	0.001
3	pH.cu	0.088	0.001
4	Mn	0.097	0.001
5	Zn	0.104	0.001
6	Ca	0.110	0.001
7	K	0.115	0.001
8	Ca.sq	0.119	0.001
9	Zn.cu	0.124	0.001
10	Ca.cu	0.128	0.001
11	K.sq	0.131	0.001
12	Mg	0.134	0.001
13	Al	0.138	0.001
14	Nmin	0.140	0.001
15	pH.sq	0.144	0.001
16	Nmin.sq	0.146	0.001
17	Fe.sq	0.148	0.001
18	Mn.sq	0.150	0.001
19	Cu	0.152	0.001
20	Cu.sq	0.153	0.001
21	Zn.sq	0.156	0.001
22	Mg.sq	0.157	0.002
23	Al.sq	0.159	0.001
24	Al.cu	0.161	0.001
25	Mn.cu	0.163	0.002
26	P.sq	0.164	0.001
27	Mg.cu	0.165	0.004
28	K.cu	0.166	0.004
29	Cu.cu	0.167	0.023
30	Fe.cu	0.167	0.024
31	Nmin.cu	0.168	0.049

Table S4. Forward selection results for the set of topographic variables for each study site. Variables are listed in order of addition to the model, along with the cumulative adjusted R^2, giving the variation explained by the variable plus all previous variables.

(a) BCI

Rank	Variable	R^2adj. Cum	P-val
1	slope	0.034	0.001
2	cos.asp	0.056	0.001
3	sin.asp	0.072	0.001
4	meanelev.cu	0.087	0.001
5	meanelev.sq	0.102	0.001
6	convex	0.108	0.001
7	slope.sq	0.115	0.001
8	slope.cu	0.122	0.001
9	meanelev	0.127	0.001
10	convex.sq	0.129	0.010

(b) Huai Kha Khaeng

Rank	Variable	R^2adj. Cum	P-val
1	sin.asp	0.034	0.001
2	meanelev	0.052	0.001
3	meanelev.sq	0.060	0.001
4	cos.asp	0.067	0.001
5	slope	0.070	0.001
6	meanelev.cu	0.072	0.004
7	convex	0.073	0.018
8	slope.cu	0.074	0.033

(c) Khao Chong

Rank	Variable	R^2adj. Cum	P-val
1	meanelev.cu	0.037	0.001
2	slope	0.093	0.001
3	cos.asp	0.111	0.001
4	meanelev	0.128	0.001
5	meanelev.sq	0.142	0.001
6	convex	0.152	0.001
7	slope.cu	0.160	0.001
8	sin.asp	0.165	0.007
9	convex.sq	0.168	0.018
10	slope.sq	0.169	0.046

(d) Korup

Rank	Variable	R^2adj. Cum	P-val
1	slope	0.115	0.001

2	meanelev	0.144	0.001
3	meanelev.sq	0.187	0.001
4	meanelev.cu	0.231	0.001
5	convex	0.255	0.001
6	slope.sq	0.261	0.001
7	cos.asp	0.266	0.001
8	convex.cu	0.271	0.001
9	sin.asp	0.275	0.001
10	slope.cu	0.278	0.001
11	convex.sq	0.281	0.001

(e) La Planada

Rank	Variable	R^2adj. Cum	P-val
1	cos.asp	0.011	0.001
2	meanelev	0.021	0.001
3	convex	0.028	0.001
4	convex.sq	0.033	0.002
5	slope	0.037	0.001
6	slope.cu	0.043	0.001
7	slope.sq	0.046	0.003
8	meanelev.sq	0.048	0.013
9	sin.asp	0.049	0.031
10	convex.cu	0.051	0.044

(f) Pasoh

Rank	Variable	R^2adj. Cum	P-val
1	meanelev	0.057	0.001
2	meanelev.sq	0.069	0.001
3	convex	0.077	0.001
4	slope	0.082	0.001
5	meanelev.cu	0.086	0.001
6	cos.asp	0.089	0.001
7	convex.sq	0.092	0.001
8	slope.sq	0.094	0.001
9	sin.asp	0.096	0.001
10	slope.cu	0.097	0.003
11	convex.cu	0.098	0.047

(g) Sinharaja

Rank	Variable	R^2adj. Cum	P-val
1	meanelev	0.147	0.001
2	convex	0.192	0.001
3	cos.asp	0.231	0.001

4	sin.asp	0.246	0.001
5	meanelev.cu	0.258	0.001
6	meanelev.sq	0.266	0.001
7	convex.cu	0.274	0.010
8	slope	0.281	0.001
9	slope.cu	0.284	0.004
10	convex.sq	0.287	0.010

(h) Yasuni

Rank	Variable	R^2adj. Cum	P-val
1	meanelev	0.058	0.001
2	convex	0.077	0.001
3	slope	0.090	0.001
4	cos.asp	0.096	0.001
5	slope.sq	0.101	0.001
6	convex.sq	0.104	0.001
7	meanelev.sq	0.106	0.001
8	sin.asp	0.107	0.001
9	slope.cu	0.109	0.004
10	meanelev.cu	0.110	0.001
11	convex.cu	0.111	0.006

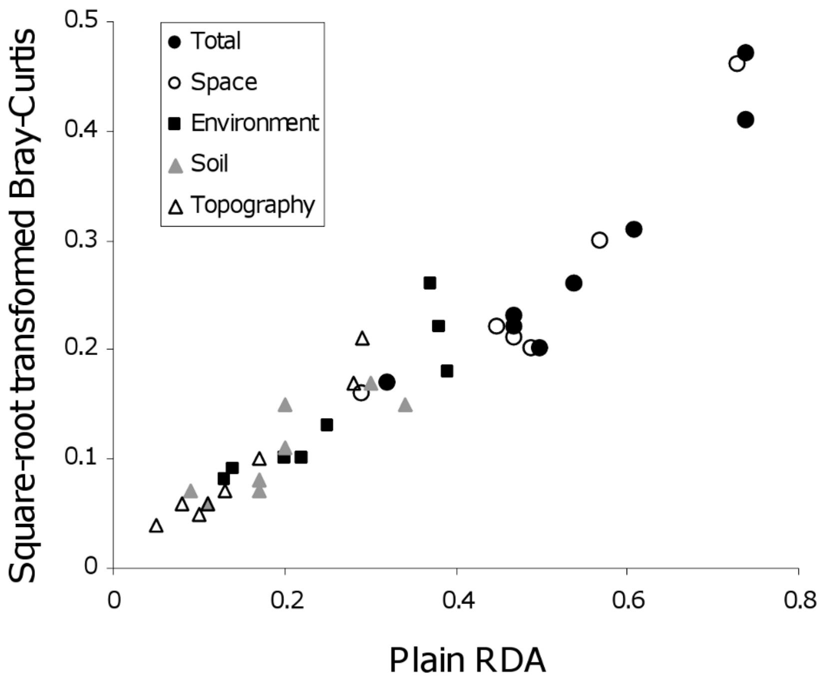

Figure S1. The proportion of variation explained calculated using plain RDA and using distance-based RDA based on square-root transformed Bray-Curtis distances among quadrats. The results are given for five explained variation fractions: total variation explained and the variation explained by spatial, environmental, soil, and topographic variables.

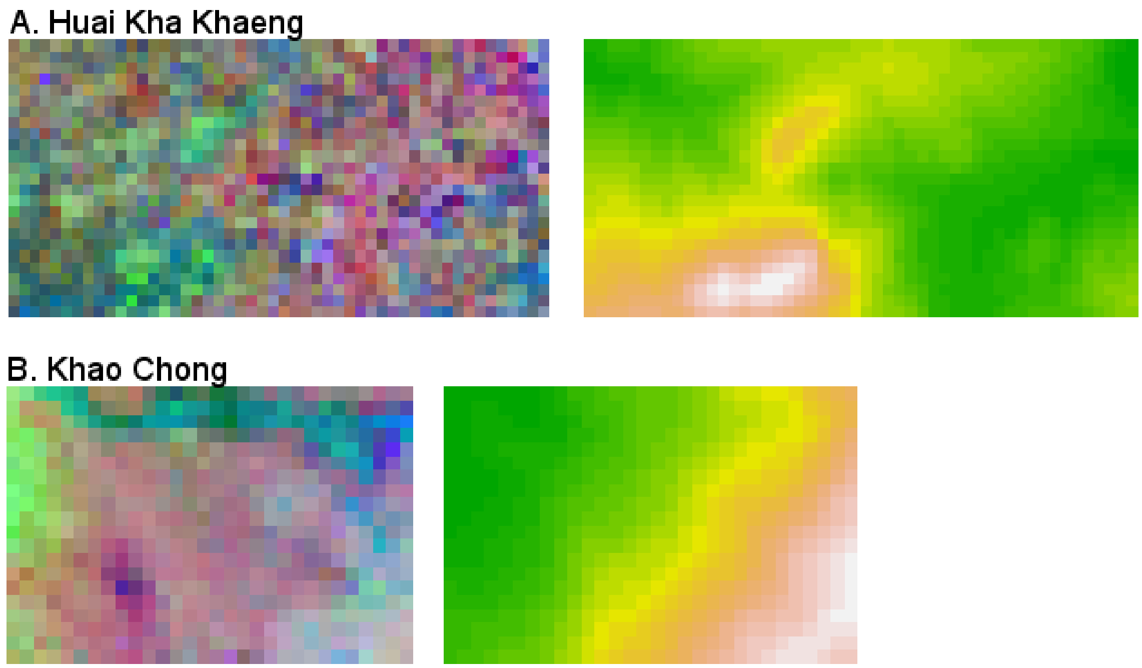

Figure S2. Beta diversity maps along with elevation maps for the two Thai study sites: A) Huai Kha Khaeng, and B) Khao Chong.