

# Better environmental data may reverse conclusions about niche- and dispersal-based processes in community assembly

LI-WAN CHANG,<sup>1,2</sup> DAVID ZELENÝ,<sup>3,5</sup> CHING-FENG LI,<sup>3</sup> SHAU-TING CHIU,<sup>1,4</sup> AND CHANG-FU HSIEH<sup>1</sup>

<sup>1</sup>*Institute of Ecology and Evolutionary Biology, National Taiwan University, 1 Roosevelt Road, Section 4, Taipei 10617 Taiwan*

<sup>2</sup>*Technical Service Division, Taiwan Forestry Research Institute, 53 Nanhai Road, Taipei 10066 Taiwan*

<sup>3</sup>*Department of Botany and Zoology, Faculty of Sciences, Masaryk University, Kotlářská 2, Brno 61137 Czech Republic*

<sup>4</sup>*Department of Biology, National Museum of Natural Science, 1 Kuan Chien Road, Taichung 40453 Taiwan*

**Abstract.** Variation partitioning of species composition into components explained by environmental and spatial variables is often used to identify a signature of niche- and dispersal-based processes in community assembly. Such interpretation, however, strongly depends on the quality of the environmental data available. In recent studies conducted in forest dynamics plots, the environment was represented only by readily available topographical variables. Using data from a subtropical broad-leaved dynamics plot in Taiwan, we focus on the question of how would the conclusion about importance of niche- and dispersal-based processes change if soil variables are also included in the analysis. To gain further insight, we introduced multiscale decomposition of a pure spatial component [c] in variation partitioning. Our results indicate that, if only topography is included, dispersal-based processes prevail, while including soil variables reverses this conclusion in favor of niche-based processes. Multiscale decomposition of [c] shows that if only topography was included, broad-scaled spatial variation prevails in [c], indicating that other as yet unmeasured environmental variables can be important. However, after also including soil variables this pattern disappears, increasing importance of meso- and fine-scaled spatial patterns indicative of dispersal processes.

**Key words:** *dbMEM; dispersal-based processes; environmental control; Lienhuachih; multiscale spatial analysis; soil variables; Taiwan; topographical variables; variation partitioning.*

## INTRODUCTION

Niche-based and dispersal-based processes have been recognized as the main actors responsible for community assembly (Cottenie 2005). The development of analytical methods that are able to distinguish the relative imprint of these processes in the structure of real ecological communities is a continuous challenge. One of the most promising approaches is the partitioning of variation in community composition into environmental and spatial components (Gilbert and Lechowicz 2004). The theoretical justification behind this is based on an assumption that environmental control on species distribution according to the niche theory will result in the variation of species composition explained by environmental variables, while dispersal limitation will generate spatial signatures in community structure that are detectable by spatial variables (spatial filters). The use of environmental and spatial predictors in variation partitioning results in four components being distinguished; namely, a pure environmental component [a], a spatially structured environmental component [b], a pure spatial component [c], and unexplained variation

[d] (Borcard et al. 1992). In this framework, variation explained by environment (components [a + b]) represents environmental control imposed on species distribution (Chase and Leibold 2003), while variation explained purely by spatial variables (component [c]) represents partly unmeasured environmental variables with spatial structure, and partly the legacy of dispersal limitation (Legendre et al. 2009). If available environmental predictors represent the most important environmental drivers of species composition, then the ratio between components [a + b] and [c] can be interpreted as the ratio between niche-based and dispersal-based processes in community assembly (e.g., Gilbert and Lechowicz 2004). However, recent simulation studies (Gilbert and Bennett 2010, Smith and Lundholm 2010) indicate that the ability of variation partitioning to disentangle these two families of processes has been overrated and the dichotomy suggested above is oversimplified. For example, component [b], which is often quite large, can also carry the legacy of dispersal processes, in the case that dispersal spatially coincides with some of the environmental variables (such as topography; Smith and Lundholm 2010). Still, partitioning of the variation into environmental and spatial component is seen as an important step toward disentangling various processes responsible for spatial community structure (Dray et al. 2012).

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<sup>5</sup> Corresponding author. E-mail: zeleny@sci.muni.cz

Recently, the variation partitioning approach has been applied on data from forest dynamics plots established by the Smithsonian Institution Center for Tropical Forest Science (CTFS) and the Chinese Forest Biodiversity Monitoring Network. Forest dynamics plots are represented by large spatially contiguous grids of subplots with permanently tagged and georeferenced individuals of all woody species (Losos and Leigh 2004). Legendre et al. (2009) applied variation partitioning of tree beta diversity into environmental and spatial components, using data from a Gutianshan forest dynamics plot (China). Their approach, based on redundancy analysis of raw abundance data, was applied by De Cáceres et al. (2012), after slight modification, on a set of 10 forest dynamics plots, distributed on three continents and ranging from tropical to temperate zones. Besides introducing the analytical framework for analysis of forest dynamics plot data using the variation partitioning method, the main goal of Legendre et al. (2009) was to “test hypotheses about the processes (environmental control and neutral) that may be responsible for the beta diversity observed in the plot, by partitioning the effects of topography and space on the distribution of species at different spatial scales . . . .” Similarly, one of the aims of the study by De Cáceres et al. (2012) was to find out “what is the contribution of environmentally-related variation vs. pure spatial and local stochastic variation to tree beta diversity . . . .” Results of such analyses, however, will be strongly dependent on the quality of environmental variables used for variation partitioning (Jones et al. 2008). The assumption that component [c] represents the role of dispersal limitation holds only in cases where all relevant environmental variables are considered; otherwise, an unknown proportion of [c] is represented by unmeasured environmental variables (Laliberté et al. 2009, Diniz-Filho et al. 2012). Both Legendre et al. (2009) and De Cáceres et al. (2012) used only topographical variables (elevation, convexity, aspect, and slope) derived from the measured elevation of corners of each grid, which are the standard components of forest permanent plot data sets. Both studies acknowledged the lack of other environmental descriptors, mainly variables describing soil chemistry, which were not available at the time of their study (or not for all plots). In the Gutianshan study, Legendre et al. (2009) assumed that, because of very rough terrain, topographical variables should play an important role, and that a large proportion of variation explained by spatial variables and not explained by the environment may indicate the operation of other factors such as neutral processes. De Cáceres et al. (2012) were more careful in their interpretations, arguing that the variation explained by topography contains at least some variation derived from environmental control, because, when compared between plots, it increases with increasing within-plot topographical roughness.

In our study, we focused on the question of how the quality of environmental data changes the conclusions drawn from the results of variation partitioning between environmental and spatial variables. In the context of previous studies of forest dynamics plots, based only on topographical variables, we ask whether it is reasonable to use topography as a surrogate for environment, and how variation explained by environment will be improved by also measuring soil variables. Soil properties are important (e.g., Jones et al. 2008, Baldeck et al. 2013), but not always available, while topography is easy to measure in the field. Soil and topography is partially correlated, but each may offer additional information relevant for plant growth. Our aim is to evaluate how important the environmental information in soil variables is and whether inclusion of soil can change or even reverse conclusions drawn from studies based only on topography.

Additional insight can be gained from more detailed analysis of component [c], namely its scale structure. This analysis is based on an assumption that broad-scale spatial structures in species data represent imprints of environmental variables, while fine-scale autocorrelation is more likely generated by community dynamics, including dispersal (Dray et al. 2012). Diniz-Filho et al. (2012) analyzed variation represented by component [c] evaluating the shape of Moran's *I* correlograms and claimed that their method can distinguish if [c] is represented by broad-scaled unmeasured environmental variables or fine-scaled dispersal processes. Here, we introduce an alternative method to analyze scale properties of the [c] component, based on its multiscale decomposition using a scalogram approach (Legendre and Legendre 2012). Using the available vegetation and environmental data, we attempt to evaluate whether, after including topographical variables as environmental predictors, the spatial information in component [c] is dominated by broad-scaled or fine-scaled spatial autocorrelation. Further, we tested how the pattern changes after also including soil variables, to reveal if soil and topography captured the most important ecological drivers of species composition.

Our study is based on detailed information about topography, soil chemistry, and soil structure, collected within 25-ha forest dynamics plot in Lienhuachih (Taiwan), which is topographically very heterogeneous (within-plot altitudinal range is 164 m). We apply the same method of variation partitioning into fractions explained by environmental and spatial variables as used by Legendre et al. (2009) and De Cáceres et al. (2012). Using these data, the main objectives are (1) to show to what extent the increase in variation in species composition is explained by environment if we also include soil variables in the analysis and how this changes the conclusion about the importance of niche-based and dispersal-based processes and (2) to demonstrate the use of multiscale decomposition of [c]

component to detect whether important environmental variables were included in the study.

#### METHODS

*Study site.*—The study was conducted in the Lienhuachih Experimental Forest (see Plate 1) in central Taiwan (23°54' N, 120°52' E), which is a part of international network of forest dynamics plots coordinated by CTFSS. The mean annual temperature is 20.8°C and the mean annual precipitation is 2285.0 mm with pronounced seasonality (89.6% of total rainfall falls in between May and September) and common typhoons (Chang et al. 2010). The forest dynamics plot of 25 ha (500 × 500 m) was set up in 2008, with methodology following the census manual of Condit (1998). All woody stems with diameter at breast height (dbh) ≥ 1 cm were measured, tagged, mapped, and identified into species. The elevation of the plot ranges from 667–845 m above sea level, with an average slope of 35.3°. Altogether 153 268 individuals and 203 316 stems were recorded within the plot (6131 individuals/ha and 8133 stems/ha, respectively). The vegetation represents subtropical evergreen broad-leaved forest with important canopy species including *Cyclobalanopsis pachyloma*, *Engelhardia roxburghiana*, *Pasania nantoensis*, *Schefflera arboricola*, and *Schima superba* (Chang et al. 2010).

*Topographical, soil, and spatial descriptors.*—As topographical descriptors, we used exactly the same type of variables as Legendre et al. (2009) and De Cáceres et al. (2012), namely, mean elevation, convexity, slope, and aspect, all derived from measured elevation of four corners of each 20×20 m cell (for details of calculations, see Appendix S2 in De Cáceres et al. 2012 and Appendix A in this paper). The aspect was further segmented into east-west and north-south directions, represented by the sine and cosine of the aspect, respectively. Mean elevation, convexity, and slope were used to construct third-degree polynomial equations, creating a total of nine monomials (see Legendre et al. 2009); in total 11 topographical variables (nine monomials and two derivatives of aspect) were available for variation partitioning. Variables calculated here differed slightly from those used (and reported) by De Cáceres et al. (2012), probably because we used the most recent version of the updated and corrected data set, while De Cáceres et al. (2012) used an older version (see Appendix A for comparison).

Soil properties are described by 16 variables, including soil chemistry (total C and N, C/N ratio, pH in 1 mol/L KCl, extractable K, Ca, Mg, Fe, Mn, Cu, Zn, and P), water content and texture (proportion of sand, silt and clay); see Appendix B for details. Third-degree polynomial equations were constructed for each soil variable, resulting into 48 monomials used in further analyses.

As spatial descriptors, distance-based Moran's eigenvector maps (dbMEM, previously known as PCNM) derived from spectral decomposition of the spatial relationships among grid cells were used (Borcard and

Legendre 2002, Dray et al. 2006). This method produces linearly independent spatial variables covering a wide range of spatial scales and allows modeling of any type of spatial structure (Borcard and Legendre 2002). Truncation distance was selected to retain links between horizontal, vertical and diagonal neighboring cells. All eigenvectors associated with Moran's *I* coefficients larger than the expected values of *I* were kept in the analysis (all together 208 eigenvectors).

*Statistical analyses.*—To decompose the variation of tree beta diversity into fractions explained by topographical, soil and spatial predictors, we used variation partitioning approach based on redundancy analysis (RDA; Rao 1964). Four variation partitioning analyses were conducted, namely (1) topographical vs. spatial variables, (2) soil vs. spatial variables, (3) soil and topographical vs. spatial variables, and (4) topographical vs. soil vs. spatial variables. The set of first three variation partitioning analyses was conducted on both the original (i.e., not transformed) species composition matrix and on the Hellinger standardized matrix (Legendre and Gallagher 2001); this dichotomy aims to make our results comparable to those of Legendre et al. (2009), who did not use any standardization, and De Cáceres et al. (2012), who used Hellinger standardization. Moreover, De Cáceres et al. (2012) compared different forest dynamics plots in terms of the amount of beta diversity attributable to particular components of variation partitioning. As a measure of beta diversity for a given forest plot, they used total variance in the Hellinger-standardized species data matrix (Legendre et al. 2005), which was consequently divided into parts according to components derived from variation partitioning. To make our results comparable, we report the results of variation partitioning of Hellinger-standardized species data by both relative values of explained variation using adjusted  $R^2$  ( $R^2_{adj}$ , Peres-Neto et al. 2006) and the absolute values of beta diversity attributable to individual components. Variation partitioning among separate topographical, soil and spatial variables was conducted only on Hellinger standardized matrix.

Multiscale decomposition of [c] component was conducted using a set of partial RDAs. We evaluated variation in species composition explained separately by each dbMEM variable in three different scenarios: (1) without any covariables (i.e., marginal variation explained by individual dbMEM variables), (2) with topographical variables as covariables (i.e., variation explained by dbMEM after accounting for topography), and (3) with topographical and soil variables as covariables (i.e., variation explained by dbMEM after accounting for all available environmental variables). The significance of each of the 208 dbMEM variables in each of the three scenarios was tested by Monte Carlo permutation test (reduced model with 9999 permutations); Holm's correction (Holm 1979) was applied to correct for multiple testing. Scenarios 1–3 differ by gradually increasing the number of environmental

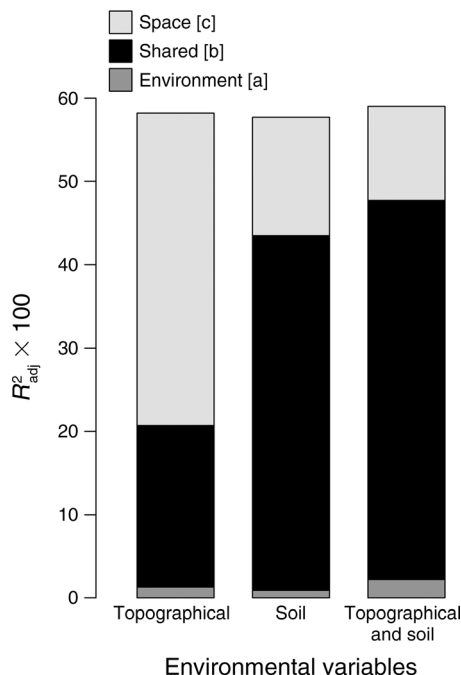


FIG. 1. Results of variation partitioning of species composition into fractions explained by environmental and spatial variables (see *Introduction* for explanation of variables), reported as adjusted  $R^2$  on percentage scale ( $R^2_{\text{adj}} \times 100$ ). Environmental variables are represented either by only topographical, only soil, or both topographical and soil variables together.

variables entering the analysis as covariables, from no variables, only topographical, and both topographical and soil variables. The focus of this analysis is on relative changes in the distribution of variation explained by individual dbMEM variables after including only topographical and both topographical and soil variables, namely whether the variation explained by broad-scaled dbMEM variables will decrease after controlling for environmental variables. Large variation explained by broad-scaled dbMEM in this analysis indicates that not all important environmental variables were included, while significant variation explained by fine-scale dbMEM variables may indicate imprints of population processes such as dispersal. Theoretically, the distribution of the explained variations will change from right skewed, with a dominance of variation explained by broad-scaled spatial variables surrogating unmeasured environmental variables, to left skewed with a prevalence of variation explained by fine-scaled spatial variables, indicating dominance of dispersal processes.

## RESULTS

Adding soil variables along with topographical variables increases the variation explained by the environment from the 20.7% explained by topography only to 47.7% explained jointly by topography and soil

(Fig. 1 and Appendix C: Table C1, considering Hellinger-standardized species data). Soil variables alone explain 43.5%, which is twice as much as the variation explained by only topographical variables. With a non-standardized species matrix, the explained variation is slightly higher: 24.5% for topographical variables only, 43.6% for soil only, and 49.0% for both (Table C1); hereafter, only results on Hellinger-standardized species data will be reported. Almost all variation explained by environmental (either topographical or soil) variables is spatially structured, meaning that an increase in variation explained by environmental factors after including soil variables decreases the variation explained purely by spatial variables (component [c]). Component [c] decreases from 37.5% if only topography is included to 11.3% if both topography and soil are included, while unexplained variation [d] remains unaffected by selection of environmental variables. If examining topographical and soil variables separately, it becomes obvious that most of the variation explained by topography is explained also by soil variables (from the 20.7% explained by topography, 16.6% is shared with soil; Fig. C1 in Appendix C), while soil explains a considerable amount of variation by itself (26.9% of variation is not shared with topography, from a total of 43.5%). From this, we can conclude that if appropriate soil variables are measured, topographical variables become highly redundant, because, from the total variation of 47.7% explained by the environment (topography and soil), only 4.2% is explained purely by topography.

If we adopt the approach of De Cáceres et al. (2012), the absolute values of beta diversity explained by topography in Gutianshan and in Lienhuachih are comparable (0.096 and 0.092, respectively, see Table S3 in De Cáceres (2012) for the first number and Table C1 in Appendix C of our paper for the second), while the part of beta diversity explained by pure space in Gutianshan is lower than in Lienhuachih (0.105 and 0.166, respectively). Adding soil among environmental variables in the case of Lienhuachih increases the beta diversity explained by environment to 0.212 and decreases those explained by pure space to 0.050.

The distribution of variation explained by individual dbMEM variables (ordered by decreasing spatial scale from broad- to fine-scaled variables) changed considerably among the three proposed scenarios. If no covariables were included, the distribution was right skewed (Fig. 2a), with broad-scaled dbMEM variables being the most important (with dbMEM 1 explaining 6.8% of variation). Filtering out topographical variables as covariables has a rather minor effect on the distribution shape (Fig. 2b), with broad-scaled dbMEM variables still prevailing. Adding soil variables along with topographical ones to the covariables changes the distribution dramatically, decreasing the importance of broad-scaled dbMEMs in favor of meso- and partly also fine-scaled dbMEMs (Fig. 2c).



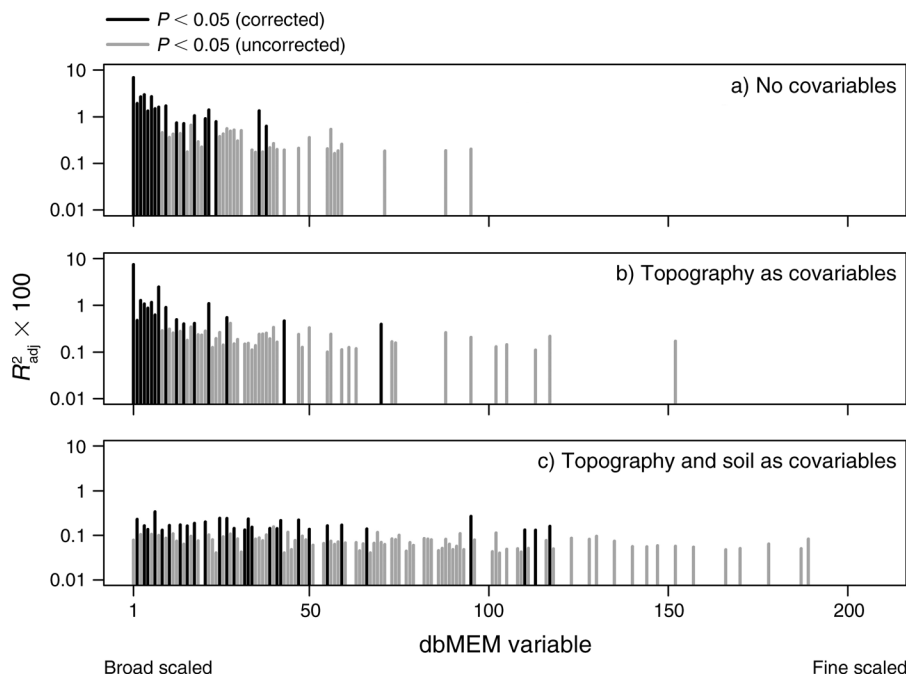


FIG. 2. Variation in species composition explained in redundancy analysis ( $R^2_{\text{adj}} \times 100$ ) by individual distance-based Moran's eigenvector maps (dbMEM) variables with (a) no covariables, (b) topographical variables as covariables, and (c) topographical and soil variables as covariables. The dbMEM variables are sorted from broad scaled to fine scaled (from left to right), and only dbMEM variables with positive  $R^2_{\text{adj}}$  are presented. Significant variables ( $P < 0.05$ , 9999 permutations) with Holm's correction for multiple testing are black lines, while variables significant at  $P < 0.05$  without correction are dark gray lines; nonsignificant variables are not displayed. Note that to facilitate readability, values of  $R^2_{\text{adj}}$  on the y-axis are multiplied by 100, and this axis is log-scaled.

#### DISCUSSION

If we follow the reasoning of Legendre et al. (2009), who attributed the components [a + b] of variation partitioning to the signature of niche processes and component [c] signature of dispersal-based processes, and apply it to data from the Lienhuachih plot, the conclusion will be very different if we include only topographical or both topographical and soil variables in the analysis. If environment is represented by only topographical variables, dispersal-based processes prevail, as the fraction [a + b] represents 24.5% and fraction [c] represents 40.8% of explained variation (non-standardized species data in Table C1). Including soil variables along with topographical variables completely reverses the interpretation in favor of niche-based processes, with 49.0% becoming much more important than dispersal-based processes, with 17.0%. In comparison, in Gutianshan at the same scale, topographical variables (components [a + b]) explain 30.7%, while the pure space (component [c]) explains 34.8% (Table 1 in Legendre et al. 2009, variation in community composition at the scale  $20 \times 20$  m). Higher variation explained by topography compared to variation explained purely by space in the case of Gutianshan can perhaps be explained by the more rugged terrain in Gutianshan when compared to Lienhuachih and hence the higher effect of topographical variables (De Cáceres et al. 2012). We assume that adding soil among environmental

variables would considerably increase the variation explained by the environment also in the case of Gutianshan, resulting into the dominance of niche- over dispersal-based processes. Although we cannot foresee how significant this increase would be, our study indicates that it may be rather dramatic.

On the other hand, the relatively high variation explained by soil variation can partly be an artifact. The variation-partitioning approach assumes that environmental variables have a causal effect on species composition. While this is definitely true in the case of topography, which can perhaps barely be modified by vegetation, in the case of soil variables, the direction of the causal relationship is not so straightforward. Soil samples are usually collected in the upper part of the soil profile, which is most strongly influenced by the litter of the aboveground vegetation. In this sense, not only does the soil chemistry influence the vegetation, but the vegetation also influences the soil chemistry. The relative proportion of this feedback changes from species to species (e.g., Finzi et al. 1998) and is hypothesized to have evolutionary context (Binkley and Giardina 1998). Therefore, the inclusion of soil variables among environmental variables in variation partitioning effect can overestimate the real effect of environmental control at the cost of the dispersal processes. The possible indication that this overestimation exists may be drawn from detailed analysis of the importance of particular



PLATE 1. View of the Lienhuachih Experimental Forest, Taiwan, from the meteorological tower, taken on 22 August 2011. Photo credit: D. Zelený.

soil properties and carefully considering if the important properties are more likely to be derived from geological substrates or from the effect of aboveground vegetation. However, the real scale of this overestimation will perhaps remain unknown, and its quantification will require an experimental approach.

Multiscale analysis of residual spatial variation in component [c] shows that topography itself is indeed not a sufficient descriptor of environmental control on the vegetation of our study site. The distribution of variation explained by particular dbMEM variables sorted from broad-scaled to fine-scaled did not change much between analysis without any environmental variables (Fig. 2a) and that including topography as covariables (Fig. 2b). Both show that there is still a considerable amount of broad-scaled spatial variation, indicating that important environmental factors have not been considered. After including soil variables, variation explained by broad-scaled spatial variables is not much higher than that explained by meso- or fine-scaled variables. Some of the broad-scaled dbMEM variables, however, remain significant, meaning that there is still some space for other environmental variables to play a role, although perhaps these are not as important as soil.

The dichotomy of broad-scaled spatial variables representing environmental variables and fine-scaled spatial variables representing dispersal processes is indeed simplified, and while it may be close to reality at certain scales, it cannot be applied universally. Ecologists tend to measure broad-scaled environmental

variables and ignore (or are unable to measure) the fine-scaled ones (Dray et al. 2012), although these may also exist. Similarly, far-distance dispersal may theoretically result in more broad-scaled spatial community patterns. Information about the spatial structure of component [c] offers additional insight in data, but does not offer a definite answer about the relative role of alternative processes causing the spatial pattern. Further studies may focus on the comparison of our method with spatial autocorrelation analysis approach proposed by Diniz-Filho et al. (2012) to see if the results are comparable, and to check its sensitivity and reliability using community data of known properties.

#### CONCLUSIONS

In the case study from the Lienhuachih forest dynamics plot, we have shown that including soil variables along with topographical variables into variation partitioning results in a more than two-fold increase in variation explained by the environment, and reverses the original conclusion about the dominance of dispersal-based processes in community assembly in the prevalence of niche-based ones. Detailed multiscale decomposition of [c] component indicates that topographical variables, when included as explanatory variables, does not explain much of the broad-scaled spatial pattern in species composition, while including soil variables does, leaving meso- and fine-scaled spatial patterns unexplained. However, we also pointed out that the variation explained by soil variables may be overestimated, because not only does soil influence the

vegetation, but vegetation also partly influences the soil properties.

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#### SUPPLEMENTAL MATERIAL

##### Appendix A

Comparison of environmental data for the Lienhuachih forest plot with those used by De Cáceres et al. (2012) ([Ecological Archives E094-200-A1](#)).

##### Appendix B

Details of soil sample analyses ([Ecological Archives E094-200-A2](#)).

##### Appendix C

Variation partitioning analysis between environmental (only topographical, only soil, or both) and spatial variables ([Ecological Archives E094-200-A3](#)).