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Key Community Assembly Processes Switch between Scales in Shaping Beta Diversity in Two Primary Forests, Southwest China

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Abstract: Environmental and dispersal-based processes have been widely investigated for the understanding of community assembly. However, the relative importance of these ecological processes across spatial scales, life history stages and forest types needs to be largely studied. We test the variability of ecological processes in shaping tree community composition across life stages and spatial scales, and in particular, the hypothesis that dispersal limitation dominates at smaller scales and early life stages, but environmental filtering at larger scales and later life stages. We used spatially explicit point process models to estimate the relative importance of environmental and dispersal processes and their combined effect on beta diversity across spatial scales and life stages in tropical and subtropical forests. These models fit the observed species distribution pattern and generated realizations of the fitted models for each species. We found that the importance of environmental and dispersal processes did not shift with life stages or vegetation types, but did with spatial scales. Dispersal provided the best explanation of large-scale patterns, but dispersal combined with environmental selection was superior for small-scale patterns. In conclusion, we confirm the importance of spatial scale for the effects and identification of community assembly mechanisms. Our results also suggest that the importance of both dispersal and environmental processes for community assembly could be pervasive across life stages and vegetation types. The generality of these findings should be tested further in different vegetation types and life stages to assess whether specific ecological processes have consistent effects on community structure across life stages and vegetation types.

Keywords: beta diversity; community assembly; dispersal limitation; ecological processes; environmental heterogeneity; life stages; subtropical forest; tropical forest

1. Introduction

Identifying the ecological mechanisms responsible for community assembly has long been a focus of ecology. Niche and neutral-based community assembly theories have been hypothesized to explain the principal underlying mechanisms for community structure. Niche theory posits the role of the environment to be dominant in removing species that are not able to respond to abiotic conditions [1] suggesting that species are mainly distributed based on their environmental requirements. Neutral community assembly theory hypothesizes that species are ecologically equal and are distributed primarily due to dispersal limitation [2]. The roles of environmental and dispersal processes or their combination for community assembly have widely been recognized [3–7]. However, relatively few studies have explicitly considered differences across spatial scales, life history stages and forest types [8].

It remains important to consider these ecological contexts to provide deep insights into community assembly mechanisms.

Previous studies have reported that the contributions of environmental and dispersal mechanisms to species diversity varied across different biogeographic regions [3,6,9–12]. Nonetheless, the relative importance of underlying processes for variation in species composition across diversity gradients within a single biogeographic region characterized by similar evolutionary history has been less studied [13]. This study examines the contribution of environmental and dispersal processes for the assembly of species beta diversity in Yunnan province, southwest China. The province contains distinct vegetation types with a clear species diversity gradient from the tropical seasonal rainforest, to the subtropical forest, to subalpine vegetation types. In addition, clear gradients of climate, elevation and topographic heterogeneity are also presented [14]. This provides a chance to test the relative importance of community assembly rules for variation in species composition across richness, climatic and topographic gradients.

Plant life stages are an important factor in estimating the contribution of environment- and dispersal-based processes to tree distributions, as ecological requirements vary across life-history stages [15]. Dispersal could be a key process at early life stages, as seed dispersal provides the first template for seedling establishment [16], while the resource requirements of seedlings during establishment are partly fulfilled by nutrients in their seeds [17]. However, the importance of dispersal could decline with tree age as the role of other ecological processes such as species interactions, environmental selection and self-thinning increases [18,19]. Although ontogeny has been found to help separate the consequences of different ecological processes for community structure [20–22], it is still not well understood how it varies across different forest types, which may obscure the wide range of the importance of underlying mechanisms over the lifespan of plants. A better understanding of this could reveal whether tree size variation in life stages alters the role of ecological processes for community assembly in different forest communities.

Spatial scale is one of the factors that could decouple the contribution of niche and neutral forces for community assembly [23]. These drivers were found to vary greatly in strength to shaping ecological patterns over a wide range of spatial scales [9]. Dispersal limitation is expected to play a more important role at small spatial scales by increasing the aggregation of conspecifics. However, its importance may decline when there is no limitation of seed dispersal [24]. On the other hand, niche processes are expected to be more important at larger spatial scales, due to habitat heterogeneity along environmental gradients [9]. The scale-dependent roles of environment and dispersal suggest that multiple driving forces are responsible for tree community assembly at the local scale [25,26]. Considering the spatial scale is, therefore, essential to avoid misunderstandings about the importance of ecological processes for community structure.

The overall goal of this study is, therefore, to test the hypothesis that the importance of ecological processes for beta diversity varies with life stages and spatial scales in tropical and subtropical forest plots, with the expectation of a strong role of dispersal limitation at smaller scales and early life stages, and a strong role of environmental filtering at larger scales and later life stages. Permanent forest dynamics plots with coordinate records of trees are ideal to test this hypothesis. Specifically, we used four spatial point processes to model random placement, niche and/or neutral processes across different life stages at 10 × 10 m, 20 × 20 m, 50 × 50 m and 100 × 100 m cell sizes. We estimated the relative importance of the four models by comparing community beta diversity in real and simulated communities at each life stage and spatial scale in each of the two plots.

2. Materials and Methods

2.1. Study Sites and Census Data

We used tree census data in the Bubeng (BB) 20 ha tropical forest plot, and the Ailaoshan (ALS) 20 ha subtropical forest plot in Yunnan province, southwest China (Figure S1). All the freestanding woody stems with a diameter at breast height (DBH) of ≥1 cm in both plots were identified, measured and mapped following the protocol of [27]. Briefly, all the woody plant species in both plots were counted with their DBH size, species identity and location map information. The census was started in 2007 for the BB plot and 2014 for the ALS plot, and they keep being censused at every five-year interval. We used the 2012 and 2014 census data, respectively, for the BB and ALS plots for this study. These plots show different forest types, climates, topographies and soil fertilities. Further characteristics of the plots are given in [14].

2.2. Environmental Data

We treated topography and soil nutrients as the source of niche differentiation. Topographical data described elevation, convexity, slope and aspect. We calculated the mean value for each topographical variable at each 20 × 20 m quadrat [28]. The elevation of each 20 × 20 m quadrat was measured as the mean value of the four corners of the 20 × 20 m quadrat. The slope was calculated as the mean angular deviation from the horizontal of each of the four triangular planes of the 20 × 20 m quadrat formed by connecting three of its corners [28].

Convexity was measured as the elevation of a focal quadrat minus the mean elevation of the eight surrounding quadrats. For edge quadrats, convexity was calculated as the elevation of the center minus mean elevation of the four corners of the quadrat [29]. Aspect was calculated using the following formula:

$$Aspect = 180 - arctan\left(\frac{fy}{fx}\right) \times \left(\frac{fy}{\pi}\right) + 90 \times \left(\frac{fy}{|fx|}\right)$$

where fx is the elevation difference from east to west in the 20 × 20 m subplot and fy is the elevation difference from north to south.

We used soil samples (only from the BB plot) taken on a 30 × 30 m grid in the 20 ha plot. By using the 252 nodes in this grid as base points, two additional sampling points paired randomly at 2 and 5 m, 2 and 15 m or 5 and 15 m in a random direction were also located. Leaf litters, branches and humus were wiped off from these sampling points, and 500 g were collected at 10 cm depth. 756 samples were collected in total for soil variable analyses and transported to the Biogeochemistry Laboratory at the Xishuangbanna Tropical Botanical Garden. From these samples, we used measured total nitrogen, available nitrogen, total phosphorus, extractable phosphorus, total potassium, exchangeable potassium, soil bulk density, soil organic matter, soil moisture and soil pH. Estimation of soil nutrients is described in detail [30]. Since soil data were only available for the BB plot, we used only topographical data for ALS. To estimate the relative effect of ecological processes on beta diversity at different scales, we divided the full 20 ha plot into various size quadrats: 10 × 10 m (n = 2000), 20 × 20 m (n = 500), 50 × 50 m (n = 80) and 100 × 100 m (n = 20). We have then calculated the abundance-based pairwise Bray–Curtis dissimilarity of trees between these quadrats.

2.3. Tree DBH Size Class

DBH class has often been used as a surrogate to determine trees' life stage effect on species distribution [31], and hence, we made comparisons between different stem sizes to evaluate the importance of ontogeny for species distribution. Based on the diameter size distribution of stems, we divided stem diameters using 1/3 and 2/3 quantiles of DBH into three size classes for the BB plot and two size classes for the ALS plot. Only abundant species in each plot were considered, as a large population size increases model accuracy [32]. We, therefore, included those species with at least 150 individuals in the BB plot (50 individuals in each size class), and 60 individuals in the ALS plot (30 individuals in each size class). To make a comparison with and without life stage effects, we combined the DBH size classes and labeled that as the "all DBH size class". In total, 97 tree species in the BB plot and 47 species in the ALS plot were included in our analyses.

2.4. Spatial Point Pattern Analysis and Null Communities

We used a spatial point pattern method based on the exact location of trees to test the relative importance of different ecological processes for species distribution [33,34]. Permanent forest dynamics plots provide coordinate records of trees, which are used to indicate the exact location of trees using a spatial point pattern method. Specifically, we used the Homogeneous Poisson process (HP), Inhomogeneous Poisson process (IP), Homogeneous Thomas process (HT) and Inhomogeneous Thomas process (IT) to estimate the role of random effect, environmental filtering, dispersal limitation and joint-effect of dispersal limitation and environmental filtering, respectively, on the distribution pattern of species [5,34].

The HP model produces a completely random pattern for each of the species with the assumption of species independence and constant density of each species per unit area [35]. The IP model simulates species distribution by relating species density with environmental factors in the sampling scales [34]. The HT model estimates the effect of dispersal limitation on species distribution [33]. This model explicitly describes the dispersal of young trees around their parents and generates clusters that are distributed randomly and independently, with Poisson-based distribution of points in each cluster.

The IT model was used to evaluate the joint effect of environmental and dispersal processes on the species distributions, and hence it is the most complex model. It predicts the effect of environmental factors on species distribution by associating species density with the corresponding environmental factors in the sampling scale in addition to the dispersal clustering process as implemented in the HT model [34].

We separately fitted these models to the observed distribution pattern of each species and generated realizations of the fitted models for each species. Each model has produced 100 simulated communities for each tree life stage at each spatial scale. Finally, we independently superimposed the simulated patterns of all species to produce one simulated community in each DBH-size class [34]. Models did not consider species interaction effects on community assembly, which is one of the limitations of this approach that needs to be addressed in the future. We have given a detailed description of each spatial point process model in the Supporting Information (Supplementary S2).

2.5. Species Beta Diversity

We calculated beta diversity both for the observed and simulated communities of each model for each DBH-size class at four different spatial scales (10 × 10 m, 20 × 20 m, 50 × 50 m, 100 × 100 m). We used the Bray–Curtis dissimilarity index to calculate the beta diversity of the species and transformed the abundance data using square root transformation before the analysis to reduce the influence of the most dominant species [36]. The Bray–Curtis dissimilarity index is one of the main indices to measure the degree of dissimilarity between communities. It is the modified version of the Sørensen index which is based on presence-absence data and uses species abundance data to calculate community dissimilarities [37]. The predicted beta diversity of each model was calculated by averaging the beta diversity of 100 simulated communities. We used Kruskal–Wallis rank sum tests to compare beta-diversity values among spatial scales.

2.6. Goodness-of-Fit of the Models

We assessed the performance of the point process models in predicting species beta diversity in two ways: first, we constructed the 95% confidence interval (CI) for the predicted beta diversity from the 100 simulated communities and compared the observed pattern of the beta diversity with the corresponding simulated patterns. If the observed values fell within the 95% simulation envelopes, the model was considered adequate and otherwise rejected [34,38]. Second, we used the Akaike's information criterion (AIC) score to compare model performance:

$$\mathrm{AIC} = n \times \ln(\mathrm{R}) + 2\mathrm{K}$$

where n is the number of sampled areas, R is the sum of residual squares and K is the number of parameters of a point process model. We used the "spatstat" package in *R* [39] and the *R* scripts provided by Shen et al. [5] for the modeling process.

3. Results

We found three key results:

First, the spatial scale was found to affect the relative importance of ecological processes in shaping beta diversity. In both plots, we found that the IT model best fitted the species beta diversity at 10 × 10 m and 20 × 20 m with low AIC values, whereas the HT performed better at 50 × 50 m and 100 × 100 m with low AIC values (Figures 1 and 2). This finding held across life stages. The random point process model (HP), however, showed the poorest fit to beta diversity in both forest types, with the highest AIC values (Table 1) and the observed pattern consistently lay outside the 95% confidence interval (Figures S3–S6). The IP model also performed poorly in both forest types (Figures 1 and 2; Table 1). All the models consistently predicted that beta diversity significantly declined as the scale of analysis increased with $p < 0.001$ (Figure S7). Therefore, the spatial scale was found to decouple the relative importance of ecological processes shaping beta diversity in both forest types.

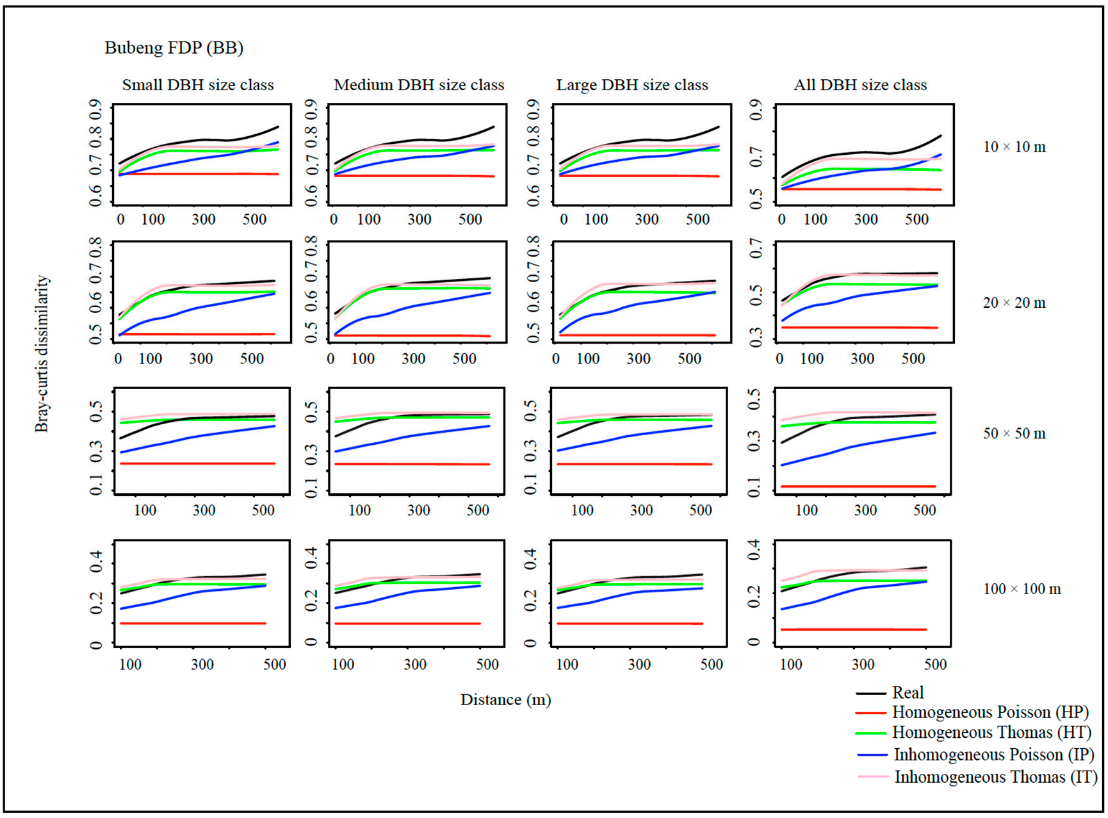

Figure 1. Real and simulated species beta diversity across DBH-size classes at different spatial scales in the Bubeng plot.

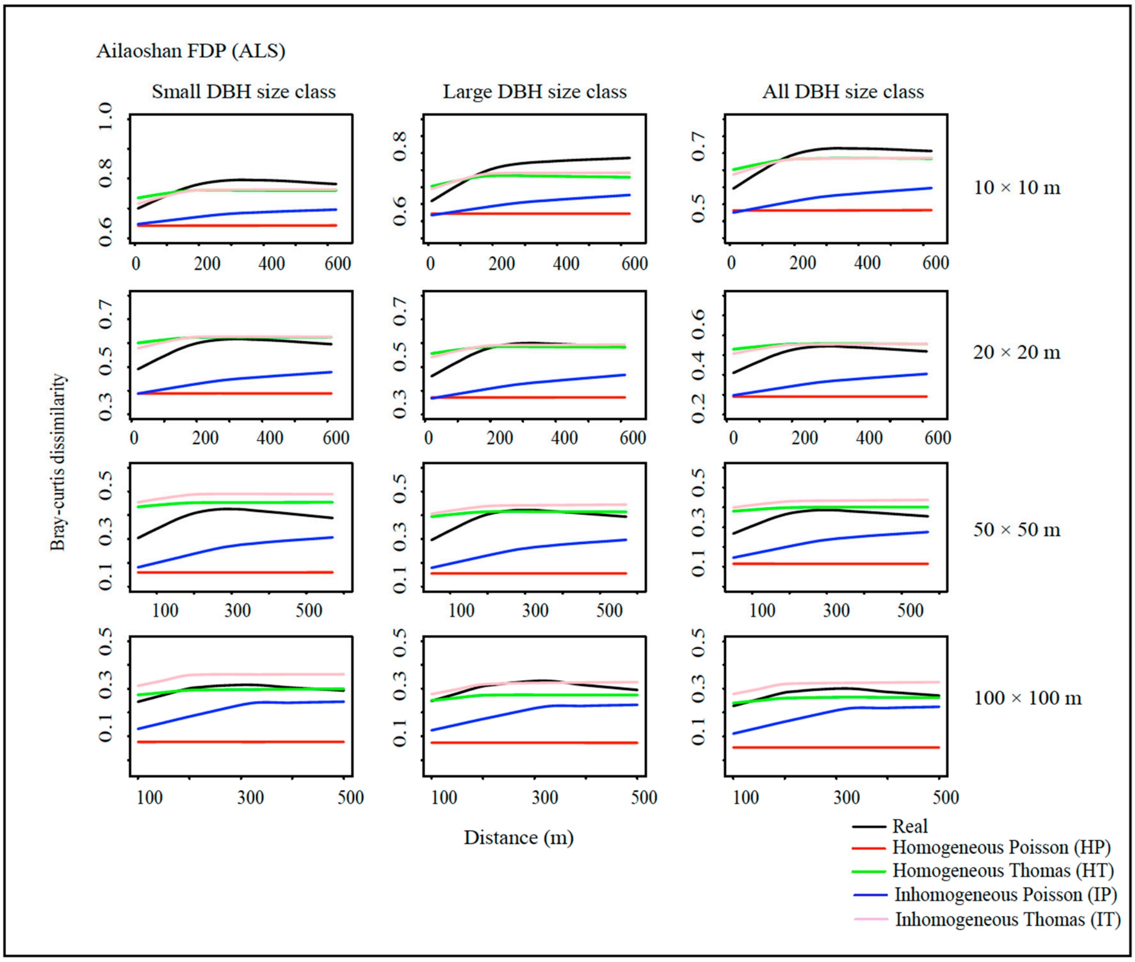

Figure 2. Real and simulated species beta diversity across DBH-size classes at different spatial scales in the Ailaoshan plot.

Table 1. Akaike's information criterion (AIC) values of the spatial point pattern models for species beta diversity across DBH-size class and scales in the two forest dynamics plots.

Plots	DBH-Size Class	Spatial Scale (m^2)	Homogeneous Poisson (HP)	Homogeneous Thomas (HT)	Inhomogeneous Poisson (IP)	Inhomogeneous Thomas (IT)
Bubeng FDP	Small	10 × 10	2251.77	367.72	991.38	**−174.68**
		20 × 20	475.98	−288.18	81.86	**−395.03**
		50 × 50	49.26	**−107.56**	−18.95	−94.76
		100 × 100	−1.61	**−32.59**	−9.65	−17.54
	Medium	10 × 10	2380.91	265.05	1002.02	**9.77**
		20 × 20	515.23	−333.94	107.16	**−389.33**
		50 × 50	51.16	**−130.41**	−17.57	−107.31
		100 × 100	−1.79	**−36.87**	−9.57	−20.88
	Large	10 × 10	2354.46	303.36	945.80	**−316.74**
		20 × 20	485.178	−279.02	3.62	**−387.11**
		50 × 50	50.33	**−107.56**	−26.45	−96.16
		100 × 100	−1.51	**−32.64**	−9.12	−16.63
	All	10 × 10	2955.40	1585.51	1600.41	**350.53**
		20 × 20	675.14	−32.64	238.58	**−276.99**
		50 × 50	64.98	**−100.18**	−6.09	−90.62
		100 × 100	−1.47	**−32.04**	−10.29	−18.22

Table 1. *Cont.*

Plots	DBH-Size Class	Spatial Scale (m^2)	Homogeneous Poisson (HP)	Homogeneous Thomas (HT)	Inhomogeneous Poisson (IP)	Inhomogeneous Thomas (IT)
Ailaoshan FDP	Small	10 × 10	2745.64	−92.39	2082.93	−33.11
		20 × 20	648.49	−334.51	428.44	−327.46
		50 × 50	55.47	−85.18	4.23	−40.44
		100 × 100	−1.91	−45.5	−15.61	−27.55
	Large	10 × 10	2803.81	517.95	2215.77	**187.8**
		20 × 20	656.93	−224.04	451.78	**−234.99**
		50 × 50	56.22	**−112.52**	9.10	−89.89
		100 × 100	−1.24	**−33.77**	−12.56	−32.97
	All	10 × 10	3172.29	286.25	2500.18	**291.82**
		20 × 20	713.26	−218.43	473.30	**−232.32**
		50 × 50	58.49	**−105.19**	3.69	−61.10
		100 × 100	−1.64	**−40.00**	−15.54	−30.94

HP, HT, IP and IT to estimate, respectively, the role of random effect, environmental filtering, dispersal limitation and joint-effect of dispersal limitation and environmental filtering.

Second, in contrast to our expectations, the life stages of trees did not affect the apparent relative importance of ecological processes. We found that the process with the lowest AIC was always the same across life stages in each of the two plots. In both plots, the IT and HT models matched the beta diversity of all life stages at small and large scales, respectively (Figures 1 and 2; Table 1). The HP and IP models were the poorest fitting across life stages with higher AIC values (Table 1).

Third, the relative importance of ecological processes was not found to change with forest types. Both the IT and HT models remained better predictors of the dissimilarity pattern of tree communities in the two forest types, with their scale-dependent effect also being consistent, as mentioned before. Our result, thus, suggests that the same underlying mechanisms may remain dominant in shaping community assembly in different forest types.

4. Discussion

We found that species are distributed non-randomly in both tropical and subtropical forests. The random placement hypothesis (HP model) was the poorest model in predicting beta diversity across life stages, which was in line with most similar point process based studies [5,38,40]. It underestimated the observed species' beta diversity across life stages and spatial scales suggesting that species tend to be more aggregated than expected by chance.

The effect of ecological mechanisms in structuring beta diversity was found to depend on the spatial scale of analysis. Our results showed that the joint-effect of dispersal limitation and environment (IT model) produced a good estimation of the observed dissimilarity pattern of trees at a small scale, while dispersal limitation (HT model) alone was superior at a large scale in both forest types (Table 1). The joint effect of dispersal and environment at small scales suggests that seed dispersal may provide the first template for tree distribution on which the local environment builds. This is consistent with other findings [9,13] that dispersal and environment leave signatures on the spatial structure of beta diversity at local scales. The detection of an environmental signal coupled with dispersal also indicates communities with strong spatial structures at fine scales, as it is also reported (for patchy diversity patterns at Wabikon plot) [38]. Furthermore, the scale-dependence of ecological drivers for beta diversity, with environment dominating at larger scales but dispersal playing a substantial role at smaller scales, has previously been identified in species diversity patterns [26]. Spatial scale, therefore, appears to decouple the importance of ecological processes for species diversity patterns.

Environmental variation (IP model) was capable of generating beta-diversity patterns with an increasing scale of analysis and habitat diversity in both forest types (Figures 1 and 2; Table 1). This is consistent with the finding that the effect of habitat heterogeneity on beta-diversity patterns increased as the spatial scale increased [9]. The environment (IP model) was expected to be the main driver for the species diversity pattern in the tropical BB plot, due to the fact that the plot is more heterogeneous in topography than the other plot. The importance of the environment in a more heterogeneous plot compared to a less heterogeneous plot has also been indicated [41]. However, we found it was more important in combination with dispersal limitation, not alone. This may suggest that environmental heterogeneity is important but not sufficient for generating observed spatial patterns of species. It has also been reported that a significant species-habitat association does not necessarily imply the habitat-based distribution of the species [41] suggesting that other processes may also be involved in shaping community structure. In relation to the topographic variability of plots, we found that the ability of the environment (IP model) to predict species beta diversity declined from a more heterogeneous tropical habitat (BB plot) to a less heterogeneous sub-tropical environment (ALS plot). This is consistent with the niche theory that different habitat heterogeneities vary in strength to explain species distribution [42,43]. The inability of the environment to reproduce beta-diversity patterns alone could be associated with its inability to generate conspecific aggregation [14]. The relative importance of the environment for beta diversity, therefore, increases with spatial scale and habitat heterogeneity.

It is widely accepted that the relative importance of assembly processes differs between life stages of trees [21]. Unexpectedly, however, we did not find evidence of shifts in the relative importance of environmental and dispersal processes to life stages in either forest type. This is consistent with previous studies (at the community level, not species level) [14,38] and suggests that adult trees carried the legacy of early life history stages. However, inconsistently with our result, several previous studies found that the relative importance of ecological mechanisms was age-specific [15,21,44,45], suggesting a shift in species' ecological preferences between life stages. One of the reasons for the inconsistency could be the criterion differences in categorizing trees into different life stages based on stem size, which perhaps limits our ability to draw general conclusions. Furthermore, plot conditions of the study sites such as the topography, soil and species composition could also be a source of discrepancies in the results. Compared to other previous studies, our results suggest that the role of underlying mechanisms to shape species diversity may not considerably differ between vegetation types and life stages.

5. Conclusions

This study provides three important findings that might improve our understanding of community assembly. First, dispersal alone and in concert with environment shapes beta diversity, respectively, at large and small spatial scales, indicating that spatial scale decouples the role of ecological mechanisms. Second, the contribution of environmental and dispersal processes did not vary with life stages suggesting that adult trees may conserve the signal of early life stages. Third, the importance of dispersal and environmental heterogeneity did not change between the tropical Bubeng (BB) plot and the subtropical Ailaoshan (ALS) plot. We conclude that the spatial scale and life stages have broad implications for our understanding of the ecological mechanisms that shape forest communities. We still, however, suggest these mechanisms need to be tested further for community assembly under different ecological contexts and vegetation types to reach agreement on the underlying mechanisms of species diversity pattern. We also suggest models be more refined to consider other components of ecological mechanisms such as biotic interaction effects. It is also important to link the role of ecological processes with spatial distance within a given scale of analysis, as the performance of models varies with distance.

Supplementary Materials: The following are available online at http://www.mdpi.com/1999-4907/11/10/1106/s1, Figure S1: Map showing the study sites; Appendix S2: Description of ecological process models; Figure S3: 95% confidence interval of models for the small DBH size class in the BB plot; Figure S4: 95% confidence interval of models for the large and all DBH size classes in the BB plot; Figure S5: 95% confidence interval of models for the small and large DBH size classes in the ALS plot; Figure S6: 95% confidence interval of models for all DBH size class in the ALS plot; Figure S7: Effect of spatial scale on the observed and predicted values of beta diversity.

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Data Accessibility: The datasets used for this study are available at www.cfbiodiv.org and www.xtbg.ac.cn.

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