RESEARCH PAPER

Community assembly processes shape an altitudinal gradient of forest biodiversity

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ABSTRACT

Aim Spatial patterns in biodiversity along environmental gradients are a central theme in ecology. However, the ways in which local assembly processes control changes in species turnover (β-diversity) along broader gradients have been less well documented. In this study, we aimed to elucidate factors and processes governing the altitudinal gradients in the β-diversity of woody plants and ground-dwelling oribatid mites.

Location Shiretoko National Park in Hokkaido, Japan.

Methods The diversity of plants and oribatids was investigated in seven plots (each containing 10 subplots) at different altitudes, and the β-diversity of the two organism groups was calculated for each altitude. The dependence of β-diversity on the size of the species pool (γ-diversity) is an issue of long-standing importance. We therefore used null modelling, which randomly shuffles individuals among subplots while preserving the γ-diversity, the relative abundance of each species per plot and the number of individuals per subplot. This approach enabled us to estimate how much the observed β-diversity deviates from the expected β-diversity under stochastic assembly processes. Environmental data were collected to evaluate the possible effects of habitat condition/heterogeneity on community processes.

Results In plants, deterministic processes dominated in the low-productivity, high-altitude stands because of the finer-scale niche partitioning seen among small individuals within less-stratified stands. In the structurally developed, low-altitude stands, the community structure was more strongly affected by stochasticity, probably resulting from one-sided competition such that the canopy trees intercept the majority of light, a primary resource for plants, and therefore the small understorey individuals had limited access to light. Among the oribatids, the altitudinal gradient of β-diversity was less evident than among the studied plants. However, this non-linearity does not support the notion that local assembly processes contribute little to the spatial pattern of β-diversity. Indeed, local-scale environmental heterogeneity favoured a more deterministic assembly of oribatids at a given altitude.

Main conclusion The biogeographical patterns of β-diversity are not independent of community processes and, in reality, are shaped by local stochastic/deterministic factors that change within a landscape.

Keywords
Beta diversity, community assembly, niche-based processes, oribatid mites, stochastic processes, woody plants.

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INTRODUCTION

Understanding spatial patterns in biodiversity along environmental gradients is a central theme in ecology (Willig *et al.*, 2003; Ricklefs, 2004); it helps to address the looming threats to biodiversity by contributing to regional-scale biological conservation activities, such as reserve design and habitat restoration. The most widely recognized biogeographical patterns of diversity are the gradients that occur along altitude and latitude. Knowledge of these patterns is also vital for predicting how climate change will affect biodiversity, as most species are expected to be forced to shift their distributions to higher altitudes/latitudes in the warmer future (Sheldon *et al.*, 2011). Despite substantial efforts, however, the underlying drivers of the spatial organization of diversity remain unknown (Mokany *et al.*, 2011). In particular, compared with local and regional species richness (α- and γ-diversity, respectively), the patterns and processes related to how local assemblages of species are differentiated (i.e. β-diversity) across environments (including altitudinal and latitudinal gradients) have been poorly explored. Generally defined as the variation in the identities of species among locations, β-diversity is at the heart of community ecology (Anderson *et al.*, 2010). Filling the knowledge gap regarding β-diversity is thus critical in our quest to reveal how biodiversity varies in space, both theoretically and practically (Mena & Vázquez-Domínguez, 2005; Baselga, 2010; Chase & Myers, 2011; Leprieur *et al.*, 2011).

The factors driving variations in β-diversity are among the most important but also the most poorly understood influences on global variations in biodiversity (Chase, 2010; Qian *et al.*, 2012). A number of explanations have been proposed for the geographical changes observed in β-diversity, including explanations based on dispersal limitation (Qian & Ricklefs, 2007; Qian, 2009), habitat specialization (Jankowski *et al.*, 2009) and environmental heterogeneity (Andrew *et al.*, 2012). The available evidence implies that multiple processes operating at various scales may control β-diversity (Carvalho *et al.*, 2011). Based on forest inventories, Kraft *et al.* (2011) claimed that the general trend in β-diversity, which shows a linear decrease with increasing altitude/latitude, is spurious and that this decrease is a simple function of α- and γ-diversity. These authors concluded that local-scale community assembly processes, such as niche partitioning, contribute little to the geographical pattern of β-diversity. However, this notion is still open to discussion (Qian *et al.*, 2012; Tuomisto & Ruokolainen, 2012). In fact, observational (Andrew *et al.*, 2012) and experimental (Chase, 2010) studies have shown that the relative impact of stochastic/deterministic processes on β-diversity varies with productivity. Given the general correlation between altitude/latitude and productivity in forest ecosystems (e.g. Nogues-Bravo *et al.*, 2008), we hypothesize that the shifts between the stochastic and deterministic processes underlying local assemblages across environmental variations drive the broad-scale spatial pattern in β-diversity in forest communities.

In forest ecosystems, resource distributions are spatially heterogeneous (Nicotra *et al.*, 1999; Lindo & Winchester, 2009).

The high heterogeneity caused by the structural complexity of forests is known to strongly contribute to the maintenance of local community structure for both plants (Kohyama, 1993; Kohyama & Takada, 2009) and animals (Tews *et al.*, 2004; Decaëns, 2010). Therefore, niche assembly probably accounts for the processes shaping forest biodiversity at broader spatial scales. In this study, we highlight different groups of organisms (woody plants and oribatid mites) because taxon-specific factors may be important in structuring communities (e.g. dispersal mode and habitat requirements; De Bie *et al.*, 2012). Considering resource partitioning among woody plant species, we focused on forest stratification, as this process determines the within-stand distribution of light, which is a primary resource for plants (Kohyama & Takada, 2009). In ground-dwelling oribatid mites, we considered the soil environment to be a determinant of deterministic community-structuring processes (Lindo & Winchester, 2007; Decaëns, 2010). Vegetation, primarily through litter input, strongly influences the soil diversity, including that of the oribatid mites, which are the most representative, species-rich group of the soil mesofauna (Hasegawa *et al.*, 2013). Incorporating these mites in addition to plants when considering community processes may thus have an important implication. That is, our multi-taxon approach will be useful for determining whether universal processes drive the distribution of β-diversity.

Based upon the above considerations, we aim to quantify the role of local community processes in creating the altitudinal pattern of β-diversity in the northern forests of the Shiretoko Peninsula in Japan (Fig. 1), which are characterized by sharp altitudinal changes in forest structure and productivity due to unique climatic conditions (see Materials and Methods). We expect that our hypothesis can best be tested in a region with a sharp environmental gradient, making our study site ideal for this purpose.

MATERIALS AND METHODS

Study site

This study was conducted in Shiretoko National Park, which is located in north-eastern Hokkaido, the northernmost island of Japan (Fig. 1). Shiretoko Peninsula is registered as a UNESCO (United Nations Educational, Scientific and Cultural Organization) World Natural Heritage Site because of its high biodiversity. This site provides one of the richest northern temperate ecosystems in the world and is an outstanding example of the interaction between marine and terrestrial ecosystems and of extraordinary ecosystem productivity (http://whc.unesco.org/en/list/1193). This site has particular importance for a number of species, some of which are endangered and endemic, such as Blakiston's fish owl (*Ketupa blakistoni*) and the Shiretoko-sumire plant (*Viola kitamiana*). Approximately 90% of the land is covered with pristine natural vegetation, which extends from the coast to above the tree line in belts graded by altitude.

On the peninsula, there is a remarkable difference in climate between the east and west sides, which are separated by central
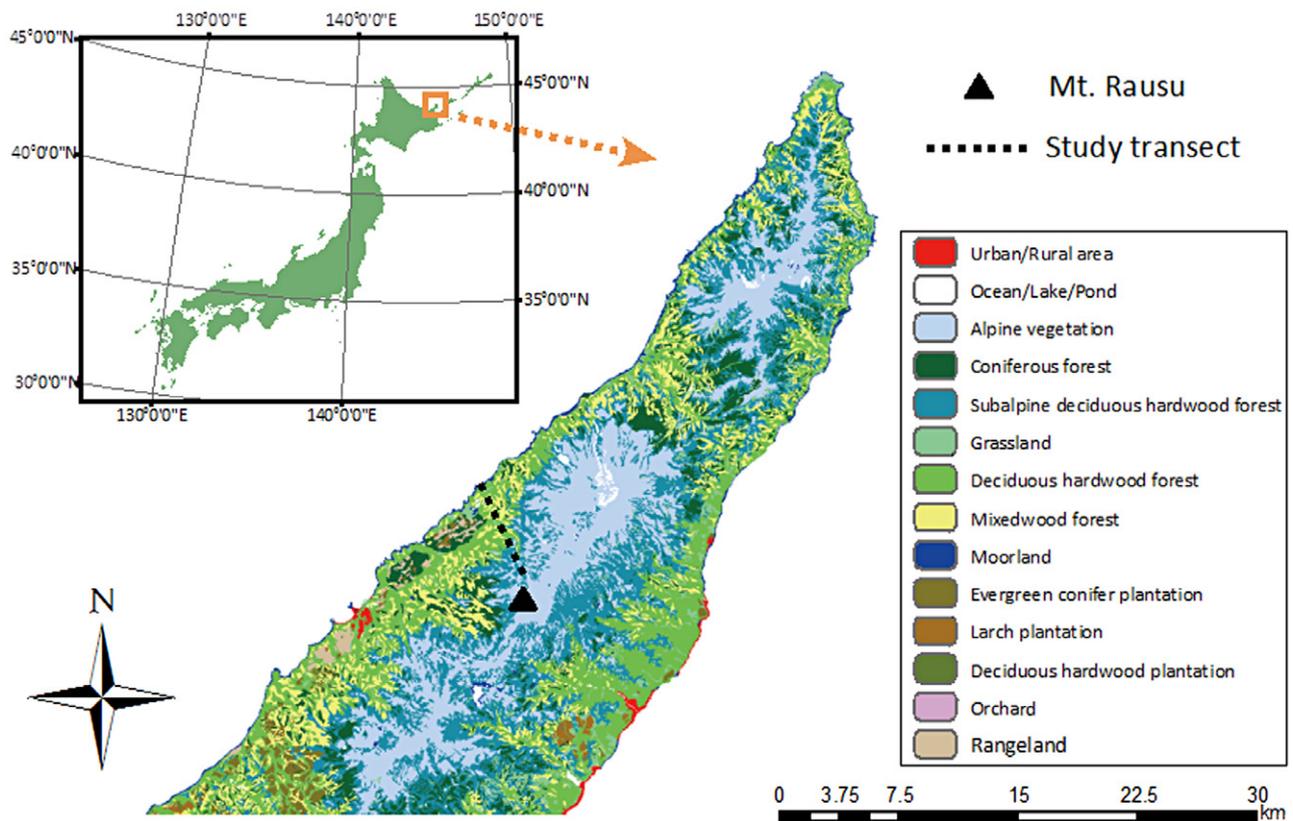
Figure 1 Map of the Shiretoko Peninsula on Hokkaido Island, northern Japan. The vegetation and land-use classifications are indicated with different colours/shades. The biodiversity analysis was conducted along the indicated altitudinal transect (black dotted line) on the western slope of Mount Rausu. We established 10 0.01-ha subplots (a total of 70 subplots, 0.7 ha) in seven altitudinal zones.

mountains. The west coast is characterized by an annual rainfall of approximately 900 mm, an average maximum temperature in August of approximately 22 °C, and average minimum temperature in February of approximately −16 °C, whereas the east coast presents annual rainfall of approximately 1600 mm, an average maximum temperature in August of approximately 19 °C and an average minimum temperature in February of approximately −11 °C. The region is dominated by the cold Northwest Asian Monsoon, which prevails from November to March. Due to the location of the peninsula, its western side is particularly exposed to strong cold winds. Because the vegetation on the western side is greatly affected by winter winds, trees in the mid-to-high altitudes generally creep leeward. We selected the forests on this side of the peninsula as our study sites because of the sharp change in forest structure observed in this area.

Sampling procedures

The diversity of woody plants and oribatid mites was investigated on the western slope of Mount Rausu (1661 m) in July 2010. Measurements were conducted at 50, 200, 400, 600, 800, 1000 and 1200 m above sea level (Fig. 1). All of the study plots were located in areas of pristine vegetation. In each plot, we established 10 subplots of 10 m × 10 m (0.01 ha). We randomly selected mature stands and avoided stands where there had been

recent disturbances to minimize the effects of differences in stand age on community composition. This scale may be smaller than those used in other studies of tree diversity. However, the size of our study subplots is the same as that used by Kraft *et al.* (2011), who indicated that the method employed to calculate the γ-correction of β-diversity (described later) is not dependent on scale. In particular, the complex fine-scale topography of the Shiretoko Mountains (which is thought to contribute to their high biodiversity) makes this scale useful, as small plots tend not to include multiple topographical characteristics, such as different slopes. This scale has also been shown to be valid when considering the distance-decay of tree β-diversity (Morlon *et al.*, 2008). The maximum distances between the subplots in each plot ranged between 311 and 435 m, with an average of 366 m. The average intervals between adjacent subplots were not significantly different among plots (ANOVA, $P > 0.10$), suggesting that our sampling scheme is designed to minimize the confounding effects of spatial factors (which can potentially lead to differences in β-diversity among locations; see also Appendix S1 in Supporting Information for further explanation). A total of 70 subplots (0.7 ha) were established.

In each subplot, we recorded the number of individuals taller than 0.5 m for all woody plant species. For all trees with a girth at breast height (GBH) > 10 cm (an approximate diameter of 3.18 cm), we measured the GBH and then estimated the total

basal area (BA) of the trees in each subplot. The height of the tallest tree in each subplot was recorded as the canopy height (CH) of the stand. In each subplot, we measured the diameter and length of all coarse woody debris (CWD; such as downed logs and branches) with a diameter of greater than 5 cm to estimate the total volume for two categories: recent CWD (decay classes 1–3) and old CWD (decay classes 4–5). For this purpose, we followed the decay-class definitions of Sollins (1982). We also measured understorey light (relative photosynthetic photon flux density, rPPFD) with a quantum sensor (LI-190SZ; LI-COR Inc., Lincoln, NB, USA) 2 m above the ground. Given the close relationships between BA, CH and understorey light, we mainly relied on BA to represent local stand structure (see Appendix S2). Furthermore, we collected four soil samples from each subplot using a soil corer (cylindrical, 20 cm^2 bottom area and 5 cm depth) and then transported them to our laboratory. Oribatid mites were extracted from the soil using Tullgren funnels with 40 W bulbs over 72 h. The oribatid mites were removed using forceps under a stereoscopic microscope (M3Z, Wild Inc., Heerbrugg, Switzerland). Their morphology was observed under a Nomarski differential interference microscope (Eclipse E-600, Nikon Corp., Ltd, Tokyo, Japan) after the specimens had been mounted on slides with gum chloral. We counted the number of individuals of all oribatid mite species. The data from the four soil cores in each subplot were combined and taken as the oribatid community data for the stand. In all of the cores, we measured the thickness and dry mass of the soil surface litter (A0 layer) remaining in the Tullgren funnel after the oribatid mites were extracted. Again, the average values for litter mass and thickness from the four cores were used as the data for each subplot. Furthermore, we collected additional leaf litter (A0 layer) from soil adjacent to the sampled locations over a surface area of 10 cm × 10 cm and measured the water content (WC), pH and carbon-to-nitrogen ratio (CN) in the laboratory. The mass of the collected litter was measured shortly thereafter, and the samples were air-dried for 1 week before the mass was remeasured to estimate the WC. Next, the soil and roots were removed from the samples using a sieve with a 2-mm mesh, and the remaining portions of the samples were dried at 105 °C for subsequent pH and CN measurements. CN was measured using an NC analyser (Sumigraph NC-22, Sumika Chemical Analysis Service, Ltd, Tokyo, Japan).

Data analyses

We calculated the changes in species diversity along the altitudinal gradient in terms of the local (α-diversity) and regional species richness (γ-diversity). The α-diversity is the species richness for each subplot and the γ-diversity is the total number of species at each altitude. We calculated β-diversity using the traditional multiplicative metric of Whittaker (1960), defined as $\beta_w = 1 - \alpha/\gamma$, where α is the mean α-diversity (mean species richness for each subplot at each altitude), and γ is the γ-diversity. Because this index is the most widely applied index of species turnover and has been described as a measure that is well suited for ecological analyses, we relied mainly on this

methodology. Furthermore, we calculated variance-based β-diversity (β_v) as proposed by Legendre *et al.* (2005), which is suitable for comparisons of the average community dissimilarity between sampling units and between different taxonomic groups within the same area. We obtained data table Y by transforming the row data in table $X_{i,j}$, which contained the number of individuals of species j in subplot i, based on the Hellinger distance. Then, we calculated the total variance in the data table with n subplots as $\text{Var}(Y) = \text{SS}(Y)/(n-1)$, where $\text{SS}(Y)$ is the sum over all species and all subplots of the squared deviations from the species means presented in table Y. This variance corresponds to β_v. The Hellinger transformation does not give high weights to rare species (Legendre & Gallagher, 2001). Given the differences in abundance among plots (described later), the Hellinger-standardized β-diversity estimate provides important information for the interpretation of overall results.

In evaluating β-diversity, the dependence of β-diversity on the species pool size (γ-diversity) is an issue of long-standing importance (Anderson *et al.*, 2010; Chase & Myers, 2011). To overcome this difficulty, we employed the null modelling approach of Kraft *et al.* (2011), which corrects local β-diversity for γ-dependence. The null model randomly shuffles individuals among subplots while preserving γ-diversity, the relative abundance of each species per plot (altitude) and the number of individuals per subplot. We calculated β-deviation (β_{dev}), defined as ($\beta_{obs} - \beta_{null}$)/$\beta_{sd}$, where β_{obs} is the observed β-diversity, β_{null} is the mean of the null distribution of β-diversity and β_{sd} is the standard deviation of the null distribution. The null distribution was calculated based on 999 randomizations. Note that β_{dev} is equivalent to a standardized effect size, which indicates the magnitude of the deviation from the expectation of a random (stochastic) assembly process, and positive and negative values indicate more and less β-diversity, respectively, than expected by chance.

Because we focused primarily on the effects of forest stratification on β-diversity for woody plants, we separated the plant communities into three layers: with layer I corresponding to canopy trees > 10 cm in GBH, layer II to large trees > 1.3 m in height, and layer III to small trees > 0.5 m in height. We calculated β_w and β_{dev} separately for individuals in layer I, for individuals in layers I and II, and for all individuals in the three layers to consider the possible changes in niche partitioning among the plants along the vertical gradient in the stand structure.

After calculating the β-diversity and β-deviation of the plants and oribatids for each altitude, we determined whether these parameters show a significant relationship with altitude. Significance was tested using the jackknife regression test because this test is suitable for a small number of observations, as no single observation can have a disproportionate influence on the results (Tukey, 1958). Linearity was tested with both linear and log-linear models, and the results with high R^2 values are shown. Furthermore, to understand the possible contributions of the extrinsic environmental variable(s) to the determination of β-diversity, we tested whether there is a linear relationship between β_{dev} and any explanatory variable(s). Here, we preliminarily conducted a canonical redundancy analysis and selected meaningful environmental variables as determinants of

community structure based on forward selection (999 permutations with an alpha criterion of 0.10) following Blanchet *et al.* (2008). The Hellinger standardization was performed again in this analysis. Altitude, soil properties (litter thickness, litter mass, WC, pH and CN) and BA were taken as candidate determinants for woody species, and the same set of variables with CWDs was included in the selection for oribatid mites. For plants, altitude and BA were selected. BA is widely used as a proxy of stand structure and represents relative dominance, competitive interactions and resource and space occupancy among plant species (Appendix S2; Kohyama, 1993; Kohyama & Takada, 2009). Additionally, this parameter clearly represents the availability of light, which is the most critical resource for plants in the understorey (Appendix S2). For oribatids, litter thickness and mass were selected in addition to altitude. Hence, we relied on these soil variables as critical local environmental factors underlying the structure of oribatid communities (Lindo & Winchester, 2007; Decaëns, 2010).

In testing the relationships between β_{dev} and the explanatory variable(s), we used the mean and coefficient of variation (CV) for each altitude to determine the possible effects of resource availability and heterogeneity on the magnitude of β_{dev}. The CV is widely employed to evaluate environmental heterogeneity (e.g. Questad & Foster, 2008). Because the spatial structure of communities differs between plants and oribatids, with the latter being less spatially structured as a result of their potential dispersibility (Appendix S1), the spatial distributions of the available resources in terms of their amount and heterogeneity are expected to have different effects on the deterministic community-structuring processes of these two groups. The significance of the relationship between β_{dev} and the explanatory variable(s) was tested with the jackknife regression test. In addition, if an environmental variable is correlated with altitude, its effects on β_{dev} may be artefacts mediated by altitudinal change. For this reason, we conducted a partial correlation test to control for the effects of altitude. The partial correlation test was simultaneously used to test for a significant relationship between β_{dev} and altitude, with an environmental variable as a controlling factor. Based on these partial correlation analyses, we determined which factor (environmental variable or altitude) determines the altitudinal changes in β_{dev}.

All of the statistical analyses were performed with R Software, version 2.14.2 (R Core Team, 2012, http://www.R-project.org/). For the null modelling we modified the code of Kraft *et al.* (2011) with the help of the 'vegan' package for additional modelling of the pairwise β-diversity indices (see Appendices S4 & S5). We used the package 'packfor' for the forward selection. We also relied on the 'vegan' package for a rarefaction approach (see the discussion and Appendix S5).

RESULTS

Species richness

We examined the species diversity of woody plants and oribatid mites along an altitudinal gradient on Mount Rausu (Fig. 1).
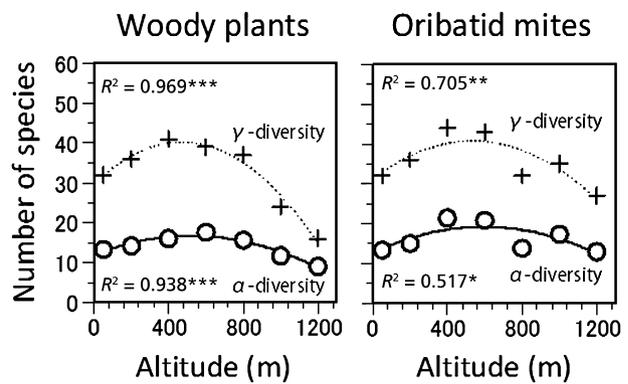
Figure 2 Altitudinal changes in species richness for woody plants and oribatid mites. The γ-diversity and mean α-diversity are shown. The R^2 values and significance were calculated using a quadratic regression. The significance levels are indicated with asterisks: ***$P < 0.001$, **$P < 0.01$, *$P < 0.05$.

Among woody plants with a height greater than 0.5 m, 59 species and 5359 individuals were recorded. Regarding oribatid mites, 77 species and 3669 individuals were recorded. Both α- and γ-diversity showed a hump-shaped (unimodal) distribution with a mid-altitude peak for both woody plants and oribatid mites (Fig. 2).

Beta diversity

The β-diversity distributions of woody plants along the altitudinal gradient are illustrated in Fig. 3. The observed β-diversity decreased with altitude, regardless of the forest-stratification category, except in layer I (for both β_w and β_v). Likewise, the expected β_w based on a random assemblage decreased with altitude for all stratification categories. The observed β_w and β_v values were always greater than would be expected for a random assemblage. Among the investigated plants, the deviation of β-diversity from a random assemblage (β_{dev}) increased with altitude (for both β-diversity indices). In particular, increases in β_{dev} with altitude became more evident when lower-layer individuals were included in the analysis. The relationship between stand structure and β_{dev} is shown in Appendix S3. The β_{dev} of plants was significantly correlated with BA and CH (for both β-diversity indices), whereas β_{dev} was not correlated with the CV values of either BA or CH. The deviations were again larger when lower-layer individuals were included. As there was a significant negative correlation between BA and altitude (Appendix S2), a partial correlation test was conducted to detect any direct relationship between β_{dev} and either BA or altitude (Table 1). The correlations between BA and β_{dev} were still significant after the effects of altitude were excluded (for both β-diversity indices). In particular, the partial correlations between BA and β_{dev} were more evident in the analyses including the lower-layer individuals. In contrast, β_{dev} did not change with altitude when BA was excluded from the correlation, except for the analysis performed in layer I with β_v, suggesting that BA, not altitude, is the major determinant of higher β_{dev} values at higher elevations.
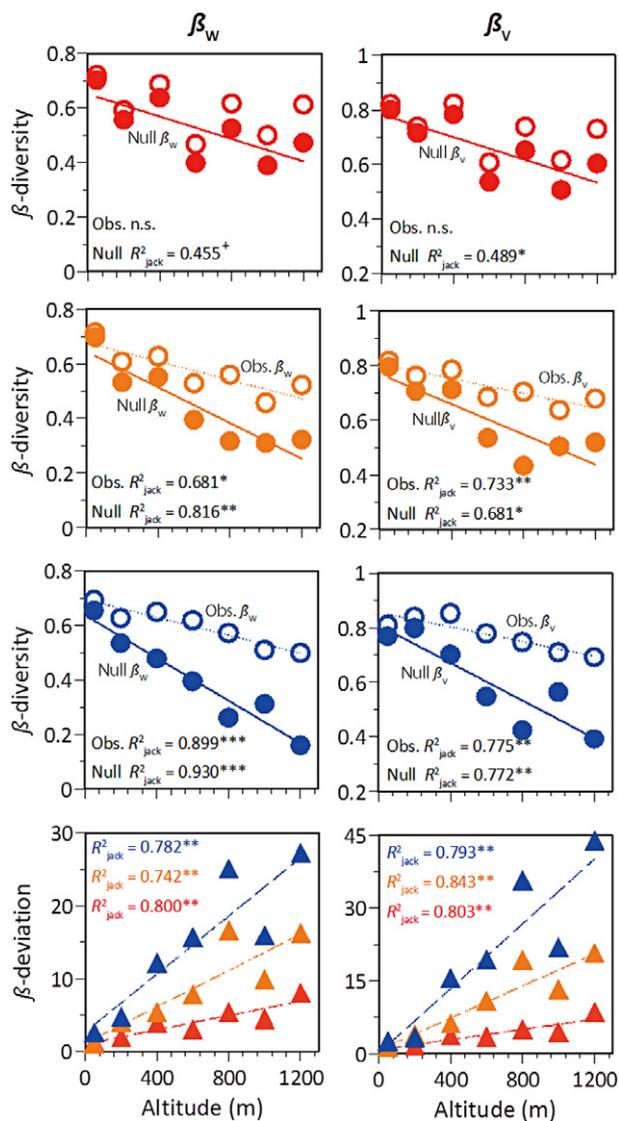
Figure 3 Altitudinal changes in β-diversity for woody plants. Results for $β_w$ and $β_v$ are shown. The circles and triangles indicate the values of β-diversity and β-deviation, respectively. The open and closed symbols indicate the observed values and those expected from the null modelling, respectively. The red, orange and blue symbols represent the results for layer I, layers I–II and layers I–III, respectively. The R^2 values based on the jackknife regression (R^2_{jack}) are shown. The significance levels are indicated with asterisks: ***$P < 0.001$, **$P < 0.01$, *$P < 0.05$.

The β-diversity distributions of oribatid mites along altitude are illustrated in Fig. 4. Both the observed and expected β-diversities decreased with altitude (for both $β_w$ and $β_v$). In contrast to what was observed for woody plants, the β-deviation of oribatids ($β_{dev}$) showed no relationship with altitude (for either β-diversity index). However, the observed β-diversity values were always greater than would be expected from a random community. The $β_{dev}$ of oribatids was not related to the mean values of the soil variables (except for a weak positive correlation of $β_{dev}$ based on $β_v$ with litter mass; jackknife regres-

sion, $R^2_{jack} = 0.438$, $P = 0.06$), whereas $β_{dev}$ significantly increased with CV values, regardless of the examined β-diversity index (Fig. 5). The CV values of these soil variables showed no linear relationship with altitude (jackknife regression, $R^2 < 0.01$ for both litter variables), suggesting that the within-plot heterogeneity of the soil environmental variables is the determinant of the nonlinear relationship of $β_{dev}$ with altitude.

DISCUSSION

We observed a positive departure of β-diversity from what would be expected for a random (stochastic) community for both woody plants and oribatid mites (Figs 3 & 4), suggesting the importance of deterministic processes in structuring the community assembly of forest biodiversity in this landscape. Interestingly, the observed β-diversity was always greater than expected at all locations for both groups of organisms (Figs 3 & 4). Although this phenomenon has been reported previously in recent works (Lindo & Winchester, 2008; Kraft *et al.*, 2011; De Cáceres *et al.*, 2012), it remains unexplained.

For woody plants, the magnitude of β-deviation increased with altitude (Fig. 3). This result contrasts with the previous report by Kraft *et al.* (2011), who found no altitudinal/latitudinal gradient in β-deviation for South American tree communities. However, their study prompted a rebuttal (Qian *et al.*, 2012; Tuomisto & Ruokolainen, 2012). Using the same dataset, Qian *et al.* (2012) detected a significant increase in β-deviation with latitude after correcting for the temperature variations within each transect. Although this method of data correction was subsequently criticized by the original authors (Kraft *et al.*, 2012), our result regarding the altitudinal increase in β-deviation for woody plants in Shiretoko supports the suggestion of Qian *et al.* (2012). In the studied landscape, higher-elevation (low-temperature) stands show greater β-deviation among the investigated plants (Fig. 3), suggesting that, consistent with previous reports (Chase, 2010; Andrew *et al.*, 2012), the role of deterministic assembly processes increases with decreasing productivity in plant communities (note that similar results were observed for different β-diversity indices; Appendix S4). As we hypothesized, the mechanisms underlying community assembly (e.g. niche versus neutral) play an essential role in creating biogeographic patterns of β-diversity (Chase & Myers, 2011).

Our results suggest that niche-based processes in plant communities should dominate in high-altitude stands. Interestingly, the altitudinal increase in β-deviation was more evident when the plants growing in lower layers were included in the analysis (Fig. 3). A similar result was found for β-deviation along a stand-structure gradient (Appendix S3). According to the partial correlation analysis, basal area, not altitude, determines the β-deviation gradient, especially when smaller understorey plants are considered in the analysis (Table 1, Appendix S4). These results imply that given the altitudinal changes in stand structure, the role of understorey plants in deterministic assembly becomes more dominant with altitude. In forests, light is the primary resource for plants, but the availability of light is

Table 1 Partial correlations (r_p) between basal area/altitude and β_{dev} for woody plants.

β-diversity	Layer	Explanatory variable	Controlling factor	r_P	P-value
β_w	I	Altitude	Basal area	−	n.s.
		Basal area	Altitude	−	n.s.
	I–II	Altitude	Basal area	−	n.s.
		Basal area	Altitude	−0.617	< 0.10
	I–III	Altitude	Basal area	−	n.s.
		Basal area	Altitude	−0.683	< 0.05
β_v	I	Altitude	Basal area	0.615	< 0.10
		Basal area	Altitude	−	n.s.
	I–II	Altitude	Basal area	−	n.s.
		Basal area	Altitude	−0.794	< 0.01
	I–III	Altitude	Basal area	−	n.s.
		Basal area	Altitude	−0.692	< 0.05

Analyses were conducted for different layers to evaluate the effects of stand stratification on β_{dev}. We employed two different β-diversity indices to evaluate β_{dev}. Values of r_p are shown with P-values (n.s. means non-significant at $P > 0.10$).
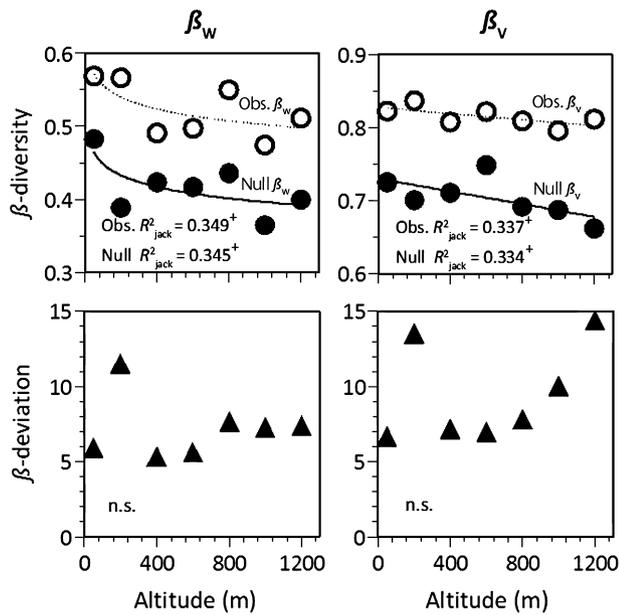
Figure 4 The altitudinal changes in β-diversity for oribatid mites. Results for β_w and β_v are shown. The circles and triangles indicate values of β-diversity and β-deviation, respectively. For β_w, the results for the observed and expected β-diversity showed a log-linear relationship (upper panel), and the lines were fitted on the log-transformed altitude for the analysis and then back-transformed to the plots. The open and closed symbols indicate the observed values and those expected from null modelling, respectively. The R^2 values based on the jackknife regression (R^2_{jack}) are shown. n.s. means that the relationship was not significant ($P > 0.10$). The significance levels are indicated by +, corresponding to $P < 0.10$.

Figure 5 The relationships between two environmental variables (litter thickness and mass) and β_{dev} for oribatid mites. Results for β_w and β_v are shown. The CV values were used to test their relationships with β_{dev}. Significance was tested with the jackknife regression test. The significance level is indicated with asterisks: $**P < 0.01$, $*P < 0.05$.

generally limited in the understorey (Canham *et al.*, 1990; Nicotra *et al.*, 1999). In the studied forests, as low-elevation stands are structurally well developed, light limitation is probably a stronger force in the understorey (Appendix S2). That is, at low altitudes, asymmetric competition for light (one-sided

competition; Kohyama & Takada, 2009) is more intense, so the majority of light resources are intercepted by canopy trees, while only a small proportion of the light is available for the understorey plants, which constitute the majority of the stand assemblage. In contrast, understorey plants have a greater potential to obtain sufficient light in high-altitude stands (Appendix S2), promoting more deterministic resource partitioning. It should be noted that because plant density increased with elevation in

lower layers ($R^2 > 0.68$, $P < 0.05$), rare species were more likely to be found at higher elevations. However, a rarefaction approach (Gotelli & Colwell, 2001) and our additional β-deviation calculations for each subplot (as opposed to the plot-level calculations) showed no significant evidence of this sampling effect (Appendix S5). Thus, we speculate that the greater abundance at higher altitudes was the consequence of finer-scale niche partitioning, which allows more individuals to exist together in a given space, rather than the cause – generating artificial (abundance-driven) altitudinal differences in diversity patterns (see Appendix S5 for further explanation). In reality, in addition to niche partitioning (limiting similarity), the local assembly of a plant community may be structured by different (and sometimes opposing) processes, such as abiotic filtering and facilitation (Spasojevic & Suding, 2012). Nevertheless, we speculate that niche partitioning is the key mechanism underlying the observed spatial pattern of biodiversity.

Several lines of evidence suggest that both predictable and random processes operate simultaneously to shape species assemblages, although the degree to which these processes contribute differs among sites (Ellwood *et al*., 2009; Chase, 2010; Gotzenberger *et al*., 2012). This finding indicates that, in addition to niche-based mechanisms, it is essential to explore a potential factor generating stochasticity in local community assemblies. Historical contingency resulting from a priority effect can create multiple stable states (Chase, 2010) or an alternative transient state (Fukami & Nakajima, 2011) at different sites, leading to high β-diversity. In this study, although we cannot discuss differences in the colonization history of the plant species among the localities, the higher stochasticity observed in the low-altitude stands may result from stronger one-sided competition for resources. In other words, because the canopy trees in old forests generally colonized a site prior to most understorey individuals, one-sided competition may play a role similar to that of priority effects in plant assemblages. The predominance of a few canopy species, which negatively influences understorey species by reducing the availability of resources and space, is more prominent in low-altitude stands, leading to the relative dominance of a quasi-random assembly. Thus, β-diversity decreases with altitude, whereas β-deviation increases with altitude. Although further studies are required, we speculate that the forest-architecture theory (Kohyama, 1993; Kohyama & Takada, 2009), which explains the importance of stand structure in creating niches allowing the successful coexistence of plant species, may explain the broad-scale pattern of β-diversity along a productivity gradient. Therefore, the altitudinal change in stand stratification associated with the change in the within-stand light distribution results in a gradual change in complementary resource use among species. Accordingly, the relative importance of stochastic/deterministic assembly processes in forest-plant communities shifts along altitude. Although our explanation for the shift in local processes is speculative, we believe that recent advances in related theories, such as coexistence theory (HilleRisLambers *et al*., 2012), have the potential to address this unsolved issue in community ecology.

Among the oribatid mites, the altitudinal changes in β-diversity were not as evident as for woody plants, and β-deviation showed no significant altitudinal gradient (Fig. 4). However, the lack of a geographical gradient is not convincing evidence that local community assembly has no role in structuring the biogeographical gradient in biodiversity (Qian *et al*., 2012). We found that the observed β-diversity was always greater than would be expected from a random community (Fig. 4), indicating that niche-based processes control the β-diversity of oribatids (see similar results for different β-diversity indices; Appendix S4). In a Mediterranean beech forest and grasslands, Caruso *et al*. (2012) recently found that the oribatid mite assemblages cannot be explained by a neutral model, suggesting dominance of a niche-based process. The diversity of plants often has a major influence on the diversity of other groups of organisms due to it determining the variety of resource and habitat elements that create niche spaces for different taxa (Hawkins & Porter, 2003), including soil fauna (Vanbergen *et al*., 2007). In this study, we calculated the stand dissimilarity index, which showed a significant partial Mantel correlation with the compositional dissimilarity of the oribatids; this pattern most likely resulted from vegetational control of the environmental conditions in the soil ecosystems (Appendix S6; St John *et al*., 2006; Decaëns, 2010). Thus, the absence of an altitudinal gradient in the β-deviation of oribatids may be a consequence of an indirect response to the spatial gradient in plant diversity (St John *et al*., 2006). Compared with plants showing a clear diversity gradient, more complex (and most likely multiple) processes may operate to structure the oribatid assemblages across the landscape gradient.

Ecological factors that play a deterministic role in diversity patterns often show nonlinear relationships with altitude/latitude (Decaëns, 2010; Qian *et al*., 2012). In this study, the two selected environmental variables explained a significant amount of the variation in the β-deviation of the oribatid communities (Fig. 5, Appendix S4). In particular, instead of mean values, the variation values determined the magnitude of deviation from a stochastic assemblage at each altitude. This result advocates an explanation for the relationship between heterogeneity and biodiversity (Tews *et al*., 2004; Decaëns, 2010; Andrew *et al*., 2012): habitat heterogeneity generates niches across sites (Kerr & Packer, 1997; Vanbergen *et al*., 2007; Questad & Foster, 2008), although some researchers have suggested that productivity may be more important than environmental heterogeneity (Chase & Leibold, 2002; Chase, 2010). Although the dispersal of the oribatids is passive, they can be moved from site to site (e.g. by the wind; Maraun *et al*., 2007; Lehmitz *et al*., 2011). Given the high microhabitat specialization of oribatids (Anderson, 1978), it is likely that high environmental heterogeneity can create more niche spaces, leading to more deterministic community assembly. In reality, the broad-scale gradient of β-diversity is the outcome of various processes, including dispersal limitation, speciation and climate differentiation among localities (Davidar *et al*., 2007; Qian & Ricklefs, 2007; Qian, 2009). Specifically, dispersal limitation is a critical factor influencing community dissimilarity among localities (Lindo & Winchester, 2009; Qian,

2009). The spatial dispersion of our sampling subplots at each altitude was small, so dispersal limitation had no major influence on local (within-plot) community structures (Appendix S1). In conclusion, our results imply that even when habitat conditions show no clear trend along a primary environmental gradient (i.e. altitude/productivity), the niche-based processes determining the local community assembly should not be undervalued.

To our knowledge, this study is the first to quantify the importance of local assembly processes in driving the altitudinal pattern of β-diversity across different taxa. In both the plants and oribatids, we observed unimodal relationships of both α- and γ-diversity with altitude (Fig. 2). The peaking of this congruent pattern of diversity at middle elevations has been widely discussed (Cardelus *et al.*, 2006; Nogues-Bravo *et al.*, 2008; Jankowski *et al.*, 2009; Li *et al.*, 2009), although the causal mechanisms underlying this pattern (e.g. climate, scale effects and human impacts) are beyond the scope of this study. In the present study, despite this concordance, we found striking differences in the altitudinal patterns of β-deviation between the two groups of taxa, emphasizing that the deterministic factors governing a biodiversity pattern along an environmental gradient differ among groups of organisms. This finding indicates that there is no universal rule shaping diversity distribution across multiple taxa. However, our study significantly contributes to the unified theory of biodiversity by explicitly providing this evidence of the importance of local assembly processes in the biogeographical pattern of β-diversity, which is an issue that is currently being actively debated.

REFERENCES

Anderson, J.M. (1978) Inter- and intra-habitat relationships between woodland Cryptostigmata species diversity and the diversity of soil and litter microhabitats. *Oecologia*, **32**, 341–348.

Anderson, M.J., Crist, T.O., Chase, J.M., Vellend, M., Inouye, B.D., Freestone, A.L., Sanders, N.J., Cornell, H.V., Comita, L.S., Davies, K.F., Harrison, S.P., Kraft, N.J., Stegen, J.C. & Swenson, N.G. (2010) Navigating the multiple meanings of beta diversity: a roadmap for the practicing ecologist. *Ecology Letters*, **14**, 19–28.

Andrew, M.E., Wulder, M.A., Coops, N.C. & Baillargeon, G. (2012) Beta-diversity gradients of butterflies along productivity axes. *Global Ecology and Biogeography*, **21**, 352–364.

Baselga, A. (2010) Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, **19**, 134–143.

Blanchet, F.G., Legendre, P. & Borcard, D. (2008) Forward selection of explanatory variables. *Ecology*, **89**, 2623–2632.

Canham, C.D., Denslow, J.S., Platt, W.J., Runkle, J.R., Spies, T.A. & White, P.S. (1990) Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. *Canadian Journal of Forest Research*, **20**, 621–631.

Cardelus, C.L., Colwell, R.K. & Watkins, J.E. (2006) Vascular epiphyte distribution patterns: explaining the mid-elevation richness peak. *Journal of Ecology*, **94**, 144–156.

Caruso, T., Taormina, M. & Migliorini, M. (2012) Relative role of deterministic and stochastic determinants of soil animal community: a spatially explicit analysis of oribatid mites. *Journal of Animal Ecology*, **81**, 214–221.

Carvalho, J.C., Cardoso, P., Crespo, L.C., Henriques, S., Carvalho, R. & Gomes, P. (2011) Determinants of beta diversity of spiders in coastal dunes along a gradient of mediterraneity. *Diversity and Distributions*, **17**, 225–234.

Chase, J.M. (2010) Stochastic community assembly causes higher biodiversity in more productive environments. *Science*, **328**, 1388–1391.

Chase, J.M. & Leibold, M.A. (2002) Spatial scale dictates the productivity–biodiversity relationship. *Nature*, **416**, 427–430.

Chase, J.M. & Myers, J.A. (2011) Disentangling the importance of ecological niches from stochastic processes across scales. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **366**, 2351–2363.

Davidar, P., Rajagopal, B., Mohandass, D., Puyravaud, J.P., Condit, R., Wright, S.J. & Leigh, E.G. (2007) The effect of climatic gradients, topographic variation and species traits on the beta diversity of rain forest trees. *Global Ecology and Biogeography*, **16**, 510–518.

De Bie, T., De Meester, L., Brendonck, L., Martens, K., Goddeeris, B., Ercken, D., Hampel, H., Denys, L., Vanhecke, L., Van der Gucht, K., Van Wichelen, J., Vyverman, W. & Declerck, S. (2012) Body size and dispersal mode as key traits determining metacommunity structure of aquatic organisms. *Ecology Letters*, **15**, 740–747.

De Cáceres, M., Legendre, P., Valencia, R. *et al.* (2012) The variation of tree beta diversity across a global network of forest plots. *Global Ecology and Biogeography*, **21**, 1191–1202.

Decaëns, T. (2010) Macroecological patterns in soil communities. *Global Ecology and Biogeography*, **19**, 287–302.

Ellwood, M.D., Manica, A. & Foster, W.A. (2009) Stochastic and deterministic processes jointly structure tropical arthropod communities. *Ecology Letters*, **12**, 277–284.

Fukami, T. & Nakajima, M. (2011) Community assembly: alternative stable states or alternative transient states? *Ecology Letters*, **14**, 973–984.

Gotelli, N.J. & Colwell, R.K. (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, **4**, 379–391.

Gotzenberger, L., de Bello, F., Brathen, K.A., Davison, J., Dubuis, A., Guisan, A., Leps, J., Lindborg, R., Moora, M., Partel, M., Pellissier, L., Pottier, J., Vittoz, P., Zobel, K. & Zobel, M. (2012) Ecological assembly rules in plant communities – approaches, patterns and prospects. *Biological Reviews*, **87**, 111–127.

Hasegawa, M., Okabe, K., Fukuyama, K., Makino, S., Okochi, I., Tanaka, H., Goto, H., Mizoguchi, T. & Sakata, T. (2013) Community structures of Mesostigmata, Prostigmata and Oribatida in broad-leaved regeneration forests and conifer plantations of various ages. *Experimental and Applied Acarology*, **59**, 391–408.

Hawkins, B.A. & Porter, E.E. (2003) Does herbivore diversity depend on plant diversity?: the case of California butterflies. *The American Naturalist*, **161**, 40–49.

HilleRisLambers, J., Adler, P.B., Harpole, W.S., Levine, J.M. & Mayfield, M.M. (2012) Rethinking community assembly through the lens of coexistence theory. *Annual Review of Ecology, Evolution, and Systematics*, **43**, 227–248.

Jankowski, J.E., Ciecka, A.L., Meyer, N.Y. & Rabenold, K.N. (2009) Beta diversity along environmental gradients: implications of habitat specialization in tropical montane landscapes. *Journal of Animal Ecology*, **78**, 315–327.

Kerr, J.T. & Packer, L. (1997) Habitat heterogeneity as a determinant of mammal species richness in high-energy regions. *Nature*, **385**, 252–254.

Kohyama, T. (1993) Size-structured tree populations in gap-dynamic forest – the forest architecture hypothesis for the stable coexistence of species. *Journal of Ecology*, **81**, 131–143.

Kohyama, T. & Takada, T. (2009) The stratification theory for plant coexistence promoted by one-sided competition. *Journal of Ecology*, **97**, 463–471.

Kraft, N.J.B., Comita, L.S., Chase, J.M., Sanders, N.J., Swenson, N.G., Crist, T.O., Stegen, J.C., Vellend, M., Boyle, B., Anderson, M.J., Cornell, H.V., Davies, K.F., Freestone, A.L., Inouye, B.D., Harrison, S.P. & Myers, J.A. (2011) Disentangling the drivers of beta diversity along latitudinal and elevational gradients. *Science*, **333**, 1755–1758.

Kraft, N.J.B., Sanders, N.J., Stegen, J.C., Anderson, M.J., Crist, T.O., Cornell, H.V., Vellend, M., Chase, J.M., Comita, L.S., Davies, K.F., Freestone, A.L., Harrison, S.P., Inouye, B.D., Myers, J.A. & Swenson, N.G. (2012) Response to comments on 'Disentangling the drivers of beta diversity along latitudinal and elevational gradients'. *Science*, **335**, 1573-d.

Legendre, P. & Gallagher, E. (2001) Ecologically meaningful transformations for ordination of species data. *Oecologia*, **129**, 271–280.

Legendre, P., Borcard, D. & Peres-Neto, P.R. (2005) Analyzing beta diversity: partitioning the spatial variation of community composition data. *Ecological Monographs*, **75**, 435–450.

Lehmitz, R., Russell, D., Hohberg, K., Christian, A. & Xylander, W.E.R. (2011) Wind dispersal of oribatid mites as a mode of migration. *Pedobiologia*, **54**, 201–207.

Leprieur, F., Tedesco, P.A., Hugueny, B., Beauchard, O., Durr, H.H., Brosse, S. & Oberdorff, T. (2011) Partitioning global patterns of freshwater fish beta diversity reveals contrasting signatures of past climate changes. *Ecology Letters*, **14**, 325–334.

Li, J., He, Q., Hua, X., Zhou, J., Xu, H., Chen, J. & Fu, C. (2009) Climate and history explain the species richness peak at mid-elevation for *Schizothorax* fishes (Cypriniformes: Cyprinidae) distributed in the Tibetan Plateau and its adjacent regions. *Global Ecology and Biogeography*, **18**, 264–272.

Lindo, Z. & Winchester, N.N. (2007) Oribatid mite communities and foliar litter decomposition in canopy suspended soils and forest floor habitats of western red cedar forests, Vancouver Island, Canada. *Soil Biology and Biochemistry*, **39**, 2957–2966.

Lindo, Z. & Winchester, N.N. (2008) Scale dependent diversity patterns in arboreal and terrestrial oribatid mite (Acari: Oribatida) communities. *Ecography*, **31**, 53–60.

Lindo, Z. & Winchester, N.N. (2009) Spatial and environmental factors contributing to patterns in arboreal and terrestrial oribatid mite diversity across spatial scales. *Oecologia*, **160**, 817–825.

Maraun, M., Schatz, H. & Scheu, S. (2007) Awesome or ordinary? Global diversity patterns of oribatid mites. *Ecography*, **30**, 209–216.

Mena, J.L. & Vázquez-Domínguez, E. (2005) Species turnover on elevational gradients in small rodents. *Global Ecology and Biogeography*, **14**, 539–547.

Mokany, K., Harwood, T.D., Overton, J.M., Barker, G.M. & Ferrier, S. (2011) Combining alpha- and beta-diversity models to fill gaps in our knowledge of biodiversity. *Ecology Letters*, **14**, 1043–1051.

Morlon, H., Chuyong, G., Condit, R., Hubbell, S., Kenfack, D., Thomas, D., Valencia, R. & Green, J.L. (2008) A general framework for the distance-decay of similarity in ecological communities. *Ecology Letters*, **11**, 904–917.

Nicotra, A.B., Chazdon, R.L. & Iriarte, S. (1999) Spatial heterogeneity of light and woody seedling regeneration in tropical wet forests. *Ecology*, **80**, 1908–1926.

Nogues-Bravo, D., Araujo, M.B., Romdal, T. & Rahbek, C. (2008) Scale effects and human impact on the elevational species richness gradients. *Nature*, **453**, 216–219.

Qian, H. (2009) Beta diversity in relation to dispersal ability for vascular plants in North America. *Global Ecology and Biogeography*, **18**, 327–332.

Qian, H. & Ricklefs, R.E. (2007) A latitudinal gradient in large-scale beta diversity for vascular plants in North America. *Ecology Letters*, **10**, 737–744.

Qian, H., Wang, X. & Zhang, Y. (2012) Comment on 'Disentangling the drivers of beta diversity along latitudinal and elevational gradients'. *Science*, **335**, 1573-b.

Questad, E.J. & Foster, B.L. (2008) Coexistence through spatio-temporal heterogeneity and species sorting in grassland plant communities. *Ecology Letters*, **11**, 717–726.

R Core Team (2012) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.

Ricklefs, R.E. (2004) A comprehensive framework for global patterns in biodiversity. *Ecology Letters*, **7**, 1–15.

Sheldon, K.S., Yang, S. & Tewksbury, J.J. (2011) Climate change and community disassembly: impacts of warming on tropical and temperate montane community structure. *Ecology Letters*, **14**, 1191–1200.

Sollins, P. (1982) Input and decay of coarse woody debris in coniferous stands in western Oregon and Washington. *Canadian Journal of Forest Research*, **12**, 18–28.

Spasojevic, M.J. & Suding, K.N. (2012) Inferring community assembly mechanisms from functional diversity patterns: the importance of multiple assembly processes. *Journal of Ecology*, **100**, 652–661.

St John, M.G., Wall, D.H. & Behan-Pelletier, V.M. (2006) Does plant species co-occurrence influence soil mite diversity? *Ecology*, **87**, 625–633.

Tews, J., Brose, U., Grimm, V., Tielborger, K., Wichmann, M.C., Schwager, M. & Jeltsch, F. (2004) Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography*, **31**, 79–92.

Tukey, J.W. (1958) Bias and confidence in not-quite large samples. *Annals of Mathematical Sciences*, **29**, 614.

Tuomisto, H. & Ruokolainen, K. (2012) Comment on 'Disentangling the drivers of beta diversity along latitudinal and elevational gradients'. *Science*, **335**, 1573-c.

Vanbergen, A.J., Watt, A.D., Mitchell, R., Truscott, A.M., Palmer, S.C., Ivits, E., Eggleton, P., Jones, T.H. & Sousa, J.P. (2007) Scale-specific correlations between habitat heterogeneity and soil fauna diversity along a landscape structure gradient. *Oecologia*, **153**, 713–725.

Whittaker, R.H. (1960) Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs*, **30**, 279–338.

Willig, M.R., Kaufman, D.M. & Stevens, R.D. (2003) Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. *Annual Review of Ecology, Evolution, and Systematics*, **34**, 273–309.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1 Spatial factors affecting β-diversity.
Appendix S2 Stand structure and understorey light.
Appendix S3 Stand structure and β-diversity of woody plants.
Appendix S4 Additional analyses of β-diversity.
Appendix S5 Effects of abundance on diversity.
Appendix S6 Pairwise community dissimilarity and stand dissimilarity.

BIOSKETCH

Akira Mori is an associate professor at Yokohama National University. He is interested in interpreting the spatial and temporal patterns of ecological and biogeographical phenomena in forest ecosystems. In particular, he is interested in understanding the roles of natural and human disturbances in determining the patterns and processes in biodiversity.

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