

ORIGINAL  
ARTICLE

# Functional redundancy of multiple forest taxa along an elevational gradient: predicting the consequences of non-random species loss

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## ABSTRACT

**Aims** Climate change can substantially alter ecological communities. However, we hypothesized that, even if novel communities emerge, those communities may not be novel in terms of functional composition. To infer the processes associated with rising temperatures, we evaluated elevational taxonomic/functional turnover of plant and invertebrate communities. Because climate change interacts synergistically with other environmental factors, and therefore is not the sole driver of change in ecological communities, we also considered how the taxonomic/functional composition of the communities would be affected by mammalian overgrazing/browsing, which has become prominent in the study region.

**Location** Shiretoko National Park, Shiretoko Peninsular, Hokkaido, Japan.

**Methods** We investigated the diversity of eight groups of organisms (taxa) in forests of northern Japan, and calculated the distance decay of taxonomic/functional similarity (Sørensen's  $\beta$ -diversity) along an elevational gradient. A null model was used to separate functional turnover from taxonomic turnover. We then simulated how taxonomic/functional turnover along the gradient would be changed after non-random loss of species sensitive to mammalian herbivory.

**Results** We found that each group showed elevational decay in taxonomic similarity. Along an elevational gradient, species groups structured by stronger dispersal limitation showed faster species turnover. This suggested differences in the process of climate-induced species reassembly among the groups. We also found that elevational turnover of communities based on functional traits tended to be lower than that based on taxonomic identity for the majority of the groups, supporting our hypothesis of functional redundancy across the elevational gradient. We thus speculated that climate-induced emergence of taxonomically novel communities may have limited influence on critical ecosystem processes supported by functional diversity. Furthermore, while random species loss did not change functional turnover, non-random loss of species attributable to mammalian herbivory substantially accelerated elevational functional turnover of the taxa. This suggested a possible loss of the functional redundancy of communities.

**Main conclusions** Future communities may be novel not simply because climates are changing at unprecedented rates but also because of the synergistic influences of other environmental changes. Thus ecological processes may be more seriously affected in the future than is generally anticipated based on

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existing climate-change scenarios, with possible consequences for ecosystem functioning.

### Keywords

Distance decay of similarity, functional beta diversity, functional traits, Japan, mammalian herbivory, multi-taxon approach, no-analogue community, non-random loss of biodiversity, novel community.

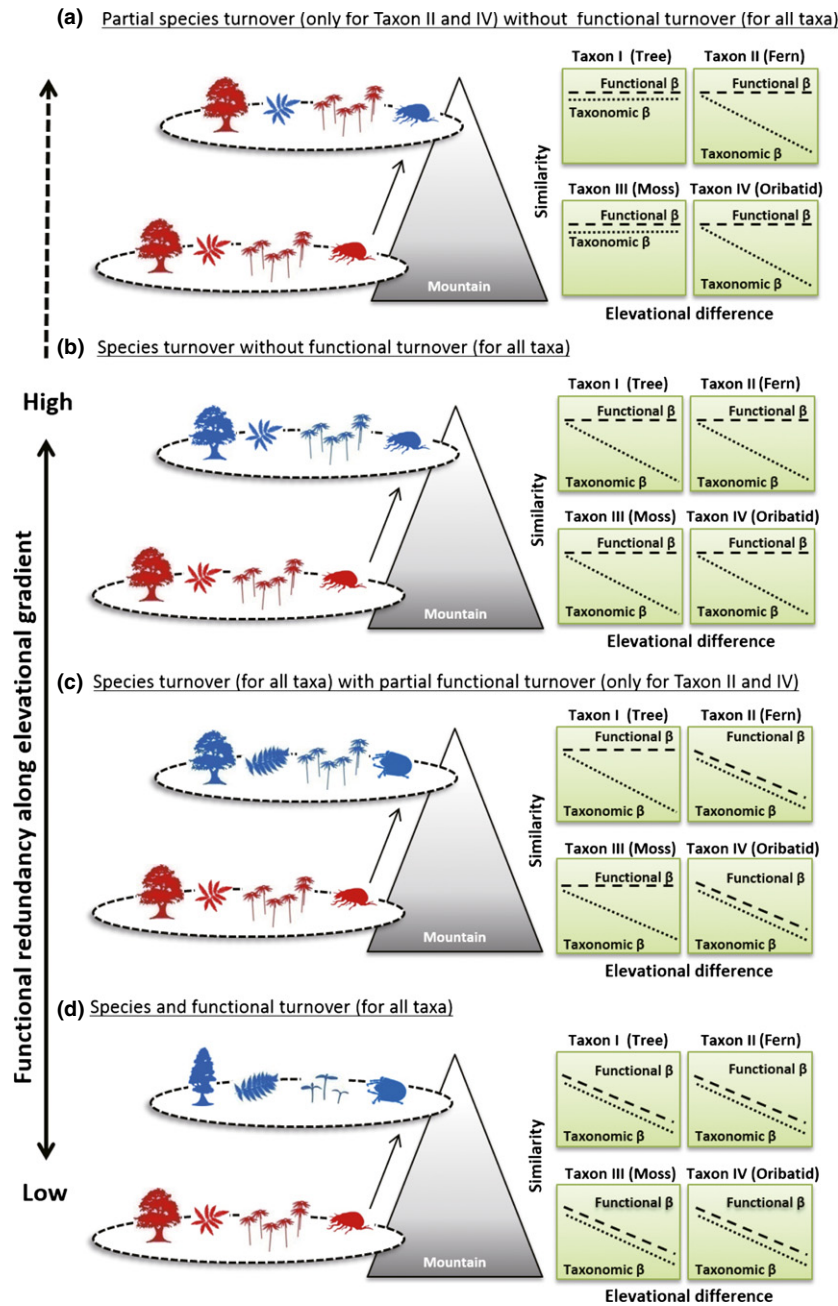
## INTRODUCTION

There is increasing evidence and awareness that changes in climate and biodiversity are of global concern (Bellard *et al.*, 2012; Mori *et al.*, 2013a). Among various climatic variables, temperature has a primary role in determining the spatial distribution of individual species. Species respond to climatic warming by shifting their ranges to higher latitudes and elevations to maintain their thermal environment, yet little is known about how shifts of individual species affect entire communities (Walther, 2010; Sheldon *et al.*, 2011). In particular, given our present understanding of how biodiversity contributes to the functioning of ecosystems (Cardinale *et al.*, 2012), climate-induced changes in the compositional characteristics of ecological communities may have serious consequences (Walther, 2010). It has been argued that a certain level of biodiversity can stabilize ecosystems, with different species providing functional complementarity under different conditions, thereby buffering the effects of environmental change (Mori *et al.*, 2013b). However, considering the evidence of historical 'community dis-assembly and re-assembly' (Williams & Jackson, 2007), an unsolved question remains: how is the functional redundancy of ecological communities (Mori *et al.*, 2013b) affected by climate change?

If future communities are substantially altered, the ecosystem functionality supported by the current combinations of species may be lost. However, recent studies suggest that terrestrial ecosystems can retain their fundamental functionality (and thus resilience) even under large changes in climatic conditions (Huntingford *et al.*, 2013; Ponce Campos *et al.*, 2013). One study of the future distributions of plant communities has suggested a high degree of functional redundancy (Gallagher *et al.*, 2013), i.e. the ability of communities to retain a similar level of ecosystem functionality despite the extinction of one or more of a set of species (Mori *et al.*, 2013b). Based on this potential for ecosystem stability following biological reorganization, we hypothesized that, even if taxonomically no-analogue communities (Jackson & Hobbs, 2009) emerge under different climate regimes, these communities may be similar in terms of functional composition. However, there is currently limited information available regarding the impacts of climate change on functional characteristics of biodiversity (Bellard *et al.*, 2012). It is thus worth exploring the mechanisms underlying species and functional reassembly along a climatic (i.e. temperature) gradient.

In particular, ecosystem functioning is not only provided by species within a single taxonomic group but is also sustained by interactions within the larger local community (a community comprising multiple organism groups). For instance, decoupling of aboveground and belowground communities resulting from differences in climate-induced community reordering may substantially alter plant–soil feedbacks, with potential consequences for biogeochemical processes (Bardgett *et al.*, 2013). When a focus is placed on multiple taxonomic groups, many possible combinations of taxonomic and functional composition exist at a given location following climate-induced reassembly (Fig. 1). Given inherent differences in the factors structuring communities among different groups of organisms (e.g. spatial versus environmental factors; De Bie *et al.*, 2012), decoupling of responses across different organism groups is likely. Although present knowledge is limited about how combinations of functional traits from different organism groups contribute to the performance and stability of ecosystem functioning, we suspect that, if there are mismatches in the rate of functional reorganization among different taxa, some ecosystem processes could be affected. A multi-taxon approach is thus important when exploring the consequences of biodiversity response to a changing climate.

We inferred the processes of climate-related community reassembly using distance decay of similarity as a framework (Nekola & White, 1999; Morlon *et al.*, 2008) for the study of plant and invertebrate communities in the northern forests of the Shiretoko Peninsula in Japan (Mori *et al.*, 2013c). Because the study area is surrounded by ocean, most terrestrial species will be forced to shift their distributional ranges upwards in a warmer future (i.e. there is no connected land area at higher latitudes). We therefore focused on taxonomic and functional changes in community composition along an elevational gradient, primarily representing a temperature gradient (Sheldon *et al.*, 2011). Our diversity dataset, collected along an elevational gradient (see Materials and Methods), does not provide a complete picture of all the consequences of reassembly, because several environmental factors, such as moisture, wind and season length, other than temperature, can change with elevation (Körner, 2007). However, comparisons of communities across different elevations provide invaluable inferences regarding temperature-related changes in the structure and function of ecosystems (Malhi *et al.*, 2010). We thus aimed to deduce scenarios of taxonomic and functional reassembly following the upward shift of species by focusing on the ele-



**Figure 1** Conceptual diagram showing taxonomic and functional turnover on a mountain. To infer processes of species and functional reassembly, we used the elevational decay of community similarity (shown in light green boxes). Each of the coloured symbols represents a species. Species with the same shape but different colours are taxonomically different but they are functionally similar based on multiple functional effect traits. Examples of four different scenarios for taxonomic and functional turnover are shown. In scenarios a and b, functionality (in terms of the presence of a function and/or the rate of an ecosystem process) supported by species assemblages within a single organism group and by those across several different groups are all maintained after a differential upward shift among taxa (despite the differences in taxonomic turnover between scenarios a and b). In scenario c, some functionality supported by either taxon I or taxon III as well as those supported by a combination of taxa I and III may be maintained, while other aspects of ecosystem functioning may be altered or even lost. In scenario d, all functionality supported by taxa I–IV individually and in any combination will be lost. Although the figures show the observed taxonomic/functional turnover, null models are necessary to separate functional turnover from taxonomic turnover (see Materials and Methods). Even functional turnover is low along the elevational gradient (represented by the small slope of the elevational decay of similarity); when functional similarity is also consistently low between locations (represented by a small intercept value of the elevational decay of similarity), functional redundancy, such as that shown in scenarios a and b, cannot exist. In addition to a low level of functional turnover, the functional redundancy hypothesized in this study needs a constantly high functional similarity along the gradient. Note that, for simplicity, although the study used eight taxa, we have only illustrated the scenarios using four taxa.

vational gradient (Fig. 1). Based on this approach, we aimed to evaluate functional redundancy. Note that the concept of functional redundancy is still rudimentary and variable (Mori *et al.*, 2013b). The specific definition of functional redundancy in this study is the ability of an assemblage to maintain the same functionality (inferred from multiple effect traits) along an elevational gradient.

It seems probable that the impact of climate change interacts synergistically with other environmental conditions (Mantyka-Pringle *et al.*, 2012; Mori *et al.*, 2013a). In particular, given that human-induced species-loss is not random and could potentially result in a critical loss of vital ecosystem functionality (Bracken *et al.*, 2008; Isbell *et al.*, 2008), it is worth assessing how a realistic loss of biodiversity can alter the taxonomic and functional characteristics of ecological communities in a changing climate. We thus modelled a realistic non-random loss of species associated with actual environmental conditions. Since the late 1980s, increasing populations of Ezo deer, *Cervus nippon yezoensis*, have seriously overgrazed and over-browsed the vegetation in the forests of northern Japan. Several underlying causes of this population expansion have been proposed, such as agricultural development (land-use change) benefiting the deer by increasing the availability of forage resources (Takatsuki, 2009). Deer herbivory is having a serious impact on coastal forests in the study area, although currently the mountain forests are relatively less affected than the lowland forests. However, the level of herbivory may be increasing in the mountain forests, because the harsh winter climate seems to be moderating as a result of climate warming, increasing the overwinter survival rate of the deer (Takatsuki, 2009). Thus, we evaluated the possible changes in taxonomic/functional turnover after the loss of plant species caused by an increased level of mammalian herbivory.

## MATERIALS AND METHODS

### Study site

The study was conducted in the western part of Shiretoko National Park, located on the Shiretoko Peninsula in north-eastern Hokkaido, Japan (Fig. 2). According to the United Nations Educational, Scientific and Cultural Organization (UNESCO), because of its high level of biodiversity, this area 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>, last accessed 5 March 2015). Approximately 90% of the park is covered with pristine natural vegetation, which extends from the coast to above the tree line in graded belts based on elevation.

The region is dominated by the cold Northwest Asian Monsoon, which prevails from November to March. The location of the peninsula exposes its western side to strong, cold winter winds. The north-west coast is characterized by

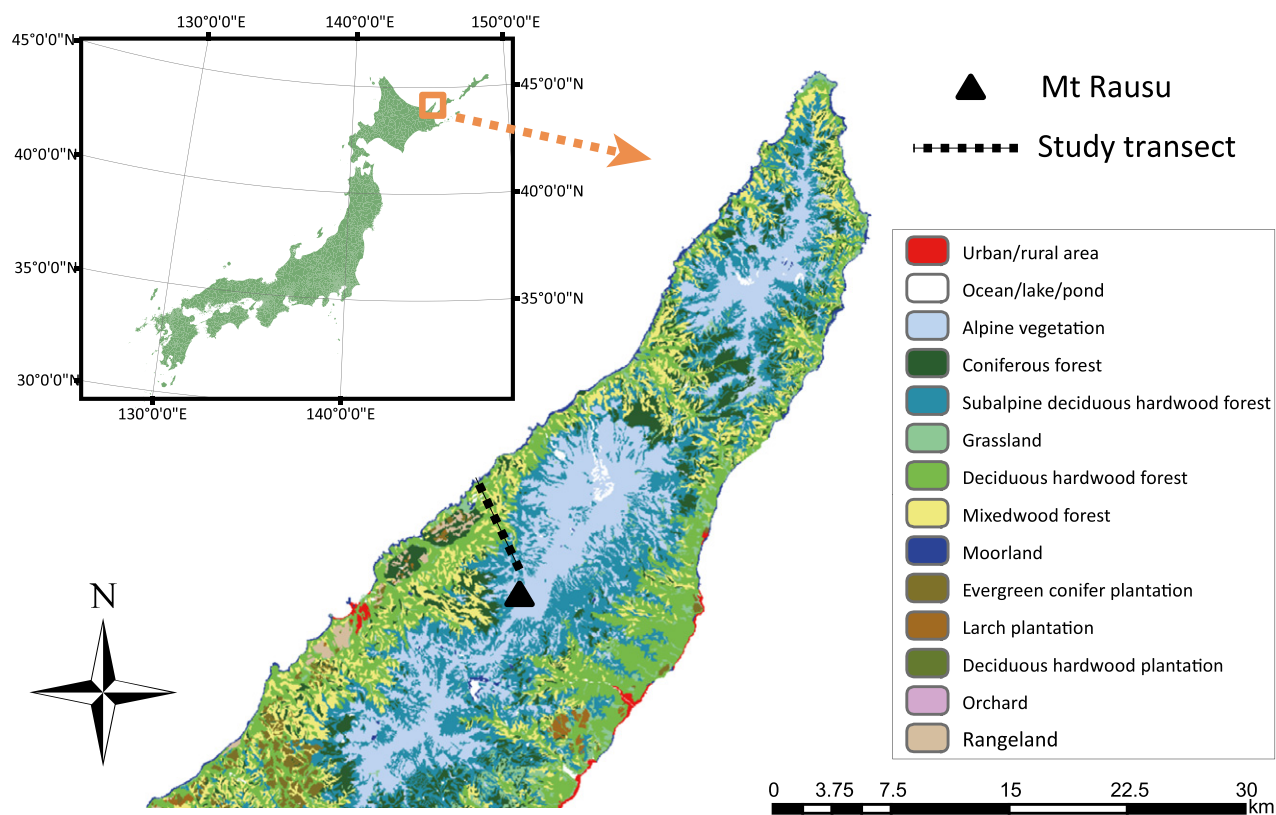
an annual rainfall of about 1090 mm, an average maximum temperature in August of approximately 22 °C, and an average minimum February temperature of about –16 °C (based on data for the last 30 years; <http://shiretoko-whc.com>, last accessed 5 March 2015). While uphill shifts of communities have been often reported as a response to climate warming, this is not always true depending on changes in other climatic variables such as precipitation (Crimmins *et al.*, 2011). We therefore created a climate surface based on an interpolation of bioclimatic variables (for the period 1950–2000, available at WorldClim; <http://www.worldclim.org>, last accessed 5 March 2015). Using these data, we confirmed with a preliminary investigation that an increase in elevation from 50 to 1200 m a.s.l. (the elevation of our study plots, see below) corresponded to an approximately 11% increase in the amount of precipitation (i.e. approximately 120 mm of annual precipitation), indicating that the precipitation gradient was relatively gentle along the elevational gradient. Furthermore, a downscaled regional climate model showed that future increases in precipitation would be smaller than those projected for temperature in this region (Tsunematsu *et al.*, 2013). Taken together, temperature was expected to be the most important environmental factor to change along the elevational gradient in our study site.

### Field data collection

In July 2010, vascular plants, mosses, oribatid mites and ground-dwelling spiders were surveyed on the western slope of Mt Rausu (1661 m a.s.l.), the highest peak in the peninsula. The surveys were taken at 50, 200, 400, 600, 800, 1000 and 1200 m a.s.l. (Fig. 2). At each elevation, we established 10 subplots of 10 m × 10 m (0.01 ha) in areas of pristine vegetation, with a total of 70 subplots (0.7 ha) (see Mori *et al.*, 2013c, for further details of the study subplots). The maximum distances between the subplots at each elevation ranged between 311 m and 435 m, with an average of 366 m. The average intervals between adjacent subplots were not significantly different across the seven elevations (ANOVA,  $P > 0.10$ ).

In each subplot, we recorded the presence of all species of woody plants, herbaceous plants and ferns. Basal area (BA) was calculated from girth at breast height (g.b.h.) of all trees > 10 cm g.b.h. The canopy height of the stand was estimated from the height of the tallest tree in each subplot. For mosses, because few field experts were available, species occurrence was recorded in only five to seven subplots for each elevation. We also collected four soil samples from five of the 10 subplots at each elevation (near the centre of each subplot, with a maximum separation of 4 m between cores), using a soil corer (cylindrical, with a 20-cm<sup>2</sup> bottom area and 5 cm depth), which were then taken to a laboratory for analysis. Oribatid mites were extracted from the soil using Tullgren funnels with 40 W bulbs over 72 h. The morphology of the oribatid mites was observed under a Nomarski differential interference microscope (Eclipse E-600; Nikon





**Figure 2** Map of the Shiretoko Peninsula on Hokkaido Island, northern Japan. Reproduced with permission from Mori *et al.* (2013c). The vegetation and land-use classifications are indicated with different colours/shades. The biodiversity analysis was conducted along the elevational transect indicated (black dotted line) on the western slope of Mt Rausu.

Corp. Ltd, Tokyo, Japan) after the specimens had been mounted on slides with gum chloral, and complete species lists were compiled. The data from the four soil cores in each subplot were combined to represent the oribatid community of the stand. For 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. Similarly, the average values for litter mass and thickness from the four cores were used as the data for each subplot. Additionally, to capture ground-dwelling spiders, we kept nine pitfall traps (7 cm diameter, about 8 cm deep with 50 mL of propylene glycol) for a week in five randomly selected subplots at elevations between 200 and 1000 m a.s.l. A reduced elevational range was used for the spiders because of the difficulties and limitations in identifying species in this taxon, which have rarely been surveyed in the peninsula. Complete species lists were compiled. The data from the nine traps in each subplot were combined and taken as the spider community for 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 > 5 cm, to estimate the total volume for two categories: recent CWD (decay classes 1–3) and old CWD (decay classes 4–5), following the decay-class definitions of Sollins (1982). We also measured understorey light (relative photosynthetic photon flux density) with a quantum

sensor (LI-190SZ; LI-COR Inc., Lincoln, NE, USA) 2 m above the ground around the centre of each subplot. We collected 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 (C:N) in the laboratory. WC was estimated by weighing the litter shortly after sampling and again after 1 week at room temperature. The soil and roots were then 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 C:N measurements. C:N was measured using an NC analyser (Sumigraph NC-22; Sumika Chemical Analysis Service Ltd, Tokyo, Japan).

### Functional traits

All recorded species (77, 110, 22, 86, 74 and 43 woody plants, herbaceous plants, ferns, mosses, mites and spiders, respectively) were classified according to a set of functional traits. Functional traits can be divided into the two major categories: effect traits and response traits (Laliberté *et al.*, 2010; Mori *et al.*, 2013b). Because our primary aim was to infer possible changes in ecosystem functioning sustained by biological communities of multiple taxonomic groups, we focused primarily on functional effect traits, which influence ecosystem processes (Hooper *et al.*, 2005). For the response

traits that can represent the responses of individual species to the environment (Elmqvist *et al.*, 2003), we relied only on information related to the dispersal mode for vascular plants (seed/spore mass and categorization of assisted/unassisted dispersal). This was because we hypothesized that the degree of turnover that causes community reassembly along an elevational gradient ( $\beta$ -diversity) would differ between taxonomic groups as a result of fundamental differences in dispersal ability between vascular plants affecting community turnover (Qian, 2009). Details about the selection of functional effect traits are summarized in Appendix S1.

### Taxonomic and functional turnover

In evaluating taxonomic and functional turnover of communities along the elevational gradient, we calculated the distance decay of similarity (Nekola & White, 1999; Morlon *et al.*, 2008) between all pairs of locations using pooled diversity data from the subplots. We used Sørensen's  $\beta$ -diversity index because it is widely used to describe the distance decay of taxonomic similarity (e.g. Davidar *et al.*, 2007; Dexter *et al.*, 2012). This index has been used previously to quantify phylogenetic (Bryant *et al.*, 2008) and functional turnover (Swenson *et al.*, 2011) between locations. To calculate taxonomic  $\beta$ -diversity, we used species-level data for all groups. To calculate functional  $\beta$ -diversity, we constructed valid functional trait dendrograms following Mouchet *et al.* (2008). We used Gower's distance throughout, which allows mixed variable types (continuous, ordinal and categorical), as well as missing values (Laliberté & Legendre, 2010). Although some studies have used ordination methods such as principal coordinates analysis to construct a functional distance matrix, we did not use this approach because of possible information loss (Schleuter *et al.*, 2010).

For the analyses of distance decay, we pooled the diversity data from all the subplots at a given elevation, because our primary interest was to quantify elevational changes in taxonomic and functional composition of communities. In other words, we did not assess local processes determining community composition at a given elevation. Using data from all seven elevations (five for spiders), we calculated two measures of distance decay. First, the slope ( $\beta_{\text{slope}}$ ) of the linear regression of the  $\beta$ -diversity index against pairwise absolute elevational differences (Nekola & White, 1999; Qian, 2009). A steeper slope (more negative values) indicates a faster turnover along the elevational gradient (Bryant *et al.*, 2008). Second, the distance (elevation separation) that halves the similarity from the initial value ( $\beta_{0.5\text{-dist}}$ ), considering both the rate of distance decay and the initial similarity (Soininen *et al.*, 2007). A smaller value of  $\beta_{0.5\text{-dist}}$  represents a faster turnover along an elevational gradient. Because there was no substantial difference in the results with and without log transformation, we chose not to log transform the data. In testing the significance of  $\beta_{\text{slope}}$  for taxonomic and functional similarity along the elevational gradient, we first conducted a

Mantel test (1000 permutations) and then, if the results were significant, we calculated  $\beta_{0.5\text{-dist}}$ .

### Environmental and spatial structure

Because we were primarily interested in taxon-dependent turnover of species (see also Qian, 2009; Qian & Ricklefs, 2012; Wang *et al.*, 2012), we evaluated our data to see whether the values of taxonomic turnover reflected the degree of dispersal limitation for each taxonomic group. Data with enough resolution were only available for vascular plants, and these were separated into five groups based on dispersal vector: woody plants dispersed by autochory, woody plants dispersed by allochory, herbaceous plants dispersed by autochory, herbaceous plants dispersed by allochory, and ferns.

For each of the eight groups of organisms (the five listed above and mosses, mites and spiders), we estimated the unique contribution of the environment (variance explained by the environment independently of space; the environmental fraction), the unique contribution of space (variance explained by space independently of environment; the spatial fraction), the contribution of the spatially structured environment (variance shared by the environment and space; environmentally structured spatial fraction) and residuals revealed by sequential subtractions (unknown fraction) to the overall meta-community structure. This provided a determination of  $\beta$ -diversity (Sørensen's index) following methods of variation partitioning (Peres-Neto *et al.*, 2006). Using subplot data we constructed spatial models using variables extracted based on Moran's eigenvector maps (MEMs; Borcard *et al.*, 2004) and used elevation, light, soil properties (litter thickness, litter mass, WC, pH and C:N), BA and CWDs as candidate environmental determinants. For details of the analysis see Appendix S2.

The fractions obtained from each group were then tested using Spearman's rank correlation on their  $\beta_{\text{slope}}$  values. We expected the fraction reflecting the overall spatial community structure to be negatively correlated with the rate of species turnover, i.e. for dispersal-limited groups controlled more by space (isolation by distance) to have a faster taxonomic turnover. Specifically, we focused on the environmentally structured spatial fraction, because environmental factors were inherently correlated with spatial isolation along the elevational gradient. The variation in species composition fitted by the environmentally structured spatial fraction could be interpreted as the outcome of local spatial control along an elevational gradient. According to De Bie *et al.* (2012), propagule size as a dispersal vector is the major determinant of the degree of dispersal limitation for passive dispersers in aquatic communities. Because our plant groups were also dispersed passively, mean seed/spore mass was tested for each fraction of the variation partitioning (see Appendix S2). Because data for the mass of seeds and spores were only available for vascular plants, we limited this analysis to only these groups. We used Spearman's rank

correlation so that our findings were comparable with those of De Bie *et al.* (2012).

### Separating functional turnover from taxonomic turnover

To separate the significance of functional turnover from taxonomic turnover, we tested whether the slope in the elevational decay of functional similarity was greater or less than expected given the taxonomic decay in similarity (see Bryant *et al.*, 2008 for the modelling of phylogenetic turnover). We compared the observed slope with a distribution of distance decay slopes obtained by randomizing the location of species at the tips of the trait dendrogram tree 1000 times. This was equivalent to sampling the species randomly while constraining the number of species in each community, the number of species shared by any two communities, and species occurrence across all communities. The observed functional  $\beta_{\text{slope}}$  was assumed to be significantly different from the null expectation if it was in the lowest or highest 2.5% values of the  $\beta_{\text{slope}}$  of the randomizations (two-tailed test,  $P < 0.05$ ). A gentler functional  $\beta_{\text{slope}}$  than the null expectation indicates that the functional traits are more evenly distributed along the elevational gradient given the taxonomic turnover, suggesting significantly less functional turnover. As the observed functional  $\beta_{\text{slope}}$  approaches zero, and functional similarity between locations is maintained at a level of high similarity, functional redundancy along the elevational gradient increases (see Fig. 1 for details).

### Scenarios of species loss

We tested possible changes in taxonomic and functional turnover along the elevational gradient under a scenario of species loss. As a proxy for species loss, we used vascular plant species identified as being negatively impacted by the intense mammalian herbivory currently occurring in Shiretoko National Park (see <http://dc.shiretoko-whc.com/data/research/report/h23/H23ezoshika-syokugai.pdf>, last accessed 5 March 2015). Our scenario assumed complete loss of these species. Although the modelled scenario could be considered extreme, it was not the worst-case scenario that could be envisioned because there is the potential for even more intensive future grazing/browsing pressure by deer. We calculated the taxonomic and functional turnover of the five vascular plant groups by excluding species sensitive to deer herbivory. Based on an analysis of covariance (ANCOVA), we first evaluated differences in  $\beta_{\text{slope}}$  before and after extirpation and then, if no significance was found, intercepts of the distance decay were compared with the changes in  $\beta_{0.5\text{-dist}}$  after extirpation.

We also evaluated how changes in functional turnover after the assumed species extirpation differed from those expected from a random loss of species. In testing this hypothesis, we randomly excluded species from our datasets. The numbers of species randomly excluded from each vascular

plant group were equivalent to those observed in the above list of species prone to grazing damage. We repeated this random extirpation and subsequent calculation of functional  $\beta$ -diversity 1000 times for all vascular plant groups, and then obtained average values for functional similarity for each pair of elevational data. The values for expected functional similarity after random extirpation were plotted against those of the present observed functional similarity, and also against those of functional similarity after the assumed extirpation. All statistical analyses were performed with the software R 2.15.3 (R Core Team, 2013). We used the APE, CLUSTER, PICANTE and VEGAN packages.

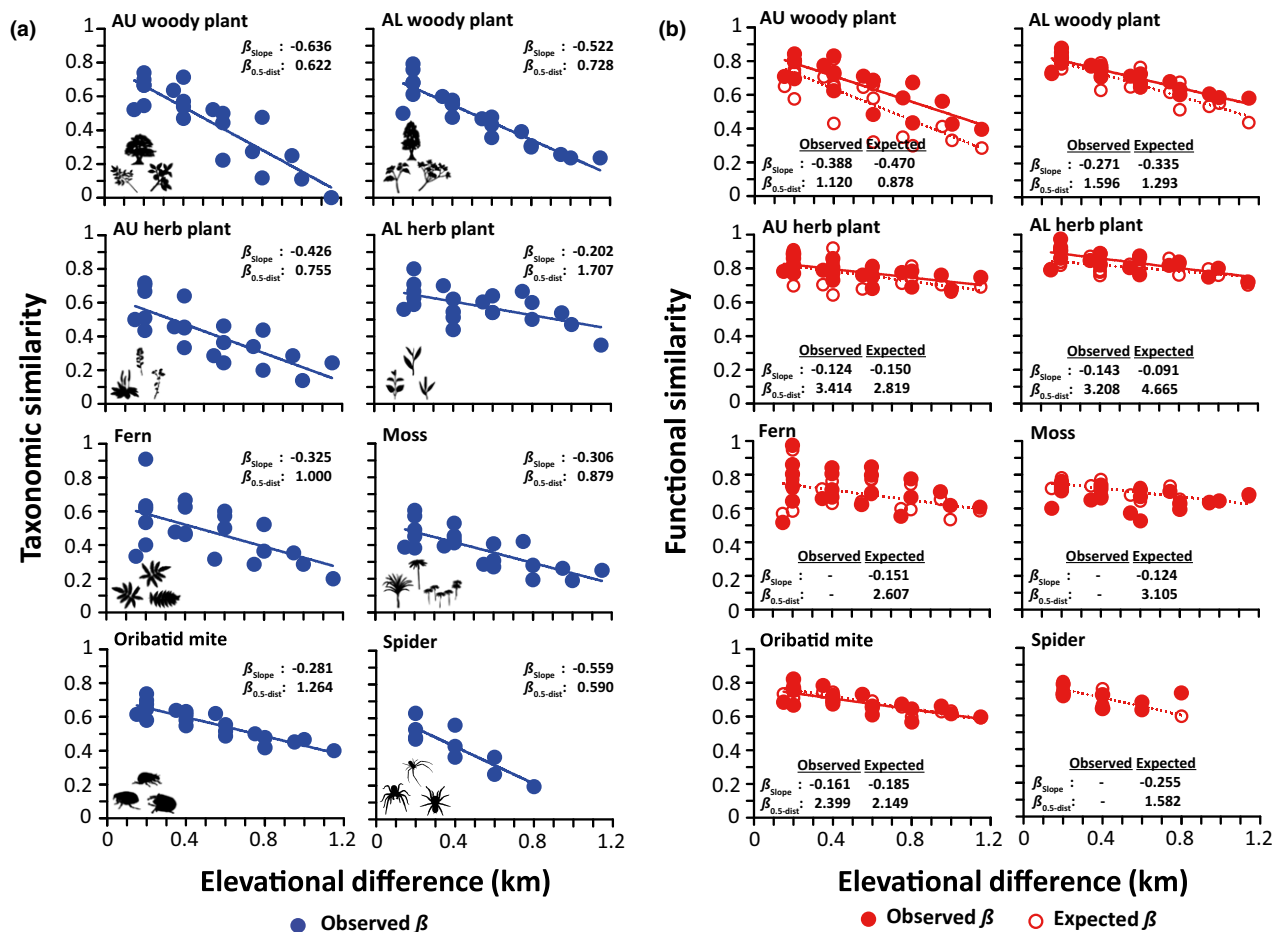
## RESULTS

### Taxonomic turnover

Along the elevational gradient, all eight groups showed significant distance decay of taxonomic similarity (Fig. 3a, Table 1). The magnitude of species turnover ( $\beta_{\text{slope}}$ ) differed among the taxa. The  $\beta_{\text{slope}}$  for all organism groups was negatively correlated with the environmentally structured space fraction and positively with the unexplained fraction (Fig. 4a). For vascular plants, there were significant correlations between the mean seed/spore mass and the fractions of variation partitioning (Fig. 4b). The environmental fraction was mediated by elevation, i.e. for all taxa elevation was selected as the most important environmental variable (see Appendix S2) while spatial isolation between sampling locations was explained primarily by elevation. Thus groups that were more structured by dispersal limitation exhibited a faster species turnover along the elevational gradient (e.g. woody plants; Table 1), while groups with a slower turnover were influenced more by factors other than elevational isolation (e.g. mites; Table 1).

### Functional turnover

For the elevational decay of functional effect similarity, a significant turnover was observed for five of the eight groups; the remaining three groups (ferns, mosses and spiders) showed no functional turnover along the elevational gradient (Fig. 3b, Table 2). For woody plants, the slopes of functional turnover were significantly flatter than those expected by taxonomic turnover alone ( $P < 0.05$  for both groups; Fig. 3b), suggesting that effect traits were more evenly distributed along the elevational gradient (i.e. functional redundancy along the gradient). For ferns, mosses and spiders, even though the expected functional turnover was significant, there was no significant elevational decay of functional effect similarity (Fig. 3b), suggesting that the communities of these groups were more functionally redundant along the gradient than expected by taxonomic turnover. Although functional turnover was attributable to taxonomic turnover for herbaceous plants and oribatid mites (Table 2), their functional  $\beta_{0.5\text{-dist}}$  values, the elevational distance that halves the



**Figure 3** Decay of taxonomic and functional similarity with elevation within forests of Shiretoko National Park, Hokkaido, Japan. The number of species recorded was 25, 52, 56, 44, 22, 86, 74 and 43 for autochorous (AU) woody plants, allochorous (AL) woody plants, autochorous (AU) herbaceous plants, allochorous (AL) herbaceous plants, ferns, mosses, oribatid mites and ground-dwelling spiders, respectively. See Appendix S3 for the species richness distributions along the elevational gradient. For taxonomic and functional similarity calculations, Sørensen's index was used. Regression lines are shown if decay of similarity was found. Tables 1 and 2 show the detailed results of the distance decay. Values for the rate of turnover along an elevational gradient ( $\beta_{\text{slope}}$ ) and the elevational distance that halves the similarity from the initial value ( $\beta_{0.5\text{-dist}}$ ; km) are shown. For functional turnover, observed and expected turnover are both shown. The expected decay of functional similarity was calculated with simulations that evaluated the significance of functional turnover compared with taxonomic turnover.

similarity from the initial value (2399–3414 m; Fig. 3b), were still large given the actual elevation of this mountain range (up to 1661 m a.s.l.). This result suggests that there is a high likelihood of the inclusion of functionally similar communities at most elevations in spite of the functional turnover along the gradient. Initial values of functional similarity for the elevational decay relationship were high overall (0.71–0.92; Table 2). As a result, the observed functional turnover was small enough to include functionally similar species at most elevations.

### Impacts of mammal overgrazing/browsing on forest biodiversity

With the scenario of extirpation of vascular plant species susceptible to mammal grazing/browsing, while there was no

change in taxonomic turnover along the elevational gradient except for herbs dispersed by allochory, a significant increase in functional turnover was observed for three of the five vascular plant groups (Fig. 5). The observed functional similarity was not different from that expected after random extirpation for all plant groups, while the scenario of non-random species loss decreased functional similarity between elevations compared with the expectations of random extirpation (Fig. 6). These results indicated that high-intensity herbivory could accelerate functional turnover along the elevational gradient.

### DISCUSSION

We found that all taxa showed a significant elevational decay of taxonomic similarity (Fig. 3a). Notably, consistent with a



previous study (De Bie *et al.*, 2012), those species groups structured more by dispersal limitation (in our case woody plants) showed a faster turnover of species assemblages along

**Table 1** Distance decay of taxonomic similarity along an elevational gradient within forests of Shiretoko National Park, Hokkaido, Japan.

Group	Distance decay of taxonomic similarity		
	$\beta_{\text{slope}}$	$\beta_{0.5\text{-dist}}$ (km)	$R^2$
Woody plants (autochory)	-0.636	0.622	0.76***
Woody plants (allochory)	-0.522	0.728	0.84***
Herbaceous plants (autochory)	-0.426	0.755	0.59**
Herbaceous plants (allochory)	-0.202	1.707	0.36**
Ferns	-0.325	1.000	0.34**
Mosses	-0.306	0.879	0.60***
Oribatid mites	-0.281	1.264	0.79***
Ground-dwelling spiders	-0.559	0.590	0.76**

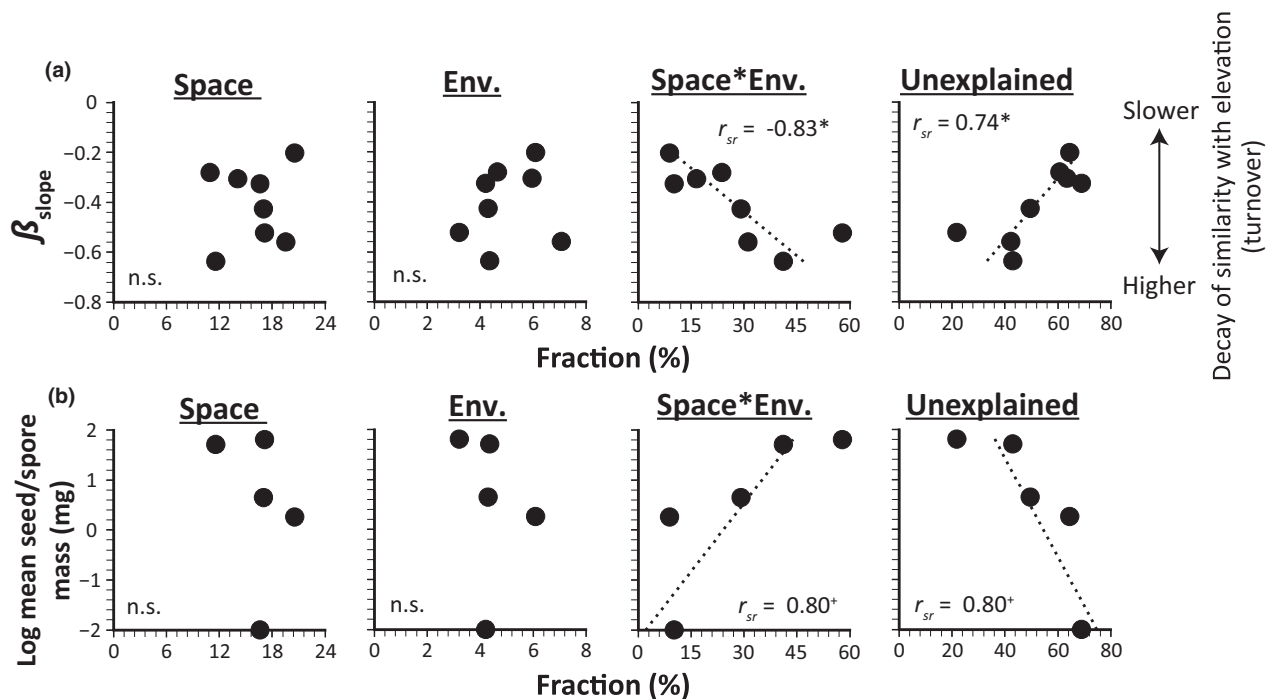
$\beta_{\text{slope}}$ , the slope of the linear regression of the  $\beta$ -diversity index against pairwise absolute elevational differences (Nekola & White, 1999; Qian, 2009).

$\beta_{0.5\text{-dist}}$ , the distance (elevation separation) that halves the similarity from the initial value, considering both the rate of distance decay and the initial similarity (Soininen *et al.*, 2007).

Significance levels: \*\*\* $P < 0.001$ , \*\* $P < 0.01$ .

elevational gradients, while those with slower elevational species turnover were influenced more by factors other than elevational isolation (Fig. 4). This confirmation is important because the taxonomic turnover along the elevational gradient for each group is inherently constrained by its dispersal ability. Possible factors structuring the more dispersive groups include historical influences and/or environmental heterogeneity (Qian & Ricklefs, 2012; Wang *et al.*, 2012), although elucidating these factors is beyond the scope of this study. Given taxon-specific dispersal abilities (Qian, 2009; Sheldon *et al.*, 2011; De Bie *et al.*, 2012), the 'complete' community (composed of multiple taxa) that appears as a result of climate-induced reassembly in a given location is expected to change substantially over time. Our study suggests a strong likelihood of the emergence of no-analogue states in terms of the taxonomic composition of the complete community in response to a changing climate.

When we expanded the same distance decay analysis to that based on functional effect traits for each species (see Table S1 in Appendix S1) i.e. those which we infer determine ecosystem processes (Elmqvist *et al.*, 2003; Hooper *et al.*, 2005; Laliberté *et al.*, 2010), we still found a significant degree of turnover for the majority of groups (Fig. 3b, Table 2). Some key traits are known to determine a species'



**Figure 4** Relationships between the fractions of variation partitioning (variance explained by the environment independently of space, Pure Env.; variance explained by space independently of environment, Pure Space; variance shared by environment and space, Space\*Env.; residuals revealed by sequential subtractions, Unexplained) and the taxonomic turnover ( $\beta_{\text{slope}}$ ) (all eight taxa) (a), and relationships between the mean seed/spore mass and the fractions of the variation partitioning (the five vascular plant groups) (b), of species along an elevational gradient within forests of Shiretoko National Park, Hokkaido, Japan.  $r_{sr}$ , Spearman's rank correlation coefficient. Significance levels: \* $P < 0.05$ , + $P < 0.1$ ; n.s., not significant. Taxonomic turnover was evaluated using the values of  $\beta_{\text{slope}}$ ; using the values of  $\beta_{0.5\text{-dist}}$  generated an almost identical result. When the Pure Space and Space\*Env. fractions were summed to help interpret the outcome of the overall spatial structure (e.g. De Cáceres *et al.*, 2012), the spatial fraction was similarly significantly correlated with slope ( $r_{sr} = -0.76$ ,  $P < 0.05$ ) and with seed/spore mass ( $r_{sr} = 0.80$ ,  $P < 0.05$ ).

**Table 2** Distance decay of functional similarity along an elevational gradient within forests of Shiretoko National Park, Hokkaido, Japan.

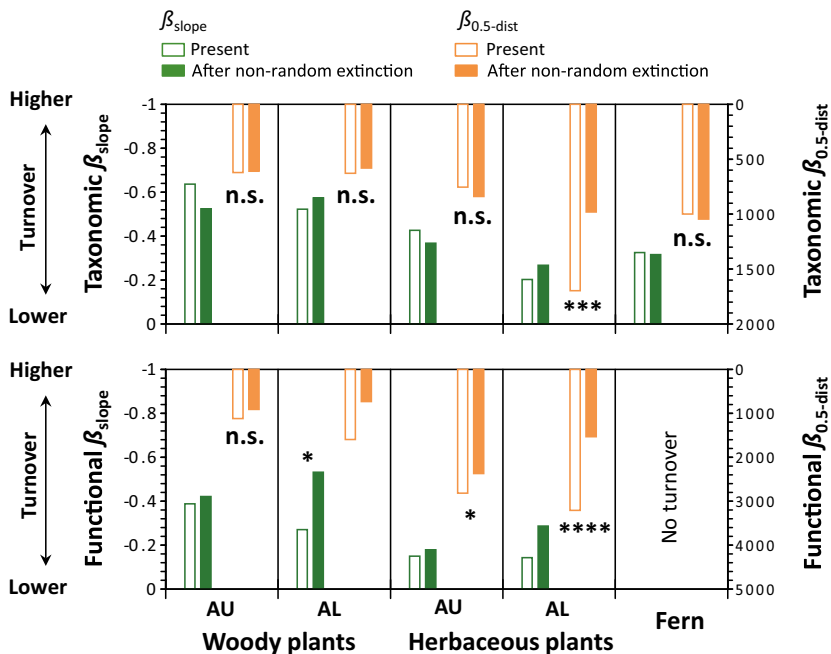
Group	Distance decay of functional similarity		Expected distance decay of functional similarity				
	$\beta_{\text{slope}}$	$\beta_{0.5\text{-dist}}$ (km)	$R^2$	Intercept	Expected $\beta_{\text{slope}}$	Expected $\beta_{0.5\text{-dist}}$ (km)	$R^2$
Woody plants (autochory)	<b>-0.388</b>	<b>1.120</b>	0.70***	0.865	-0.470 [-0.562;-0.395]	0.878 [0.786;0.968]	0.57**
Woody plants (allochory)	<b>-0.271</b>	<b>1.596</b>	0.83***	0.864	-0.335 [-0.402;-0.273]	1.293 [1.190;1.404]	0.79***
Herbaceous plants (autochory)	-0.124	3.414	0.39*	0.847	-0.150 [-0.233;-0.010]	2.819 [1.877;12.080]	0.26*
Herbaceous plants (allochory)	-0.143	3.208	0.48**	0.917	-0.091 [-0.201;-0.065]	4.665 [1.942;25.964]	0.34*
Ferns	-0.124	3.168	0.11 <sup>n.s.</sup>	0.782	-0.151 [-0.270;-0.063]	2.607 [1.497;6.071]	0.20*
Mosses	-0.074	4.749	0.13 <sup>n.s.</sup>	0.707	-0.124 [-0.221;-0.042]	3.105 [1.806;8.647]	0.60**
Oribatid mites	-0.161	2.399	0.54**	0.771	-0.185 [-0.258;-0.130]	2.149 [1.589;3.232]	0.79***
Ground-dwelling spiders	<b>-0.091</b>	<b>4.049</b>	0.15 <sup>n.s.</sup>	0.737	-0.255 [-0.299;-0.160]	1.582 [0.983;3.267]	0.74*

Slopes of the distance decay were estimated using kilometres for clarity (instead of metres). Significance levels of the distance decay were calculated with the Mantel test; n.s.,  $P > 0.05$  (not significant), \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ .

Expected  $\beta_{\text{slope}}$  and  $\beta_{0.5\text{-dist}}$  were estimated from mean values of regressions for distance decay of functional similarity under the null modelling, which randomized species information from a trait distance tree. Values of 95% confidence intervals are shown within parentheses.  $\beta_{\text{slope}}$  and  $\beta_{0.5\text{-dist}}$  values significantly smaller and larger than the expected values are highlighted with bold letters. For groups showing no significant functional turnover (no distance decay of functional similarity),  $\beta_{\text{slope}}$  and  $\beta_{0.5\text{-dist}}$  values are shown in italics.

$\beta_{\text{slope}}$ , the slope of the linear regression of the  $\beta$ -diversity index against pairwise absolute elevational differences (Nekola & White, 1999; Qian, 2009).

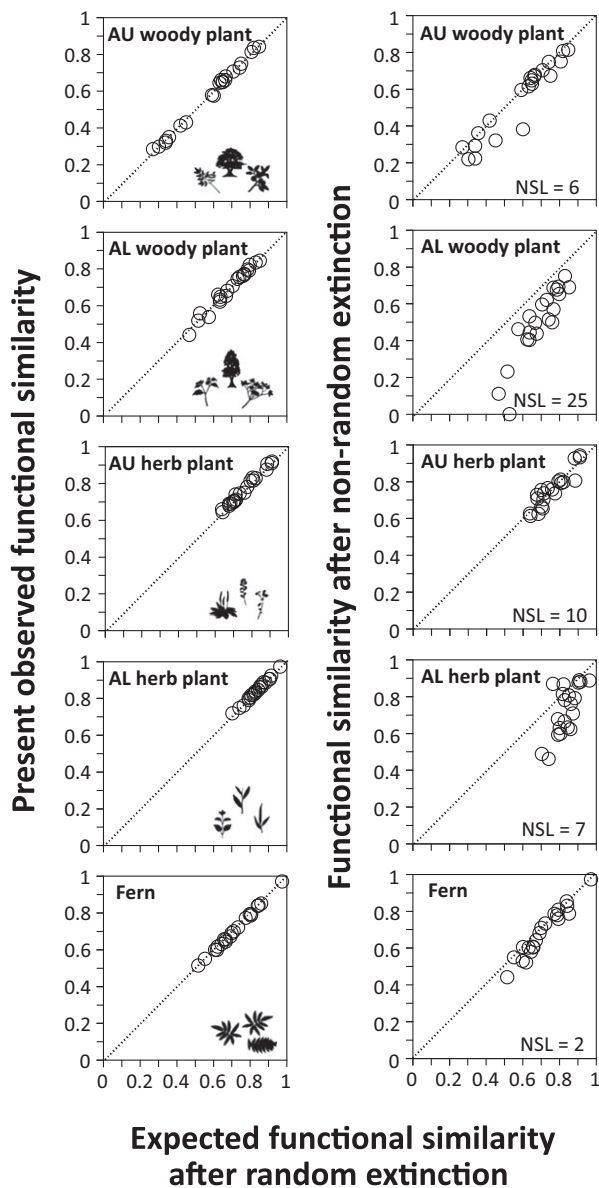
$\beta_{0.5\text{-dist}}$ , the distance (elevation separation) that halves the similarity from the initial value, considering both the rate of distance decay and the initial similarity (Soininen *et al.*, 2007).



**Figure 5** Changes in taxonomic and functional turnover between the present (open bars) and the scenario based on non-random extirpation of vascular plant species susceptible to mammal grazing/browsing (solid bars). Differences in  $\beta_{\text{slope}}$  and  $\beta_{0.5\text{-dist}}$  were tested with analysis of covariance; if there was a significant difference in  $\beta_{\text{slope}}$  between the present and the scenario of non-random species loss, differences in  $\beta_{0.5\text{-dist}}$  were not tested because of the changes in inherent turnover rate. AU, autochory; AL, allochory. Significance levels: \*\*\*\* $P < 0.0001$ ; \*\*\* $P < 0.001$ ; \* $P < 0.05$ ; n.s., not significant.

ability to cope with stressful conditions, such as may be found at high elevation (Hoiss *et al.*, 2012), generating functional turnover. However, we found that the observed functional turnover was small enough to include functionally similar species at most elevations even after taking into account the extent of change in elevation that can be anticipated as a function of a warming climate in the coming decades (Fig. 3b). Based on this functional redundancy along

the elevational gradient, we speculate that our findings may be more general and that ecosystems might be able to retain fundamental functionality despite the emergence of taxonomically novel communities associated with climate change. In the earlier work of Bryant *et al.* (2008), phylogenetic turnover along an elevational gradient was higher than taxonomic turnover alone, resulting from environmental filtering specific to each elevation. In contrast, our results suggest



**Figure 6** Functional similarity between elevations for observed results (present, right column) and under an assumed extirpation scenario (non-random loss of species, left column) compared with the results expected from a non-random species extirpation. AU, autochory; AL, allochory; NSL, number of species listed in the records as susceptible to grazing by deer. The present numbers of species of woody plants dispersing by AU and AL, herbaceous plants dispersing by AU and AL, and ferns are 25, 52, 56, 44 and 22, respectively. The expected functional similarity after random extirpation is the mean value of 1000 simulations that randomly excluded species in a group (the number of species excluded in each run corresponded with NSL).

limiting similarity arising from biotic interactions such as interspecific competition, which is often dominant in the later seral stage of forest stands (e.g. Purschke *et al.*, 2013).

Most studies of biodiversity–ecosystem functioning have focused on the diversity effects of a single taxonomic group (e.g. plant diversity effects on productivity) but many func-

tions are in reality performed by a combination of different groups of organisms (e.g. nitrogen fixation by a symbiotic relationship of bacteria with plants; Velázquez *et al.*, 2010; St John *et al.*, 2012). For example, climate-induced vegetation changes may lead to community-wide shifts in foliar traits. Suppose the vegetation shift leads to increases in foliar tannin, phenolic and lignin content; as a result, important soil processes such as decomposition would be expected to occur more slowly (Mouillot *et al.*, 2013). The accumulation of additional organic matter on the forest floor as a consequence of slower decomposition may benefit a group of oribatid species that feed predominantly on litter, as suggested by Gan *et al.* (2013). As a result, this functional group of oribatids contributes to fragmentation of the accumulated litter, potentially stabilizing the rate of decomposition. Elucidating the mechanisms that control ecosystem functioning through specific combinations of species across multiple taxa is a future topic in the study of biodiversity–ecosystem functioning. It is somewhat surprising that ours is apparently the first such study. Our results for functional redundancy imply that, in addition to ecological functions supported by a single group, the functionality shown by a complete community may also be minimally affected by species reassembly (corresponding to scenario b in Fig. 1).

Considering the potential difficulties in elevational studies of inferring biological phenomena linked with climate change (Körner, 2007) our study has, without doubt, limitations in illustrating scenarios under different climatic conditions. In particular, because our data provide only a snap-shot of community similarity along an elevational gradient, the actual reassembly processes are more likely to be structured by complex factors other than elevational shifts of species. For instance, tree diversity has a strong influence on the distribution and diversity of other forest taxa (e.g. Vanbergen *et al.*, 2007), such that range shifts of many species in other taxa may be largely limited by trees. Moreover, responses to environmental changes are expected to be different among different groups. Such temporal perspectives are lacking from our study. Furthermore, the knowledge gained from our study may not always be applicable to other forest biomes, such as tropical forests, which have high endemism (Jansson, 2003) and narrow elevational ranges of species (Sheldon *et al.*, 2011). However, given the usefulness of the distance decay framework for inferring taxon-specific range shifts associated with climate change (Qian & Ricklefs, 2007; Baselga, 2010), we speculate that ecosystems have, to some degree, redundancy that may buffer the effects of climate-induced species reassembly to maintain their fundamental functionality (see also Gallagher *et al.*, 2013).

We found a significant increase in functional turnover along the elevational gradient after the simulated extirpation of vascular plant species prone to overgrazing/browsing (Fig. 5). As most of these groups showed no change in taxonomic turnover, this decreased functional redundancy along the gradient is mainly caused by a non-random loss of biodiversity. Notably, while random loss of species did not change functional turnover for all taxa, non-random loss of species could sub-

stantially accelerate functional turnover across different elevations (Fig. 6). Because deer feed on vegetation non-randomly, reflecting the palatability of plant species (Boulanger *et al.*, 2009; Mason *et al.*, 2010; White, 2012), plant species sensitive to this herbivore damage are functionally aggregated. Boulanger *et al.* (2009) report that the order of sensitivity of woody species to deer browsing reflects wood density and height, which our study also focused on as effect traits. More recently, Mouillot *et al.* (2013) implied that community-wide trait shifts induced by mammalian herbivory may change critical ecological processes such as decomposition and photosynthesis. With a strong vegetational control on associated taxa such as oribatids (Decaëns, 2010; Mori *et al.*, 2013c, 2015), loss of particular traits from plant communities may not only affect ecosystem functions performed by plants but also impact on functions supported by other groups (e.g. biogeochemical processes). Taken together, we conclude that a non-random loss of biodiversity has the potential to seriously erode the functional redundancy of communities, which is important for responding to a changing climate.

Clearly, climate change has historically reshuffled biological organization, generating novel communities (Williams & Jackson, 2007). To our knowledge, this study is the first that sheds light on such reassembly patterns from the functional characteristics of communities across multiple taxa. Specifically, although our data do not have an actual spatio-temporal perspective, our approach focusing on multiple taxonomic groups is important because such an approach is often lacking in field-based studies. In other words, it is somewhat surprising that no one has conducted such a study; biodiversity implies a broad array of organisms, yet studies have traditionally focused on a single or a few taxa. We believe that a true understanding of the causes and consequences associated with changes in biodiversity will come from studies incorporating diverse taxonomic groups.

Our results suggest that future communities may be more novel or idiosyncratic than currently anticipated, not simply because of the unprecedented rate of climate change but also because of the synergetic influence of other environmental changes. In the case of our study area, the vegetation damage attributable to human activities is a potential threat not only to biodiversity itself but also to the ecological resilience of the ecosystem that buffers it against the impacts of climate change. Although our study did not quantify the rate of any ecosystem process, the knowledge gained from our study focusing on the potential non-random loss of species as a result of human activity is widely applicable. Intensification of mammalian herbivory has been reported across the globe, often accompanied with slow ecosystem recovery, deviation from historical conditions and possible irreversibility of ecosystem characteristics in severely damaged habitats (Mason *et al.*, 2010; St John *et al.*, 2012; White, 2012). Policies are generally designed to protect and restore vegetation, but our findings suggest that functional consequences could be reinforced by the combination of herbivory and climate change issues. The interactions between an environmental stressor

and climate change suggest that ecological processes may currently be more seriously affected than is generally believed based on existing climate change scenarios.

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## SUPPORTING INFORMATION

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

**Appendix S1** Details of the functional effect traits.

**Appendix S2** Analysis of variation partitioning methodology.

**Appendix S3** Changes in species richness of the eight taxonomic groups along the elevational gradient.

## BIOSKETCH

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