

Deer herbivory as an important driver of divergence of ground vegetation communities in temperate forests

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Ungulate herbivory can fundamentally affect terrestrial vegetation at the landscape and regional levels, but its impact has never been analyzed from meta-community perspectives. Here, we study a meta-community of forest ground-layer plants in a warm-temperate region along a clear gradient of deer density interplaying with gradients of other environmental factors (forest type, sky openness and topographic wetness). Canonical corresponding analysis showed that deer density was the most important determinant of species distributions. These distributions conformed to a two-directional filtering model, which selects for competitive species at low deer density but favours herbivory-tolerant plants at high deer density, with these two directions counterbalancing each other when herbivory is intermediary. This resulted in a bi-directionally nested meta-community, in which local species richness was highest at intermediate levels of deer density, conforming also to the intermediate disturbance hypothesis. Our results suggest that herbivory can be the most important driver of meta-community structure in mesic systems; this contrasts with the results of earlier studies conducted in harsh environments, where species sorting by abiotic factors at early life stages reduced the role of biotic interactions, including herbivory.

Ungulate herbivory exerts a profound influence on vegetation, both directly and indirectly (Olf and Ritchie 1998, Augustine and McNaughton 1998, Rooney and Waller 2003, Tanentzap et al. 2012), and can fundamentally change terrestrial ecosystems (Rooney and Waller 2003, Wardle 2004, Côté et al. 2004, Bråthen et al. 2007). Species composition of plant communities depends on the intensity of herbivory, which filters species according to their herbivory-tolerance and competitiveness (Augustine and McNaughton 1998). Some studies found the relationship between herbivory intensity and species richness to be hump-shaped (Milchunas and Lauenroth 1993, McIntyre et al. 2003, Frank 2005, Mainer and Hobbs 2006, Sebastià et al. 2008), as predicted by the intermediate disturbance hypothesis (IDH; Grime 1973, Connell 1978). Because ungulate populations span through regional or higher spatial scales (Austrheim and Eriksson 2001, Adler et al. 2001, Shea et al. 2004), herbivory can also have strong effects on biodiversity patterns at these scales and is manifested in meta-community structure. Yet, ungulate herbivory has been rarely studied as a driver of meta-community structure (but see de Bello et al. 2007, Komac et al. 2011), and its importance remains underestimated in comparison with other environmental factors.

Ungulate herbivory can act as a bi-directional filter that selects tolerant species under heavy herbivory pressure but favours competitive species where herbivory is light and thus the role of plant–plant competition is important (Augustine and McNaughton 1998). According to the IDH, these two directions can counterbalance each other when herbivory is intermediate to allow for mixed compositions of species with different life histories, thus boosting local species richness (Milchunas et al. 1988, Huston 1994, Cingolani et al. 2005). However, when considered from the meta-community perspective, this same mechanism suggests additional insights about species distributions along the herbivory gradient. In particular, other environmental factors being equal, two-sided filtering can produce a bi-directionally nested meta-community structure (Fig. 1). In this meta-community, the local species compositions at high and low herbivory intensities are dissimilar, but at the same time, they are the subsets of richer communities found when herbivory is intermediary.

In nature, however, strong abiotic factors can also sort species in early life stages before biotic filtering occurs (Austrheim and Eriksson 2001). Many previous studies conducted in relatively unproductive environments found that physical factors, rather than herbivory, were the primary

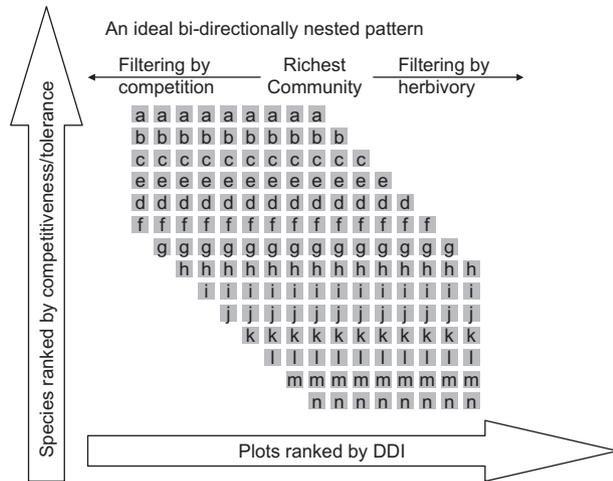


Figure 1. A hypothetical meta-community with a bi-directionally nested structure. Species richness decreases toward both ends of the herbivory intensity gradient and is maximized at intermediate herbivory levels, where two directions of the filtering species pool (plant competition and herbivory) counterbalance each other.

drivers of community structure (Cingolani et al. 2003, Barbaro et al. 2004, Sebastià et al. 2008). Conversely, in relatively more productive systems, the dependence of species richness on herbivory was hump-shaped (Milchunas et al. 1988, Huston 1994, Cingolani et al. 2005). Overall, most of the large-scale studies were conducted in low productive environments such as dry rangelands and alpine grasslands where abiotic factors seem to have overridden biotic filters. Comparable examples from productive environments such as warm-temperate forests are absent (but see Väre et al. 1995).

A meta-community of forest ground-layer plants in Boso Peninsula, Japan, is an ideal system to examine the potential effects of herbivory at the regional scale. Deer herbivory is an important factor here as elsewhere throughout Japan. Indeed, the wild population of Sika deer *Cervus nippon centralis* in this region is dramatically increasing because of stricter hunting regulations after World War II, and caused significant change in natural ground-layer vegetation (Kabaya 1988, Chiba Prefecture 2004). Our previous experimental study suggested that species distributions across this region depends more on species sorting than on dispersal limitation ('SS-type' sensu Cottenie 2005, Suzuki unpubl.). Forests in Boso Peninsula form a mosaic landscape representing two major forest types: conifer plantations and secondary broad-leaved woods. In both of these forest types, species richness of ground-layer plants responds to herbivory in a hump-shaped manner, as predicted by the IDH, whilst the dependence on the light and water availability was found weak (Suzuki et al. 2008). Here, we use these data to reveal how herbivory can shape the meta-community structure of forest ground-layer vegetation, interacting with other environmental factors (forest type, light and water availability). In particular, we tested two hypotheses:

1. Herbivory is the most important driver of species distributions, which sort local floristic composition from the regional species pool.

2. The meta-community has a bi-directionally nested structure as illustrated in Fig. 1: local communities at both ends of the herbivory intensity gradient are subsets of those at intermediate herbivory, where local species richness reaches its maximum as predicted by the IDH.

Hypothesis 1 was tested using canonical correspondence analysis (CCA) for estimating the relative contribution of multiple species filters. To test hypothesis 2, we analyzed its nestedness based on species spatial covariance.

Material and methods

Study site

Boso Peninsula is located in Chiba prefecture, central Japan (35°N, 140°E) and is characterized by a warm-temperate climate. Here, forests cover 323 km² from 9 to 339 m a.s.l., with the mean elevation being 208 m. Forests currently represent a mosaic of small patches of <0.1 km², composed of either conifer plantations (*Cryptomeria japonica* and *Chamaecyparis obtusa*) or secondary broad-leaved woodlands (dominated by *Castanopsis sieboldii* and *Quercus* spp.). In the absence of deer, evergreen shrubs (e.g. *Aucuba japonica*, *Eurya japonica*), forbs (e.g. *Rubus buergeri*), grasses, and ferns dominate ground vegetation. Owing to deer herbivory, these ground-layer plants are decreasing at different rates in order of preference to deer (Kabaya 2001, Suzuki et al. 2008). The deer population native to this region occupied 40 km² in 1974, but their range had expanded to 440 km² by 2001 (Chiba Prefecture 2004). Even at the core area of deer population, where almost all forest floor vegetation disappeared under herbivory pressure, common species of the peninsula rapidly re-established in deer-exclosure experiments (Suzuki unpubl.). This fact suggests that species composition of local communities is primarily determined by species sorting rather than dispersal limitation (Cottenie 2005).

Data collection

In late September 2005, we sampled ground vegetation in 30 coniferous plantations and 34 broad-leaved woods. Sites were scattered across the entire range of deer habitat to weaken spatial autocorrelation and to represent a wide range of deer densities. We set five quadrats of 2 × 2 m, each 2–3 m apart, within an area of visually homogeneous ground-layer vegetation and recorded the projective cover of each plant species within the quadrats. The projective cover was used as a measure of abundance of ground-layer species. Hemispherical photographs were taken at the centre of each quadrat at a height of 2 m to calculate sky openness (%).

Deer density index (DDI) represents the mean density of recent faecal pellets monitored every second year (pellets m⁻² year⁻¹, data published by Chiba Prefecture 1997–2005). Direct observations (block-count method) proved that this index correlates tightly with the local density of deer population (Maruyama and Nakama 1983). Monitoring was based on counting faecal pellets along 1 km transects. There were 92 transects; the nearest ones being 1.6 km apart and covering most of the range of deer population.

Counting was completed during December–January, when the decomposition rate of faeces is almost negligible. DDI values for each vegetation-sampling site were calculated using inverse distance weighted interpolation (Shepard 1968).

We calculated a topographic wetness index (TWI) for each vegetation-sampling site as an indicator of water availability (Moore et al. 1993). TWI links topography with hydrological conditions and hence can characterize biological processes such as vegetation productivity (Sørensen et al. 2005). We produced 25-m digital elevation data (DEMs) of Boso Peninsula by inverse distance weighted interpolation of 50-m mesh elevation data provided by the Geographical Survey Institute. Then we estimated the TWI for each 25-m cell as $\ln(A \tan B^{-1})$, where A was the upslope area around the target cell per unit contour length (25 m) and $\tan B$ was the slope of the target cell, respectively. The TWI of each vegetation-sampling site was estimated as the mean value within a 25-m radius of the target point.

We examined whether the two forest types (coniferous versus broad-leaved) were uniform in terms of sky openness, DDI, and TWI. We calculated the mean values of these variables for each forest type and compared these values between the forests by using a nonparametric Wilcoxon rank-sum test.

Determination of major species

Based on the abundance distributions in the species-by-site matrix, we calculated proportions (relative abundance) of each species and used them to determine major species on the basis of Simpson's dominance index (Kikvidze and Ohsawa 2002). First, we pooled the data of all sites together and calculated Simpson's dominance, and then rounded its reciprocal value to integers:

$$\text{number of co-dominants} = \text{round} (1/\sum p_i^2)$$

where p_i is the proportion of the i th species. We then ranked species in the order of descending abundance and selected the number of the most abundant species equal to the rounded value generated by the above equation. Hereafter, we refer to these species as major species.

Canonical correspondence analysis

Variability of species composition along environmental gradients was analyzed with Canonical correspondence analysis (CCA) by using the package *vegan* (Oksanen et al. 2011) on R-2.11.0 (R Development Core Team). We used percent ground cover as the score of abundance for each species and included all species with a >1% cover per plot. For the 'environmental' matrix, we used the following data: DDI, forest type (coniferous plantations or broad-leaved woods), sky openness, and TWI. The elevation of vegetation-sampling sites was not considered as an environmental variable because it was significantly correlated with TWI (Pearson's product-moment correlation: $r^2 = -0.27$, $p = 0.03$) and had less explanatory power than TWI.

Meta-community matrix analysis

We constructed a presence–absence matrix of dominant species and examined species co-occurrence, using variance-covariance analysis. Net covariance of a binary matrix is calculated as follows:

$$\text{net covariance} = (V_{\text{obs}} - V_{\text{exp}})/2,$$

where V_{obs} refers to the observed variance of species richness in plots, and V_{exp} is the value expected from random distribution of species across plots; and V_{exp} is calculated as the sum of variance of each species' frequencies (Palmer 1987, Kikvidze et al. 2005). Positive values of net covariance indicate a nested matrix, where species co-occur more often than expected from the random null-model; negative covariance points to over-dispersion of species in the matrix. Then, we reordered the covariance matrix along distributional trends by ranking species according to their mean DDI values, which were calculated for each species from the plots where this species occurred. From this covariance matrix, we tried to discern sub-matrices with predominantly positive covariance species pairs corresponding to the two hypothesized groups of nested communities.

Results

In all, 372 species were recorded. Among them, 63 species were very rare, with less than 1% cover per plot. We excluded these very rare species and performed the analyses with the remaining pool of 309 species. Abundance distributions of these species in the pool were considerably uneven, and the use of Simpson's dominance index produced 29 major species (Supplementary material Appendix A Table A1). Across sites, the cover of each of these major

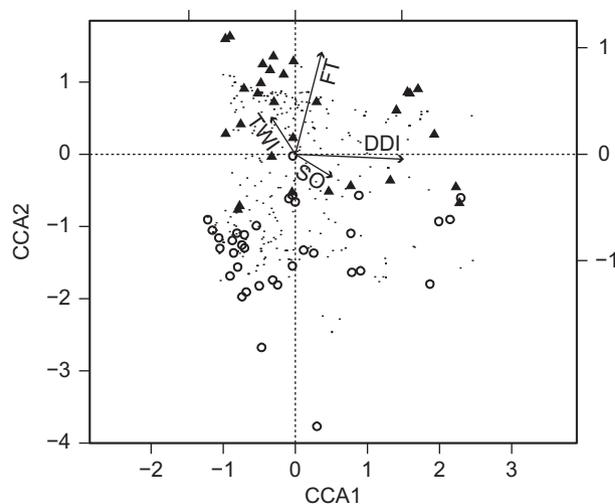


Figure 2. Biplot of CCA ordination of plots and species. Triangles and circles represent sites of coniferous plantations and broad-leaved woods, respectively. Dots show the species. Arrows represent contribution of environmental axes: Deer density index (DDI), Forest type (FT), Sky openness (SO), and Topographic wetness index (TWI).

Table 1. Correlation coefficients between environmental variables and CCA axes, with the proportion explained by CCA axes. DDI: Deer density index; Forest type: planted conifers or natural broadleaved; TWI: Topographical wetness index.

| | DDI | Forest type | Sky openness | CCA1 | CCA2 | CCA3 | CCA4 |
|------------------------|--------|-------------|--------------|--------|--------|-------|--------|
| DDI | | | | 0.996 | -0.044 | 0.017 | 0.066 |
| Forest type | 0.041 | | | 0.244 | 0.940 | 0.204 | -0.098 |
| Sky openness | 0.027 | 0.042 | | 0.330 | -0.203 | 0.846 | -0.379 |
| TWI | -0.112 | 0.284 | -0.262 | -0.216 | 0.333 | 0.102 | 0.913 |
| Eigenvalue | | | | 0.684 | 0.480 | 0.337 | 0.278 |
| Proportion explained | | | | 0.385 | 0.270 | 0.189 | 0.156 |
| Cumulative explanation | | | | 0.385 | 0.655 | 0.844 | 1.000 |

species was >15%, and together they accounted for over 72% of the total cover (i.e. cover values of all species across all plots summed). Net covariance of this meta-community equalled 2.58, suggesting considerably positive co-occurrence of species in the matrix.

Canonical correspondence analysis detected strong relationships of species composition with deer density and forest type in local communities. The DDI clearly associated with the CCA1 axis (Fig. 2, Table 1), suggesting its primary importance. Correlation between the forest type and CCA2 axis was also tight. We found somewhat lower but still considerable correlations between sky openness and the CCA3 axis and between the TWI and CCA4 axis. Significant correlations were found between the TWI and forest type and between the TWI and sky openness (Table 1; Wilcoxon rank-sum test, $p < 0.05$), but these correlations were unlikely to affect the results of CCA (Palmer 1993). In addition, we used CCA to analyze data from two forests types separately and see whether the results suggesting the highest relative importance of DDI were robust. Both in coniferous plantations and broad-leaved woods, we found a high correlation between the DDI and CCA1 axis, whilst sky openness and TWI were correlated with CCA2 and 3 axes, respectively (data not shown).

While CCA1 described species distributions along herbivory gradient, we interpreted CCA2 as showing species' preference for a forest type. These distributions were graphically analyzed as relationships between species' ranges along the DDI gradient and their preference for forest type (Fig. 3). Species strongly preferred by deer (and hence sensitive to herbivory; Kabaya 2001), such as *Aucuba japonica* and *Arachniodes standishii*, were restricted within sites of low DDI (Fig. 3). In contrast, *Arachniodes aristata* and *Maesa japonica*, known as species unpalatable to deer (Kabaya 2001; Appendix 1 of Suzuki et al. 2008), were common at high DDI. Other species such as *Eurya japonica*, *Lindera umbellate* and *Carex lenta* were mostly found at sites with intermediate DDI levels. Many other species also peaked at intermediate DDI, where species richness was maximized (50–55 species found at DDI = 0.5–1.0 pellets $m^{-2} year^{-1}$). Some of these species were ubiquitous, co-existing with other dominant species, although their contributions to plant cover remained low. Remarkably, certain herbivory-sensitive plants were split between the coniferous (e.g. *A. standishii*, *Iris japonica*) and broad-leaved sites (e.g. *Ophiopogon japonicus*, *Castanopsis sieboldii*). In contrast, species tolerating high DDI levels did not show notable preferences for forest type (e.g. *A. aristata*,

M. japonica), although these species tended to be relatively more abundant in conifer plantations.

Covariance analysis showed a pattern (Fig. 4) that conforms to the predicted bi-directionally nested meta-community structure (Fig. 1). Indeed, species found at high- and low-DDI areas tended to co-occur as indicated by positive covariance (along the diagonal of the level-plot, Fig. 4). Covariance values between these two groups were mostly negative (close to right upper or left lower corners, Fig. 4), indicating significantly low overlap between them. Species with distribution centred at intermediate DDI levels, such as *R. buergeri* and *Oplismenus undulatifolius* (Fig. 3), showed positive co-occurrence with many species (Fig. 4). Yet, there were species specialized in different

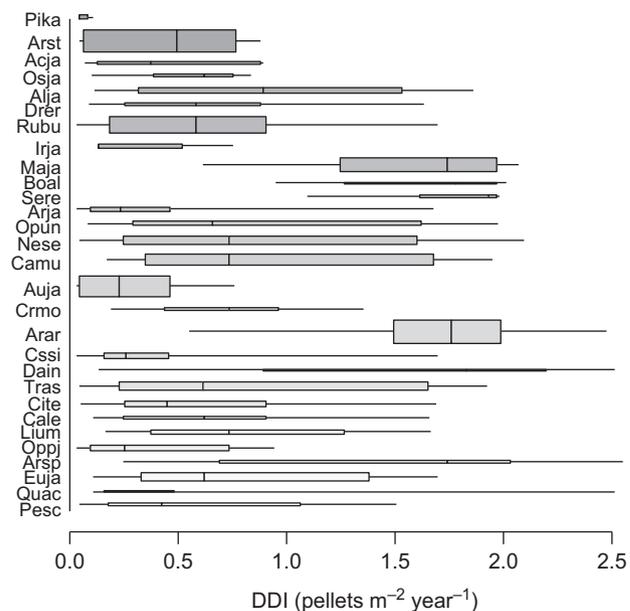


Figure 3. The distribution of 29 major species along the deer density gradient (DDI) and across forest types. Horizontal bars and boxes with vertical lines indicate the 10, 25, 50, 75 and 90th percentiles of the DDI values of the plots where a given species was recorded. The box height shows the proportional cover of the given species. Species are ranked by their preference for forest type (as measured by v -values of CCA2 axis) and are expressed by the colour gradation of the boxes: dark-coloured boxes show the species characteristic to coniferous plantations, bright-coloured boxes show the species more common in broadleaved forests, and intermediate colour corresponds to species common in both forest types (see Supplementary material Appendix A1 Table A1 for species name abbreviations).

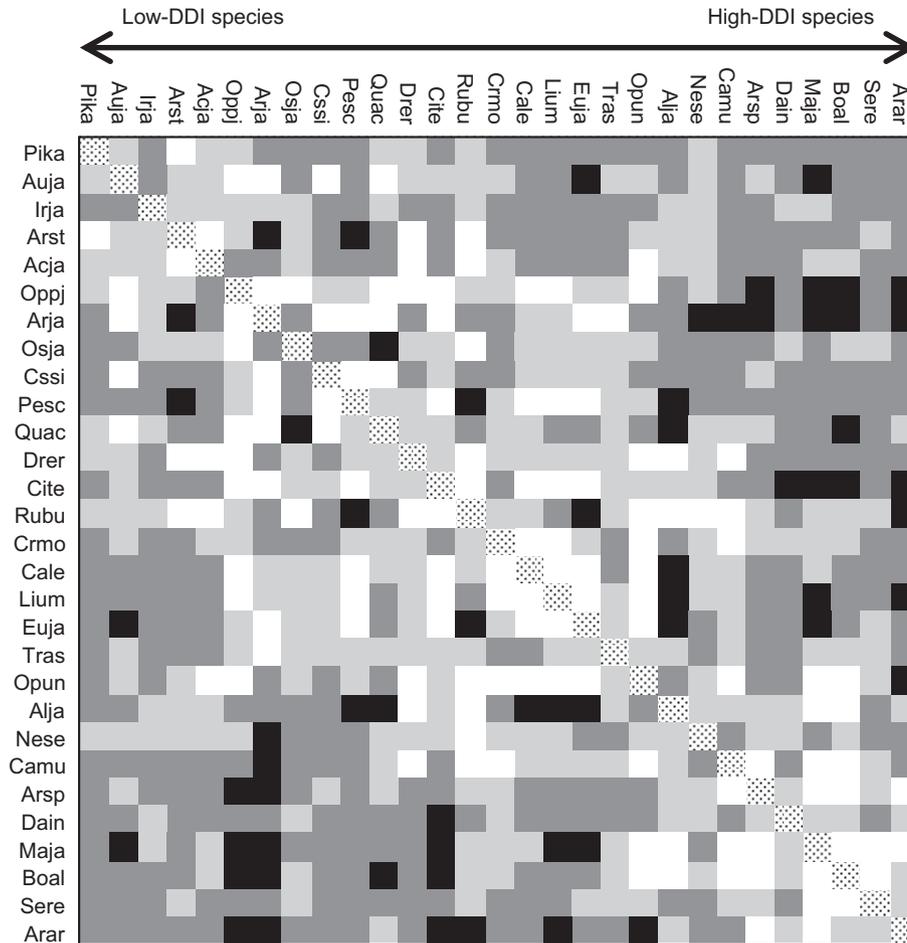


Figure 4. A level-plot of the covariance matrix for 29 species pairs. Species are ranked by mean DDI values calculated for the plots where species were recorded. Levels of covariance values (cov) are expressed with black-gray-white gradation: black for negative co-occurrence ($cov < -1 \text{ SD} = -0.0336$), dark-gray for marginally negative ($-1 \text{ SD} \leq cov < 0$), light-gray for marginally positive ($0 \leq cov < +1 \text{ SD}$), and white for positive co-occurrence ($+1 \text{ SD} \leq cov$).

extremes of the DDI gradient and thus co-occurred negatively. In addition, other environmental factors such as forest type also contributed to habitat segregation (Fig. 3), which resulted in negative co-occurrence between species occurring at sites with similar levels of DDI. Therefore, local communities at the ends of the DDI gradient were not nested in those at intermediate DDI as ideally as shown in Fig. 1.

Discussion

This study showed that herbivory intensity can be the most important determinant of floristic composition patterns in certain regions, contrary to the trends observed in previous studies in less productive environments (Cingolani et al. 2003, Barbaro et al. 2004, Sebastià et al. 2008, Sasaki et al. 2009, Aarrestad et al. 2011). Deer herbivory explained the largest proportion of variation in floristic composition across local assemblages better than other environmental factors (hypothesis 1 in the Introduction). This suggests weaker effects of abiotic environmental filters working at early life stages (seeds and seedlings) relative to herbivory-induced biotic filtering at later life stages. The warm, mesic climate

of the temperate forests characterizing Boso Peninsula seem to increase the relative importance of biotic interactions, including herbivory and plant-plant competition, in determining meta-community structure (Kikvidze et al. 2011). It is noteworthy that deer density in studied forests remains high even though overgrazing has reduced the biomass of forest ground vegetation (Miyashita et al. 2008). This is because deer have access to food resources outside of forests, and the input of such allochthonous resources makes the relationship of deer and ground-layer vegetation donor-controlled (Miyashita et al. 2008). This might also contribute to the strong effects of herbivory on ground vegetation structure.

One mechanism of species turnover along the deer density gradient can be the two-sided filtering of major species: competitive species dominant at the low end of the deer density gradient disappear at the high end where herbivory-tolerant species become dominant (Milchunas et al. 1988, Huston 1994, Cingolani et al. 2005). This conforms to the IDH, which predicts a peak of richness at intermediate herbivory intensity, where competitive and herbivory-tolerant species coexist (Connell 1978, Huston 1979). However, the non-equilibrium coexistence of two species groups with different strategies was not the only

reason of the observed hump-shaped pattern. Some species such as *L. umbellata*, *C. lenta* and *E. japonica* showed a preference for the intermediate levels of DDI boosting the 'humpedness'. Thus, the meta-community approach helped reveal specific mechanisms that generate the hump-shaped pattern, which are invisible in analyses based on species richness only.

Overall, the bi-directionally nested meta-community structure observed in our study strongly supports the idea of two-sided filtering by herbivory and hence the IDH: many species found at high and low DDI levels also occurred at intermediate DDI levels, supporting hypothesis 2. However, local communities at high and low DDI levels were not complete subsets of those at intermediate DDI. This can be partly explained by the existence of species thriving at intermediate deer density as well as by the sporadic emergence of relatively minor species (chance-dependent immigration, Hanski 1982). In addition, species could replace each other by responding to changes in forest type, sky openness and TWI. Each of these environmental factors had smaller contributions than deer density, but their cumulative effect was higher than that of deer density. Such multiple environmental filtering of a regional species pool might have increased beta and gamma richness, boosting the anti-nestedness of the meta-community structure (Leibold and Mikkelsen 2002, Almeida-Neto et al. 2007).

Among the environmental filters, forest type was the second important driver of species distributions. This is not surprising because the mosaic structure of upper-story tree canopy can be a primary determinant of heterogeneous ground-layer vegetation (Roberts 2004). Conifer plantations and broad-leaved woods seem to have a common species pool of ground-layer plants (Hirata et al. 2006). The dissimilarity in ground-layer species compositions between forest types might have arisen from differences in soil types, nutritional status (Nagaike 2000, Kato and Yachi 2003), or thickness of litter layers (Yanagi et al. 2008). Interestingly, the range of plants preferring coniferous forest was restricted to low-DDI sites, unlike the plants preferring broad-leaved forests. The rich, stable soil under thick litter cover in conifer forests (Yanagi et al. 2008) might have allowed water-demanding, competitive species that are intolerant to herbivory to establish in conifer plantations. Consequently, ground-layer plants in conifer plantations appeared to have responded more sensitively to herbivory pressure than those in broad-leaved forests.

The variables determining productivity (light and water availability) were less important to species distributions than biotic factors such as herbivory and forest type. This conforms well to our previous study, which shows that species richness and foliar cover of local communities depend more on herbivory and forest type rather than light and water availability (Suzuki et al. 2008). Such weak effects of productivity-related variables might be attributed to the uniform forest environment of our study region. In other words, the relative importance of herbivory to meta-community structure was brought about by the highly variable herbivory intensity in a relatively homogeneous and benign environment (Kikvidze et al. 2011). As the rapid increase in and range expansion of ungulates

becomes a worldwide trend (Côté et al. 2004), it seems likely that herbivory will generally be found the most important driver of meta-community structure in productive forest environments.

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Supplementary material (available online as Appendix O20431 at <www.oikosoffice.lu.se/appendix>). Appendix A1.