

Management and micro-scale landform determine the ground flora of secondary woodlands and their verges in the Tama Hills of Tokyo, Japan

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Abstract

We investigated the influence of management and micro-scale landform on the species composition and richness of ground flora in secondary woodlands and their verges next to paddy fields in the Tama Hills, Tokyo, Japan. Sites representing various micro-scale landforms and different management regimes were sampled. The results of Detrended Correspondence Analysis and Indicator Species Analysis showed that there was no significant difference between management regimes on species composition in head hollow sites. However, species composition was unique in other landform types having the same management regimes. Micro-scale landform units had less effect on species composition than management regime on crest slopes and side slopes of secondary woodlands. A large variation in species composition of verges, all on the lowermost side slopes, was found within sites, but the composition was different when compared with other sites. We recognized five habitat types associated with species composition that resulted from the combined effects of landform and management regimes. Among habitat types, the verges and the well-managed woodlands had high species richness. Management practices within woodlands have enhanced the species richness on crest slopes and side slopes. High beta diversity of ground flora could be due to the variation in micro-scale landform along soil moisture regimes. Intensive management involving clear-cutting on the lower side slopes (an ecotone of mesic and wet environments) accompanied by paddy cultivation on valley bottoms enhanced the diversity of herbaceous vegetation in the verges.

Key words

Coppice woodland, Ground flora, Micro-scale landform, Species richness, Vegetation management, Verge to paddy field

Introduction

Secondary woodlands in Japan have originated mostly from coppice woodlands, commonly known in Japan as ‘satoyama’ (Takeuchi 2001). These coppice woodlands have been one of the major elements of Japan’s traditional rural landscapes (Fukamachi et al. 2001). For many centuries, they were used to produce firewood and charcoal for home use and compost from fallen leaves and twigs. The compost was generally used as organic fertilizer in traditional agriculture. Since the 1960s, however, these traditional practices have diminished drastically owing to the introduction of chemical fertilizers and fossil

fuels. As a consequence, the coppice woodlands have been either abandoned or converted into urban land uses like dormitory suburbs that require huge land modifications (Tamura and Takeuchi 1980). The neglect of coppice management and the conversion of woodlands into urban land uses have caused the loss or destruction of habitat, resulting in a drastic decrease in plant species diversity. The issue of biodiversity reduction in abandoned coppice woodlands has been raised not only in Japan but also in Europe and other countries (Brown and Yokohari, 2003).

The mechanisms of how plant diversity develops in managed forests are well summarized by Roberts and Gilliam (1995). Washitani (2001) summarized the mechanisms relevant to coppice woodlands in Japan, including periodic anthropogenic disturbances—succession interventions accompanied by coppice management and exploitation of biomass resources. These issues have important roles in suppressing physically competitive exclusion by predominant species, improving light availability in the understory, and keeping soil nutrition low by removing litter; thus, both competitive and less-competitive species (e.g. light-demanding or shade-tolerant species) can coexist within the same habitat.

Light condition is considered an important factor affecting understory flora. Several previous researchers have emphasized the importance of light in ensuring understory diversity in coppice woodlands (Ash and Barkham 1976; Barkham 1992; Gondard et al. 2001; Mason and Macdonald 2002). In addition, results of work done in the inland Kanto District by Iida and Nakashizuka (1995) provided evidence that the diversity of forest floor plants in abandoned coppice woodlands declines with an increase in the population or density of dwarf bamboo (*Pleioblastus chino*). This bamboo species grows rapidly, and hence would become exclusively dominant once coppice woodland management is stopped. Competitive species dominance is also known to negatively affect bird diversity (Ichinose and Katoh 1998).

Aside from light condition as an important factor affecting ground floral composition and diversity, topographic variations also create different habitat conditions that can enhance such diversity (Takeuchi et al. 1995). Landform variations in hilly and mountainous forests are considered sufficient indicators of edaphic properties like nutrients and soil moisture (Cowell 1993; Garten et al. 1994; Burns and Leathwick 1996; Enoki et al. 1996; Rubio et al. 1999), soil disturbance frequency (Kikuchi and Miura 1993; Yoshida and Ohsawa 1996; Nagamatsu and Miura 1997), and microclimate mainly associated with slope aspects (Small and McCarthy 2002) that can affect vegetation structures.

Previous studies by Tamura and Takeuchi (1980), Kikuchi (1990), and Kikuchi and Miura (1993) showed a relationship between micro-scale landforms and species composition of both the overstory and understory flora in secondary woodlands located in hilly areas of Japan. In these studies, however, management in relation to ground flora was not included, because the secondary woodlands were abandoned. To determine alternative strategies to enhance floristic diversity in secondary woodlands located on hilly areas, the effects of both the landforms and management practices on the flora, especially the ground flora, should be considered.

This study sought to answer the following:

- (1) How species composition and richness of ground flora differ among micro-scale landforms and management regimes.
- (2) How interactions of landform and management affect ground flora.
- (3) How their variations and synergistic effects enhance beta diversity.

Materials and methods

Study area

The study area is located in the Tama Hills of Tokyo, central Japan. The Tama Hills lie in the southwestern part of the Kanto Plain and extend from the Kanto Mountains to the Miura Peninsula at an elevation decreasing from approximately 200 m to 50 m above sea level (Fig. 1). The bedrock of the Hills is semi- or unconsolidated sedimentary rocks that originated from the Pliocene to the Middle Pleistocene, known as the ‘Kazusa’ Group. This group consists of several formations with a sedimentary cycle of fluvial gravels, tidal flats and inner bay silt, and littoral to upper neritic sand from the lower to the upper part (Takano 1994). The bedrock is overlain by aeolian volcanic ashes or tephra usually called the “Kanto Loam” layers (Fig. 2). In the study area, the weathered sandstone of the upper part of the Oyamada Formation (Takano 1994) is highly dissected, and the mudstone of the lower part of the formation forms an impermeable layer beneath the valley bottoms.

The study site lies within the 33.2-ha Zushi-Onoji Historic Environmental Conservation Area (35°35′N, 139°25′E; Fig. 1), which was designated in 1978 as a Greenery Conservation Area by the Tokyo Metropolis. The mean annual precipitation is approximately 1540 mm, the mean temperature is 14 °C, and the monthly minimum temperature is –2 °C (Japan Meteorological Agency 2003). The original vegetation belongs to the Warm Temperate Forest Zone (*Camellietea japonicae* in the phytosociological definition; Miyawaki et al. 1978). Thus, the potential climax vegetation would be evergreen broadleaved forests such as *Quercus myrsinaefolia*, *Q. glauca*, and *Castanopsis sieboldii*. The secondary woodlands in the area, even more than 30 years after abandonment, still consist of mixed deciduous broadleaved trees, mainly *Q. serrata*, *Q. acutissima*, and *Castanea crenata*, which are the commonly dominant species in managed coppice woodlands.

The woodlands on the hillsides and their verges next to paddy fields on the valley bottoms were used for this study (Photo 1). The woodlands were managed as coppices and the paddy fields were cultivated until the late 1960s. Since 1996, a management organization mostly consisting of local farmers has revived the management of both woodlands and paddy fields using traditional practices with financial support from the Tokyo Metropolis (Kitagawa 2003).

Micro-scale landform classification

The micro-scale landform classification was based on the definition of Tamura (1974) and parts of Nagamatsu and Miura (1997). Preliminary stereo-pair aerial photographs (approximately 1:8000 scale) taken in 1974 by the Geographical Survey Institute of Japan were used to roughly delineate the landform boundaries on a 1:2000 topographic map published by the Bureau of Environment, Tokyo Metropolis, in 1996.

The micro-scale landform classification was finalized following cross-sectional slope measuring with a slope-angle meter (TRS-10, Tokyo Research Service Co. Ltd., Tokyo, Japan) along seven survey transects (mentioned below). The soil profile was surveyed at approximately 5-m intervals with a soil auger (40 mm diameter, 2 m long). Five micro-landform units were distinguished in the area: crest slope (CS); upper side slope (USS); lower side slope (LSS); head hollow (HH); and valley bottom (VB) (Fig. 2). VB was excluded from the micro-landform classification, since it is the location of the paddy fields.

Field surveys

Seven survey transects were established from hill ridges to the ends of slopes. All surveys started in inner woodland and ended in the verge next to the paddy fields. In the woodland, all transects were set up under closed canopies of mixed deciduous trees of similar height

(about 15 m) to reduce overstory effects on ground flora. To determine the effects of micro-scale landforms, two transects were set up in valley head areas, and five were set up in side slope areas.

Four management regimes were observed: no management (NM); moderate management (MM), comprising thinning the shrub layer and mowing the ground layer on a 4- or 5-year cycle (most recently during the winter of 1998–99); intensive management (IM), similar to MM but yearly; and highly intensive management (HM), in which management was done by cutting all trees and shrubs and mowing the ground layer twice a year, normally in May and October. The last HM was done in May 2001 on the lowermost side slopes, where cultivated paddy fields on valley bottoms are contiguous. HM is done to avoid shading of the paddy fields; the management was strongly associated with paddy cultivation (see Photo 1).

Of the two transects that were set up in valley heads, one was in the MM area and the other was in the NM area. Of the five transects that were established on side slopes, two were in the IM area, two in the MM area, and one in NM area. All five transects placed in the lowermost side slope area incorporated the HM area (Photo 1; Fig. 2). In addition to these, four short transects of the HM area were established on the lowermost side slopes in order to give sufficient basis for statistically acceptable comparison with the other site conditions. No transect was set on slopes facing north in order to reduce slope-aspect effects on the light condition and soil moisture. Actually, there were three aspects in the eight slope directions: southeast; southwest; and west.

Along each transect, quadrats measuring 2 m × 2 m were established continuously. A total of 168 quadrats were established (Table 1). In each quadrat, all the plant species in the herbaceous layer (< 1 m high from ground surface) were noted and classified according to their life forms: annual or biennial herb species (annual); perennial herb species (perennial); deciduous broadleaved trees or shrubs (deciduous); evergreen broadleaved trees or shrubs (evergreen); and coniferous trees (conifer). All species were recorded as present or absent during summer, from July to August 2001.

To characterize the environment, the light condition and soil moisture were measured. The photosynthetically active photon flux density (PPFD) at ground level was measured with a point sensor (LI-190SA, LI-COR, Lincoln, Nebraska, USA). Relative PPFD was calculated against reference PPFD measured in an uncovered dry field on the hill-ridge within the study area. Volumetric water content (VWC) of the surface soil was measured with a time domain reflectometry (TDR) probe (TRIME-EZ, IMKO Micromodultechnik GmbH, Ettlingen, Germany). Both the PPFD and VWC were measured in five replicates, one each at 0.5 m inside the four corners and one at the center of each quadrat. The measurements were made during overcast days from 11:00 a.m. to 1:00 p.m. in September 2001.

Data analysis

We recorded 225 species in the 168 quadrats. To understand the effects of micro-scale landform and management regime on ground flora, we analyzed species compositional data by using the ordination method of Detrended Correspondence Analysis (DCA; Hill 1979; Hill and Gauch 1980). To detect the representative species in each habitat type, we used Indicator Species Analysis (INSPAN; Dufrêne and Legendre 1997). Plant species that appeared in only one quadrat were excluded from the two analyses to avoid ordination distortion by serendipitous species because of the use of presence/absence data.

Consequently, data on 174 species were analyzed by DCA and INSPAN. The potential species richness in each habitat type was estimated by means of species–area curves and a first-order jackknife estimator (Heltshel and Forrester 1983; Palmer 1990). In these

analyses, the analytical program PC-ORD for Windows Version 4 (McCune and Mefford 1999) was used. All settings of DCA and INSPAN were set to the software's defaults.

The relationships among DCA axis scores, environmental parameters, and species richness were compared with nonparametric statistical methods—Kruskal–Wallis test and Mann–Whitney *U*-test—with SPSS Base for Windows Version 10.0 (SPSS Inc., Chicago, Illinois, USA).

To compare diversity and species turnover between habitat types, we calculated beta diversity in terms of species compositional dissimilarities of every quadrat combination within or between habitat types. The distance matrix for every quadrat pair (14 028 combinations) was obtained by measuring the compositional dissimilarities by the Sørensen or Bray–Curtis index (McCune and Mefford 1999) with PC-ORD.

Results

General description of micro-scale landforms

Figure 2 shows schematic cross-sections of head hollow and side slope areas. Average slope angles and surface water contents in each micro-scale landform unit are summarized in Table 2. Both parameters were significantly different among landform units ($P < 0.01$, Kruskal–Wallis test).

Crest slopes (CS) are found around hill ridges and consist of gentle convex slopes. The present morphogenic processes are rather inactive in CS (Tamura and Takeuchi 1980), so that the loam layer overlies the bedrock thickly (> 2 m). The type of the soil is classified as Andosol according to the World Reference Base for Soil Resources (WRB; Driessen 2001). The soil moisture is the driest among the micro-scale landform units but is mesic under the tree canopies.

Upper side slopes (USS) are situated on the lower boundary of CS and are conjoined with convex break lines of slopes in hillside areas. These slopes have convex sections and become steeper as the depth of the loam layer declines, and the weathered sandstone appears within 1 m deep. The soil is classified as Andic Cambisol according to WRB. The soil moisture was not different from that of CS ($P > 0.05$, Mann–Whitney *U*-test with Bonferroni's correction).

Lower side slopes (LSS) are separated from USS with convex break lines of slopes on the upper boundary, and from the valley bottom (VB) with concave break lines of slopes on the lower boundary. These slopes have straight or slightly convex sections and the steepest slope (sometimes up to 55°) among the micro-scale landform units in the area. Therefore, the frequency of surface soil disturbance might be high (Nagamatsu and Miura 1997); the loam layer is very thin or sometimes lacking. In the WRB classification, this soil type is considered as Mollic Cambisol. The soil moisture is moderately high because the lowermost part is close to VB. A gleyic horizon appears within 1 m deep.

Head hollows (HH) are embayed by CS with convex break lines in valley heads, and delineated against VB with concave break lines. The unit has concave sections. The steepness of slopes is larger at the upper part and gradually declines toward the lower part; the slope range is wide, from 15° to 44° . The surface soil layer, consisting of admixtures of sand from weathered sandstone and redistributed volcanic ash, has a sandy loam texture and is thick. Although the soil type in the WRB classification is considered as Mollic Cambisol, the lower parts of the unit have a gleyic horizon similar to that of LSS.

Species composition as influenced by micro-scale landform and management regime

Preliminary analyses were conducted to confirm if the slope aspect affects the light

condition and soil moisture (Small and McCarthy 2002). The results show that the soil water contents were not significantly different among three slope aspects in each micro-scale landform unit ($P > 0.05$, Kruskal–Wallis test). With regard to the light condition, adequate quadrat samples for each landform unit within the same management regime were not available for comparison (see Table 1). However, the relative PPFs were not significantly different among slope aspects when compared in HM sites ($P > 0.05$, Kruskal–Wallis test), where the effects of the slope aspect on light condition might be more distinct than in other sites covered by tree canopies. These results imply that the slope aspect within the range from southeast to west in clockwise direction would have little influence on the light condition as well as on soil moisture. We therefore excluded the slope aspect from further analyses as a factor influencing ground flora.

The results of DCA ordination of quadrats are shown in Figure 3. The scores of the first and second DCA axes were reasonably well correlated with relative PPF and soil water content, respectively (Table 3). With regard to micro-scale landforms (Fig. 3a), quadrats in HH had small scores in the first axis and big scores in the second axis. This supports the positive correlation between the second axis scores and soil water content. In HH, variation of the second axis scores was large because of the difference in soil moisture between lower and upper parts of the unit. Quadrats in CS and USS had little variation; both, however, had small scores in the second axis. Quadrats in LSS were widely scattered because all management regimes were included. Across the first DCA axis, there was a gradient in management regimes within woodlands in the order of NM, MM, and IM (Fig. 3b). Although HM sites were widely scattered along the first axis despite being located only on a single micro-scale landform type, about half of the sites had higher scores than IM sites. These reflect the positive correlation between the first axis scores and relative PPF, which was modified by management practice.

Average scores of micro-scale landform units versus management regimes (except NM in CS) are plotted in Figure 3c. In HH, no significant difference was found between management regimes in influencing species composition as manifested in the ordination scores ($P > 0.05$ on both axes, Mann–Whitney U -test). The mean relative PPF of NM (2.51%) was not significantly different from that of MM (2.53%). In CS, USS, and LSS, there were significant differences among management regimes in their effects on species composition in each micro-scale landform unit in the first ordination scores ($P < 0.01$, Kruskal–Wallis test). In contrast, there were no significant differences among these micro-scale landform units within the same management regime. This means that management regimes in CS, USS, and LSS (except in HM) were more influential than micro-scale landform in affecting the ground flora composition. HM in LSS was situated on the higher part of both the first and second axes. This suggests that the sites were light-filled and moist.

Habitat types as a result of the combined effects of landform and management regime

Five habitat types were classified on the basis of the combination of landform and management regime: (1) IM quadrats in CS, USS, and LSS ($N = 44$); (2) MM quadrats in CS, USS, and LSS ($N = 45$); (3) NM quadrats in CS, USS, and LSS ($N = 27$); (4) HH regardless of management regime ($N = 30$); and (5) HM quadrats in the lowermost LSS ($N = 22$). The relative PPFs were significantly different between most habitat types except between Types 2 and 3 ($P < 0.05$, Mann–Whitney U -test with Bonferroni's correction; Fig. 4).

The representative species of each habitat type having statistical significance at $P < 0.01$ with the Monte Carlo test (McCune and Mefford 1999) were identified by INSPAN (Table 4). The numbers of the representative species for Habitat Type 1 to Habitat Type 5

were 19, 9, 9, 15, and 31. This means that Habitat Type 5 had the most ‘unique’ species, followed by Habitat Type 1 and Habitat Type 4.

In Habitat Type 1 (IM in CS, USS, and LSS), we selected pioneer species of trees and shrubs as ‘indicator species’: *Pinus densiflora*, *Morus bombycis*, *Fagora mantchuria*, *Clerodendron trichotomum*, *Rubus palmatus*, *Rhus javanica* var. *roxburghii*, *Aralia elata*, and *Albizia julibrissin*, and grassland or forest-edge herbs such as *Paederia foetida*, *Lysimachia clethroides*, and *Lespedeza pilosa*.

In Habitat Type 2 (IM in CS, USS, and LSS), we selected typical species of secondary woodlands (Miyawaki et al. 1978): *Ilex macropoda*, *Acer crataegifolium*, and *Viburnum dilatatum*.

In Habitat Type 3 (NM in CS, USS, and LSS), we considered many evergreen broad-leaved trees, shrubs, and herbs as representative species of potential natural vegetation in the area (Miyawaki et al. 1978): *Quercus myrsinaefolia*, *Castanopsis sieboldii*, *Ligustrum japonicum*, *Ilex integra*, *Eurya japonica*, *Ophiopogon ohwii*, and *Polygonatum lasianthum*.

In Habitat Type 4 (HH regardless of management regime), the indicator species were perennial herbs and ferns such as *Viola bisseti*, *Pertya robusta*, *Deparia lasiopteris*, *Salvia nipponica*, and *Syneilesis palmata*, as well as the shrub *Hydrangea hirta*, most of which prefer wet conditions.

In Habitat Type 5 (HM in LSS), many annual and perennial herbs could be selected as indicator species. However, only species with special preference in terms of habitat selection were included. We selected *Potentilla freyniana*, *Aster scaber*, *Thalictrum minus* var. *hypoleucum*, *Scilla scilloides*, *Arundinella hirta*, *Eupatorium makinoi* var. *oppositifolium*, and *Gentiana scabra* var. *buergeri* as representative species of *Miscanthus sinensis* grassland; *Justicia procumbens*, *Setaria glauca*, *Oxalis corniculata*, and *Clematis terniflora* as representative herbs of waysides or dry-field weedy vegetation; and *Ligustrum obtusifolium*, *Deutzia crenata*, *Houttuynia cordata*, *Hydrocotyle maritima*, *Astilbe microphylla*, and *Duchesnea chrysantha* as representative shrub and herb species that prefer wet conditions or forest-edge habitats.

Species richness and beta diversity

We found a total of 225 species in the 168 quadrats. Habitat Type 5 had the highest average number of species per quadrat (22.6), followed by Type 1 (20.8), Type 4 (19.7), and Type 2 (18.6). However, no significant differences were found between or among these four habitat types. On the other hand, Type 3 had the significantly lowest number of species (13.6) ($P < 0.05$, Mann–Whitney U -test with Bonferroni’s correction).

Comparing species richness at the 22-quadrat line (Fig. 5), Habitat Type 5 had the highest number (126) followed by Type 1 (91.3 ± 4.5), and Type 3 had the lowest (62.8 ± 1.7). Use of the first-order jackknife estimator showed a similar trend in potential species richness (Fig. 6).

Between-habitat dissimilarity values were significantly higher than within-habitat values ($P < 0.01$, Mann–Whitney U -test with Bonferroni’s correction; Table 5). This shows only that species turnover had occurred between habitats. Each habitat contributed to maintaining beta diversity. Although dissimilarity was larger within Habitat Type 5 than within other habitat types, dissimilarities between Habitat Type 5 and other types were much larger than most other between-habitat dissimilarities. Large dissimilarities were also found between Habitat Types 1 and 3, and between Types 1 and 4.

Discussion

This study reveals that both light condition and surface soil moisture are important factors that control ground flora. Light condition was improved by appropriate management (Fig. 4). Although the research approach was indirect because the actual response of the flora was not monitored, the findings concur with the results of previous studies (Gondard et al. 2001; Mason and Macdonald 2002). Unlike in those previous studies, however, coppice woodland management such as clearing canopy trees was not practiced except on the lowermost hill slopes. Thus, anthropogenic disturbance within these woodlands was comparatively less.

Thinning of shrubs and mowing of the herbaceous layer have a marked effect on ground flora. Species found at intensively managed sites, such as *Morus bombycis* and *Rhus javanica* var. *roxburghii*, are also found at selective tree-felling sites in secondary woodland of central Japan (Bhujii and Ohsawa 1999). This means that enough light reaches the herbaceous layer to allow the growth of pioneer species (mean relative PPF, 27.0%; Fig. 4). As there is vertical variation in light condition under the tree canopy (Lieffers et al. 1999), removing the understory would reduce the light competition with shrub layer species. In addition, anthropogenic soil disturbance by trampling associated with yearly management practices would have effects on ground flora (Bhujii and Ohsawa 1998).

The micro-scale landforms have, in effect, made ground flora differ. In particular, the head hollow (HH) sites had a significantly different species composition from those of the other landform units. Previous studies that focused on the relationship between micro-scale landform and vegetation in hilly secondary woodlands of Japan also found unique species compositions in each landform unit (Tamura and Takeuchi 1980; Nagamatsu and Miura 1997). This is because of differences in soil moisture. The HH unit is wetter because it receives runoff from surrounding units (Tamura 1981), and hence different species can be expected.

Management in the HH unit had less effect on the variation in species composition than in the crest slope (CS) and upper side slope (USS) units. This is because HH is shaded by ridges on three sides, and management cannot improve the light condition. The geomorphic situation in HH is responsible for the high soil disturbance frequency (Nagamatsu and Miura 1997). Soil disturbance may affect the ground flora at all sites irrespective of anthropogenic disturbance. Soil disturbance has strong negative effects on vegetation development, especially in the shrub layer (Swanson et al. 1988; Sakai and Ohsawa 1993; Hara et al. 1996), reducing the competition for resources such as light between the shrub layer and the ground flora. Furthermore, disturbed soil accumulates in the lower parts of landform units, so the nutritional condition in HH would be better than in CS and USS (Enoki et al. 1996). These factors, therefore, may increase species richness in HH (e.g. Habitat Type 4), even without intensive management.

In the other micro-scale landform units, no distinction in species composition was observed except in highly intensive management (HM) sites involving clear-cutting on the lower side slopes (LSS). Our results correspond to the findings of previous studies that the change in species composition of the ground flora was slight or gradual between CS and USS (Tamura and Takeuchi 1980; Kikuchi 1990; Kikuchi and Miura 1993; Nagamatsu and Miura 1997). In contrast, these studies found significant differences between LSS and both CS and USS, owing to the greater soil disturbance in LSS. This makes our result not really consistent. In our study, all of the lowermost LSS sites were HM, which was steepest and subject to the greatest erosion. The species composition here under tree canopies, therefore, could not be researched and compared with that in the other landform units. If quadrats were established on the forest floor of the lowermost LSS sites, the ground flora might be different.

Highly intensive management (HM) sites on the lowermost LSS (e.g. Habitat Type 5) had the highest species richness (Figs. 5 and 6). In addition, the species composition was distinctive from that of the other habitat types (Tables 4 and 5). This is because the plant community is herbaceous and is managed in the most intensive way, by mowing twice a year. Kitazawa and Ohsawa (2002), in their study of herbaceous communities without tree-canopy cover in a 'satoyama' landscape on the Shimousa Plateau in central Japan, found that the maximum species richness of meadows mown more than twice a year was 76 species (quadrat size was 26 m², the smallest area in which no additional species appeared). This was the highest species richness among vegetation types. These meadows were also verges between paddy fields and secondary woodlands. This species richness value was similar to our result: the mean species richness value at the 6.5-quadrat line (= 26 m² / 2 m × 2 m) on the species–area curve for the same habitat type was approximately 80 species (Fig. 5). Unlike in their study, however, the species–area curve in our study was not saturated at this point, reaching 126 in the field (Fig. 5), and an estimated maximum of 152.7 (Fig. 6).

In HM, grassland species such as *Miscanthus sinensis* and some representative species that thrive in wetland conditions such as *Hydrocotyle maritima* and *Astilbe microphylla* were recorded. On the other hand, Kitazawa and Ohsawa (2002) found the grassland species dominant only in verges or meadows. The differences in the results may be caused by the variation in topography and other environmental factors; their research was done on a low-relief plateau, whereas ours was done on high-relief hills. The hills have a larger environmental gradient from the ridge to the valley bottom (especially soil moisture gradient), because the elevation relief is larger. The verges that we studied are situated on steeper slopes and in an environmental transition zone with a large moisture gradient. Nagamatsu and Miura (1997) noted that the variation in the type of vegetation on lower slope areas depended on soil disturbance frequency and disturbance type (aggradation or degradation) rather than on micro-scale landform unit. In addition to management regime, higher species richness can be attributed to the high soil disturbance frequency brought about by slope steepness and abruptness in the soil moisture gradient—an ecotone of soil moisture.

Conclusion

Our results show how micro-scale landform and management regimes affect ground flora. The variety of landforms with different soil moisture and soil disturbance regimes contributes to variation in species composition. Although the effectiveness of management practice varies among landform units, it has been found to enhance species richness. We distinguished five habitat types on the basis of management regime and landform unit. The high regional diversity of ground flora can be attributed to these habitat types.

To conserve diversity, it is therefore important that the whole system of micro-scale landforms consisting of the hills and the rural landscape be preserved *in toto*. The HM sites on the lowermost LSS are the most important habitat, because they have the highest species richness and have contributed greatly to enhancing beta diversity on a regional scale. Moreover, management practices and the cultivation of rice on the valley bottoms should be sustained.

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References

- Ash J.E. and Barkham J.P. 1976. Changes and variability in the field layer of a coppiced woodland in Norfolk, England. *Journal of Ecology* 64: 697–712.
- Barkham J.P. 1992. The effects of coppicing and neglect on the performance of the perennial ground flora. In: Buckley G.P. (ed), *Ecology and Management of Coppice Woodlands*. Chapman & Hall, London, pp. 115–145.
- Bhaju D.R. and Ohsawa M. 1998. Effects of nature trails on ground vegetation and understory colonization of a patchy remnant forest in an urban domain. *Biological Conservation* 85: 123–135.
- Bhaju D.R. and Ohsawa M. 1999. Species dynamics and colonization patterns in an abandoned forest in an urban landscape. *Ecological Research* 14: 139–153.
- Brown R.D. and Yokohari M. 2003. Ideological contribution of satoyamas. In: Takeuchi K., Brown R.D., Washitani I., Tsunekawa A. and Yokohari M. (eds), *Satoyama: The Traditional Rural Landscape of Japan*. Springer-Verlag, Tokyo, pp. 1–7.
- Burns B.R. and Leathwick J.R. 1996. Vegetation–environment relationships at Waipoua Forest, Northland, New Zealand. *New Zealand Journal of Botany*: 34: 79–92.
- Cowell C.M. 1993. Environmental gradients in secondary forests of the Georgia Piedmont, USA. *Journal of Biogeography* 20: 199–207.
- Driessen, P.M. 2001. *Lecture Notes on the Major Soils of the World*. World Soil Resources Reports 94, FAO, Rome.
- Dufrêne M. and Legendre P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs* 67: 345–366.
- Enoki T., Kawaguchi H. and Iwatsubo G. 1996. Topographic variations of soil properties and stand structure in a *Pinus thunbergii* plantation. *Ecological Research* 11: 299–309.
- Fukamachi K., Oku H. and Nakashizuka T. 2001. The change of a satoyama landscape and its causality in Kamiseya, Kyoto Prefecture, Japan between 1970 and 1995. *Landscape Ecology* 16: 703–717.
- Garten C.T. Jr., Huston M.A. and Thoms C.A. 1994. Topographic variation of soil nitrogen dynamics at Walker Branch Watershed, Tennessee. *Forest Science* 40: 497–512.
- Gondard H., Romane F., Grandjanny M., Li J. and Aronson J. 2001. Plant species diversity changes in abandoned chestnut (*Castanea sativa*) groves in southern France. *Biodiversity and Conservation* 10: 189–207.
- Hara M., Hirata K., Fujihara M. and Oono K. 1996. Vegetation structure in relation to micro-landform in an evergreen broad-leaved forest on Amami Ohima Island, south-west Japan. *Ecological Research* 11: 325–337.
- Heltshe J.F. and Forrester N.E. 1983. Estimating species richness using the jackknife procedure. *Biometrics* 39: 1–12.
- Hill M.O. 1979. *DECORANA: a FORTRAN program for detrended correspondence analysis and reciprocal averaging*. Cornell University Press, New York.
- Hill M.O. and Gauch H.G. Jr. 1980. Detrended correspondence analysis: an improved ordination technique. *Vegetatio* 42: 47–58.
- Ichinose T. and Katoh K. 1998. Factors influencing bird distribution among isolated

- woodlots on a heterogeneous landscape in Saitama Pref., Japan. *Ekologia (Bratislava)* 17: 298–310.
- Iida S. and Nakashizuka T. 1995. Forest fragmentation and its effect on species diversity in suburban coppice forests in Japan. *Forest Ecology and Management* 73: 197–210.
- Japan Meteorological Agency. 2003. Monthly data in an average year (1983–2000) at Hachioji Meteorological Station (<http://www.data.kishou.go.jp/>).
- Kikuchi T. 1990. A DCA analysis of floristic variation of plant communities in relation to micro-landform variation in a hillside area. *Ecological Review* 22: 25–31.
- Kikuchi T. and Miura O. 1993. Vegetation patterns in relation to micro-scale landforms in hilly land regions. *Vegetatio* 106: 147–154.
- Kitagawa Y. 2003. Regeneration of satoyama landscape. In: Takeuchi K., Brown R.D., Washitani I., Tsunekawa A. and Yokohari M. (eds), *Satoyama: The Traditional Rural Landscape of Japan*. Springer-Verlag, Tokyo, pp. 129–142.
- Kitazawa T. and Ohsawa M. 2002. Patterns of species diversity in rural herbaceous communities under different management regimes, Chiba, central Japan. *Biological Conservation* 104: 239–249.
- Lieffers V.J., Messier C., Stadt K.J., Gendron F. and Comeau P.G. 1999. Predicting and managing light in the understory of boreal forests. *Canadian Journal of Forest Research* 29: 796–811.
- Mason C.F. and Macdonald S.M. 2002. Responses of ground flora to coppice management in an English woodland: a study using permanent quadrats. *Biodiversity and Conservation* 11: 1773–1789.
- McCune B. and Mefford M.J. 1999. *PC-ORD: Multivariate Analysis of Ecological Data*, Version 4. MjM Software Design, Gleneden Beach, Oregon, USA.
- Miyawaki A., Okuda S. and Mochizuki R. 1978. *Handbook of Japanese Vegetation*. Shibundo, Tokyo (in Japanese).
- Nagamatsu D. and Miura O. 1997. Soil disturbance regime in relation to micro-scale landforms and its effects on vegetation structure in a hilly area in Japan. *Plant Ecology* 133: 191–200.
- Palmer M.W. 1990. The estimation of species richness by extrapolation. *Ecology* 71: 1195–1198.
- Roberts M.R. and Gilliam F.S. 1995. Patterns and mechanisms of plant diversity in forested ecosystems: implications for forest management. *Ecological Applications* 5: 969–977.
- Rubio A., Gavilán, R. and Escudero A. 1999. Are soil characteristics and understorey composition controlled by forest management? *Forest Ecology and Management* 113: 191–200.
- Sakai A. and Ohsawa M. 1993. Vegetation pattern and microtopography on a landslide scar of Mt. Kiyosumi, central Japan. *Ecological Research* 8: 47–56.
- Small C.J. and McCarthy B.C. 2002. Spatial and temporal variability of herbaceous vegetation in an eastern deciduous forest. *Plant Ecology* 164: 37–48.
- Swanson F.J., Kratz T.K., Caine, N. and Woodmansee R.G. 1988. Landform effects on ecosystem patterns and processes. *BioScience* 38: 92–98.
- Takano S. 1994. Stratigraphy of the Lower Pleistocene Kazusa Group in the Tama Hills, central Japan. *Journal of Geological Society of Japan* 100: 675–691 (in Japanese with English abstract).
- Takeuchi K. 2001. Nature conservation strategies for the ‘satoyama’ and ‘satoti’, habitats for secondary nature in Japan. *Global Environmental Research* 5: 193–198.
- Takeuchi K., Ide M., Yokohari M. and Brown R.D. 1995. Relationships of landform and biological diversity in landscape ecology. *Transactions of the Japanese*

- Geomorphological Union 16: 215–225.
- Tamura T. 1974. Micro-landform units composing a valley-head area and their geomorphic significance. *Tohoku Chiri* 26: 189–199 (in Japanese with English abstract).
- Tamura T. 1981. Multiscale landform classification study in the hills of Japan: II Application of the multiscale landform classification system to pure geomorphological studies of the hills of Japan. *Science Reports of Tohoku University, 7th Series (Geography)* 31: 85–154.
- Tamura T. and Takeuchi K. 1980. Land characteristics of the hills and their modification by man: with special reference to a few cases in the Tama Hills, west of Tokyo. *Geographical Reports of Tokyo Metropolitan University* 14/15: 49–94.
- Washitani I. 2001. Traditional sustainable ecosystem ‘satoyama’ and biodiversity crisis in Japan: conservation ecological perspective. *Global Environmental Research* 5: 119–133.
- Yoshida N. and Ohsawa M. 1996. Differentiation and maintenance of topo-community patterns with reference to regeneration dynamics in mixed cool temperate forests in the Chichibu Mountains, central Japan. *Ecological Research* 11: 351–362.

Figures and Tables



Photo 1. Woodlands and their verges next to paddy fields on the valley bottom. The left photo was taken from the valley head to the mouth. The right photo shows highly intensive management involving clear-cutting on the lowermost side-slopes, where cultivated paddy fields on valley bottoms are contiguous in order to avoid shading of the fields. Both photos were taken at the beginning of June 2001, during the transplanting of rice seedlings.

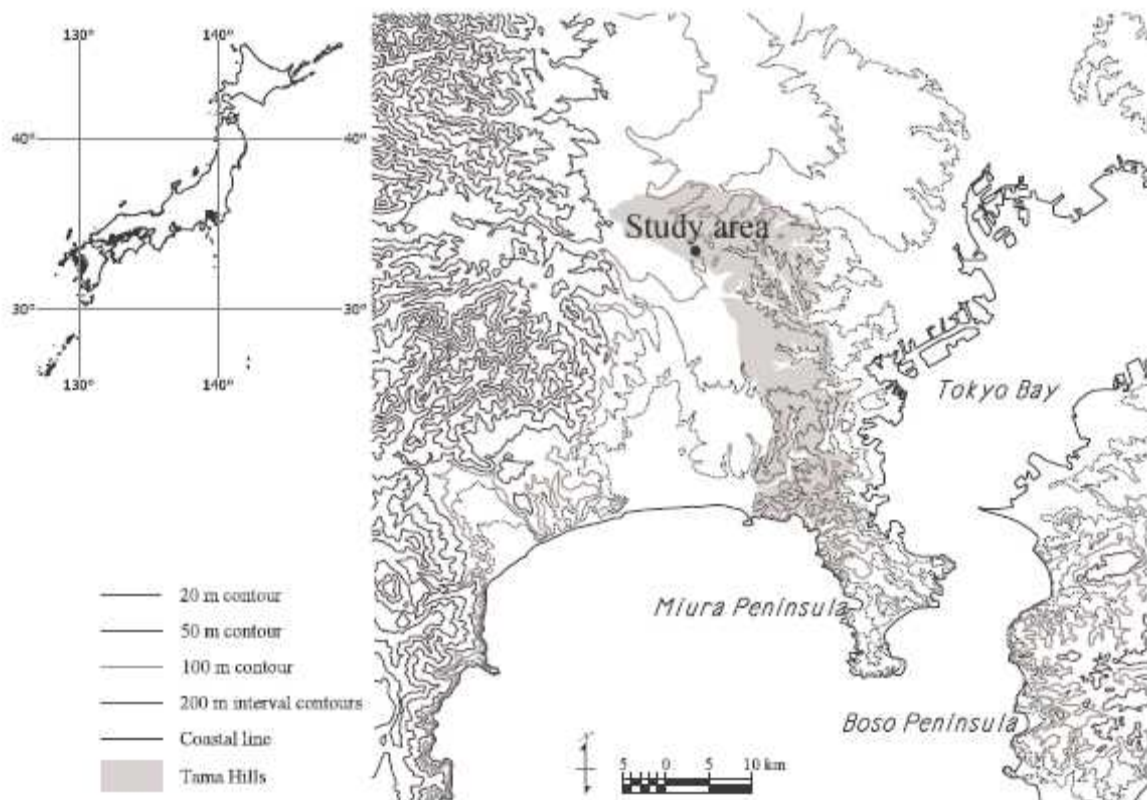


Figure 1. Location map of the study area.

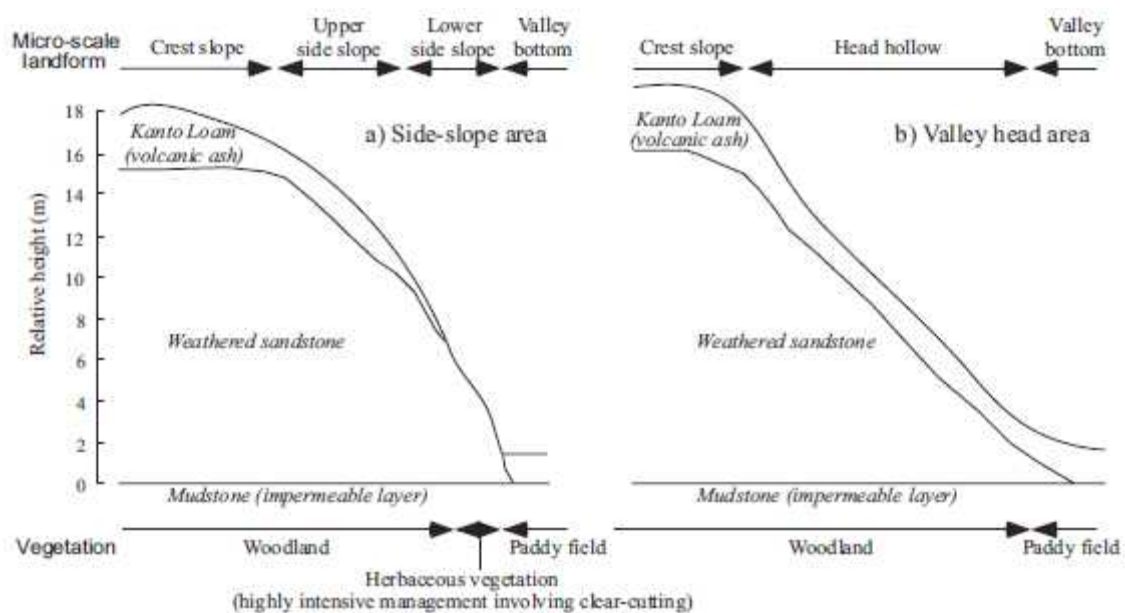


Figure 2. Schematic cross-sections of hillside slopes and valley head area with surface geological profiles and vegetation.

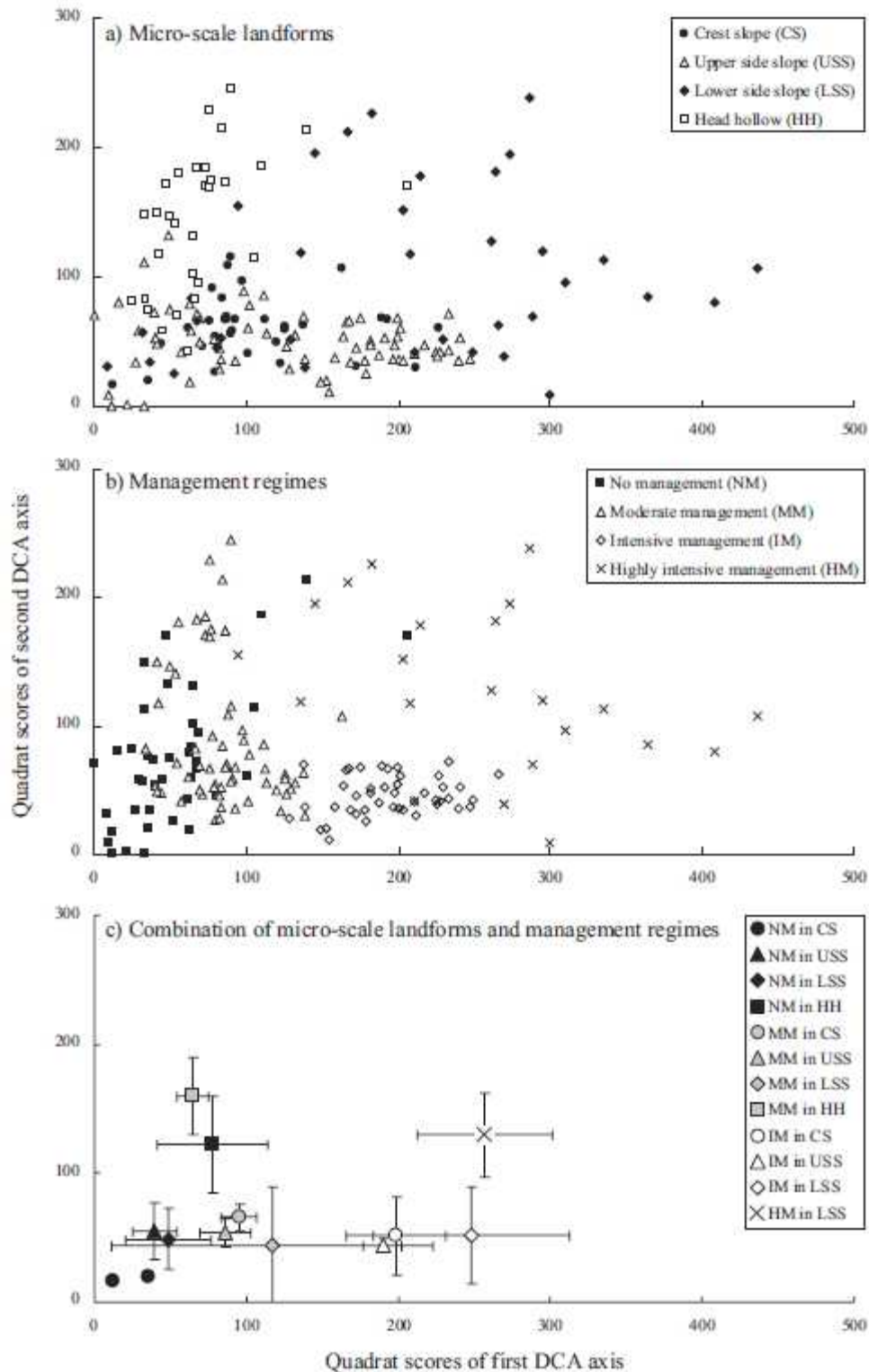


Figure 3. Scatter-plots of ordination scores for each quadrat by Detrended Correspondence Analysis (DCA) in the first two dimensions. (a) Quadrats marked by micro-scale landform units. (b) Quadrats marked by management regimes. (c) Average scores and error bars with 95% confidence coefficient for both scores by the combination of landform and management regime. For “no management” sites in the crest slope (NM in CS), actual data ($N = 2$) are plotted; no average score is shown.

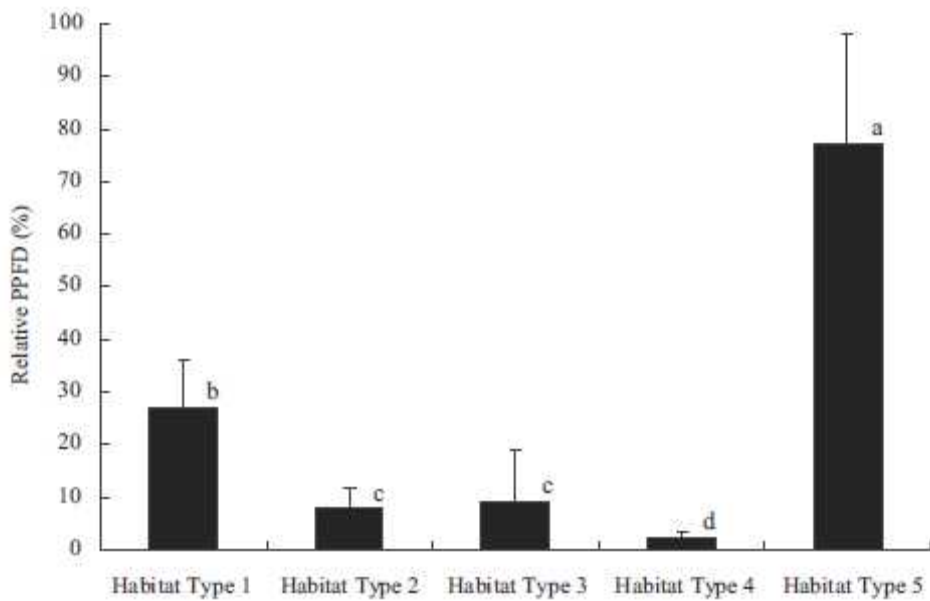


Figure 4. Differences in relative PPFD among the five habitat types. Letters above each bar graph indicate statistical differences ($P < 0.05$, Mann–Whitney U -test with Bonferroni’s correction).

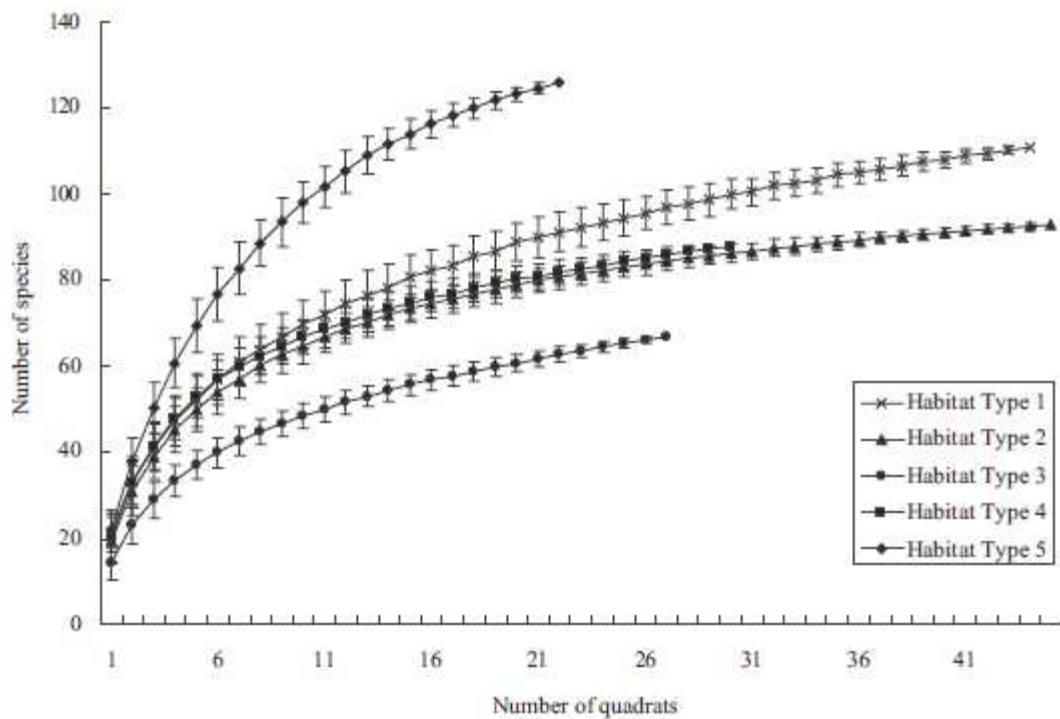


Figure 5. Species–area curves for each habitat type. Curves show mean species number by area. Error bars show ± 1 standard deviation.

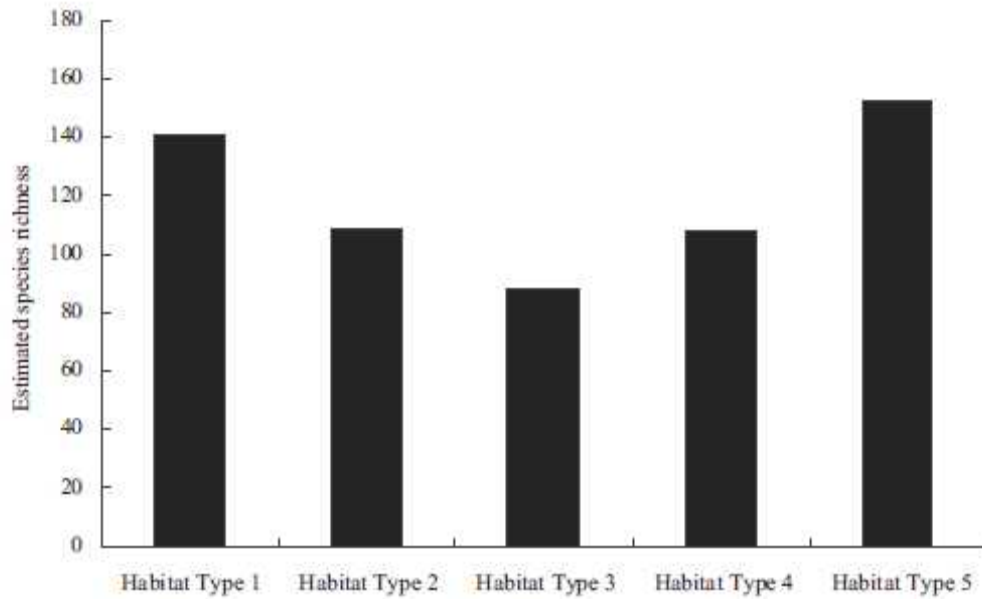


Figure 6. Estimated species richness by first-order jackknife estimator for each habitat type.

Table 1. Number of quadrats for each micro-scale landform and vegetation management type

	Crest slope			Upper side slope			Lower side slope			Head hollow		
	SE *	SW *	W *	SE	SW	W	SE	SW	W	SE	SW	W
Forest floor												
Intensive management	4	1	0	21	15	0	3	0	0	0	0	0
Moderate management	0	0	26	0	0	16	0	0	3	0	0	17
No management	0	1	1	0	18	0	0	7	0	0	0	13
Verge												
Highly intensive management	0	0	0	0	0	0	4	8	10	0	0	0

* Slope aspect in eight directions: southeast (SE); southwest (SW); and west (W)

Table 2. Environmental conditions in each micro-scale landform type

	Number	Slope (°)		Soil water content (volume %)	
		Mean	S.D.	Mean	S.D.
Crest slope (CS)	33	7.4	4.4	32.1	3.6
Upper side slope (USS)	70	20.9	7.5	33.7	5.2
Lower side slope (LSS)	35	34.7	9.9	37.9	8.0
Head hollow (HH)	30	31.4	6.2	37.9	9.3

Table 3. Spearman's correlations between DCA scores and environmental factors (*: $P < 0.05$, **: $P < 0.01$)

	DCA axis 1	DCA axis 2	Slope	Relative PPFD	Soil water content	Species richness
Slope	0.070	0.274 **	1.000			
Relative PPFD	0.618 **	-0.234 **	0.141	1.000		

Soil water content	0.315 **	0.327 **	0.195 *	0.092	1.000		
Species richness	0.329 **	0.199 **	0.211 **	0.136	0.248 **	1.000	

Table 4. Indicator species for five habitat types and their life forms. Species shown are ones that showed statistical significance by the Monte Carlo test ($P < 0.01$).

Representative habitat type *	Species name	Life form	Indicator values for habitat types **				
			Type 1	Type 2	Type 3	Type 4	Type 5
Type 1	<i>Pinus densiflora</i>	conifer	11	0	0	0	0
Type 1	<i>Callicarpa mollis</i>	deciduous	41	3	1	3	14
Type 1	<i>Morus bombycis</i>	deciduous	43	0	0	0	16
Type 1	<i>Fraxinus sieboldiana</i>	deciduous	20	12	2	0	0
Type 1	<i>Fagara mantchurica</i>	deciduous	66	0	0	0	1
Type 1	<i>Clerodendron trichotomum</i>	deciduous	30	0	0	11	0
Type 1	<i>Rubus palmatus</i>	deciduous	17	0	1	1	6
Type 1	<i>Euscaphis japonica</i>	deciduous	21	4	0	0	1
Type 1	<i>Rhus javanica</i> var. <i>roxburghii</i>	deciduous	35	0	0	0	5
Type 1	<i>Aralia elata</i>	deciduous	35	0	0	0	0
Type 1	<i>Celtis sinensis</i> var. <i>japonica</i>	deciduous	23	1	0	0	0
Type 1	<i>Stachyurus praecox</i>	deciduous	13	0	0	0	1
Type 1	<i>Albizia julibrissin</i>	deciduous	12	0	0	0	1
Type 1	<i>Callicarpa japonica</i>	deciduous	16	0	0	0	0
Type 1	<i>Paederia foetida</i>	perennial	37	3	0	1	21
Type 1	<i>Oplismenus undulatifolius</i>	perennial	33	8	0	0	17
Type 1	<i>Carex lanceolata</i>	perennial	23	3	0	2	2
Type 1	<i>Lysimachia clethroides</i>	perennial	33	0	0	0	7
Type 1	<i>Lespedeza pilosa</i>	perennial	21	0	0	0	6
Type 2	<i>Akebia trifoliata</i>	deciduous	15	25	7	12	9
Type 2	<i>Viburnum dilatatum</i>	deciduous	9	23	11	9	1
Type 2	<i>Wisteria floribunda</i>	deciduous	0	22	0	14	2
Type 2	<i>Acer crataegifolium</i>	deciduous	0	23	0	10	0
Type 2	<i>Ilex macropoda</i>	deciduous	0	11	0	0	0
Type 2	<i>Dioscorea japonica</i>	perennial	2	29	0	7	9
Type 2	<i>Ophiopogon japonicus</i>	perennial	2	37	0	2	3
Type 2	<i>Hosta montana</i>	perennial	0	18	1	0	13
Type 2	<i>Cocculus trilobus</i>	perennial	5	14	0	0	0
Type 3	<i>Eurya japonica</i>	evergreen	26	1	34	4	0
Type 3	<i>Quercus myrsinaefolia</i>	evergreen	0	6	27	5	0
Type 3	<i>Ligustrum japonicum</i>	evergreen	1	1	20	2	0
Type 3	<i>Castanopsis sieboldii</i>	evergreen	0	0	15	1	0
Type 3	<i>Ilex integra</i>	evergreen	0	0	15	0	0
Type 3	<i>Parthenocissus tricuspidata</i>	deciduous	3	0	18	0	1
Type 3	<i>Nandina domestica</i>	deciduous	0	0	13	0	0
Type 3	<i>Ophiopogon ohwii</i>	perennial	0	0	49	6	0
Type 3	<i>Polygonatum lasianthum</i>	perennial	0	0	16	0	6

Type 4	<i>Trachelospermum asiaticum</i> var. <i>intermedium</i>	evergreen	0	7	2	21	2
Type 4	<i>Viburnum erosum</i> var. <i>punctatum</i>	deciduous	0	0	3	19	0
Type 4	<i>Hydrangea hirta</i>	deciduous	0	0	0	21	0
Type 4	<i>Carex multifolia</i>	perennial	0	0	0	33	12
Type 4	<i>Carex conica</i>	perennial	4	16	0	21	0
Type 4	<i>Disporum smilcinum</i>	perennial	0	16	0	29	0
Type 4	<i>Dumasia truncata</i>	perennial	0	0	1	48	3
Type 4	<i>Viola bisseti</i>	perennial	0	0	4	57	0
Type 4	<i>Osmunda japonica</i>	perennial	0	1	0	19	11
Type 4	<i>Pertya robusta</i>	perennial	0	7	0	17	0
Type 4	<i>Dryopteris erythrosora</i>	perennial	0	0	0	29	3
Type 4	<i>Deparia lasiopteris</i>	perennial	0	0	0	43	0
Type 4	<i>Tricyrtis macropoda</i>	perennial	0	0	0	37	0
Type 4	<i>Salvia nipponica</i>	perennial	0	0	0	23	1
Type 4	<i>Syneilesis palmata</i>	perennial	0	0	0	13	0
Type 5	<i>Lonicera japonica</i>	deciduous	0	0	0	0	30
Type 5	<i>Ligustrum obtusifolium</i>	deciduous	0	0	0	0	12
Type 5	<i>Deutzia crenata</i>	deciduous	0	0	0	1	11
Type 5	<i>Indigofera pseudo-tinctoria</i>	deciduous	0	0	0	0	9
Type 5	<i>Justicia procumbens</i>	annual	0	0	0	0	27
Type 5	<i>Setaria glauca</i>	annual	0	0	0	0	14
Type 5	<i>Pueraria lobata</i>	perennial	12	1	0	0	20
Type 5	<i>Viola grypoceras</i>	perennial	13	0	0	11	21
Type 5	<i>Miscanthus sinensis</i>	perennial	6	0	0	0	25
Type 5	<i>Houttuynia cordata</i>	perennial	0	0	0	5	48
Type 5	<i>Cirsium nipponicum</i> var. <i>incomptum</i>	perennial	2	0	0	0	41
Type 5	<i>Potentilla freyniana</i>	perennial	0	0	0	0	41
Type 5	<i>Lysimachia japonica</i> var. <i>subsessilis</i>	perennial	1	0	0	0	28
Type 5	<i>Aster scaber</i>	perennial	0	0	0	0	30
Type 5	<i>Thalictrum minus</i> var. <i>hypoleucum</i>	perennial	0	0	0	0	12
Type 5	<i>Oxalis corniculata</i>	perennial	0	0	0	0	18
Type 5	<i>Clematis terniflora</i>	perennial	0	0	0	0	18
Type 5	<i>Geum japonicum</i>	perennial	0	0	0	0	18
Type 5	<i>Scilla scilloides</i>	perennial	0	0	0	0	18
Type 5	<i>Arundinella hirta</i>	perennial	0	0	0	0	18
Type 5	<i>Angelica decursiva</i>	perennial	0	0	0	0	18
Type 5	<i>Hydrocotyle maritima</i>	perennial	0	0	0	0	18
Type 5	<i>Eupatorium makinoi</i> var. <i>oppositifolium</i>	perennial	0	0	0	0	12
Type 5	<i>Deparia pseudoconilii</i> var. <i>pseudoconilii</i>	perennial	0	0	0	0	18
Type 5	<i>Miscanthus sacchariflorus</i>	perennial	0	0	0	0	14
Type 5	<i>Euphorbia pekinensis</i> var. <i>onoei</i>	perennial	0	0	0	0	14
Type 5	<i>Astilbe microphylla</i>	perennial	0	0	0	0	14
Type 5	<i>Cirsium nipponicum</i> var. <i>incomptum</i>	perennial	0	0	0	0	14
Type 5	<i>Duchesnea chrysantha</i>	perennial	0	0	0	0	14

Type 5	<i>Campanula punctata</i>	perennial	0	0	0	0	14
Type 5	<i>Gentiana scabra</i> var. <i>buergeri</i>	perennial	0	0	0	0	14

* Habitat Type 1: intensive management sites (IM) in crest slope (CS), upper side slope (USS) and lower side slope (LSS); Type 2: moderate management sites (MM) in CS, USS and LSS; Type 3: no management sites (NM) in CS, USS and LSS; Type 4: head hollow sites (HH) regardless of management regimes; Type 5: highly intensive management sites (HM) in LSS.

** Indicator values were calculated as relative abundance \times relative frequency \times 100 for each species in each group (see McCune and Mefford 1999).

Table 5. Dissimilarity matrix of within- or between-habitat type calculated for every pair of quadrats (14 028 combinations) by Sørensen's index. Mean \pm S.D. and the number of combinations in parentheses are shown.

	Habitat Type 1	Habitat Type 2	Habitat Type 3	Habitat Type 4	Habitat Type 5
Habitat Type 1	0.551 \pm 0.101 (946)				
Habitat Type 2	0.721 \pm 0.083 (1980)	0.589 \pm 0.101 (990)			
Habitat Type 3	0.775 \pm 0.087 (1188)	0.710 \pm 0.096 (1215)	0.607 \pm 0.126 (351)		
Habitat Type 4	0.781 \pm 0.081 (1320)	0.703 \pm 0.104 (1350)	0.731 \pm 0.109 (810)	0.634 \pm 0.146 (435)	
Habitat Type 5	0.746 \pm 0.109 (968)	0.799 \pm 0.092 (990)	0.862 \pm 0.086 (594)	0.821 \pm 0.085 (660)	0.739 \pm 0.133 (231)