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**Urban shade as a cryptic habitat: Fern distribution in building gaps in
Sapporo, northern Japan**

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Abstract

Biodiversity conservation and restoration in cities is a global challenge for the 21st century. Unlike other common ecosystems, urban landscapes are predominantly covered by gray, artificial structures (e.g., buildings and roads), and remaining green spaces are scarce. Therefore, to conserve biodiversity in urban areas, understanding the potential conservation value of artificial structures is vital. Here, we examined factors influencing the distribution of ferns in building gaps, one of the more common artificial structures, in urban Sapporo, northern Japan. We observed 29 fern species, which corresponds to 30% of all fern species previously recorded in Sapporo. The four dominant species were *Equisetum arvense*, *Matteuccia struthiopteris*, *Dryopteris crassirhizoma* Nakai, and *Athyrium yokoscense*. Statistical analyses showed that their distribution patterns in building gaps were associated with both local- and landscape-scale environmental factors. Although ground cover type and distance from continuous forests were the most important determinants, other factors such as the amount of solar radiation, habitat age (years after building development), and urban district type also affected fern distribution. These results suggest that building gaps act as an important habitat for ferns in highly urbanized landscapes. Policy makers and city planners should therefore not overlook these cryptic habitats. Clarifying the ecological functions of artificial structures will both further our understanding of novel ecosystems and develop a new framework for conserving and restoring biodiversity in human-modified landscapes.

Keywords: Building gaps; Ground cover; Isolation effect; Novel ecosystems; Urban matrix; Urban maturation

Introduction

Urbanization is one of the main causes of global biodiversity decline in the 21st century (McKinney 2002; Grimm et al. 2008). Although urban areas around the world arguably represent the most intensive land-use type (Foley et al. 2005), they have potentially high ecological value for regional biological communities (Imhoff et al. 2004; Yamaura et al. 2011). Indeed, the distributions of rare and endemic plants and animals are often spatially overlapped with urbanized areas (e.g., Kowarik 2011). Urban biodiversity is also essential for the maintenance and improvement of human well-being and health (Fuller et al. 2007; Irvine et al. 2013). Even in urban areas, contact with nature has a crucial role in engaging and reconnecting people with the natural world (i.e., preventing the “extinction of experience”; Miller and Hobbs 2002; Miller 2005). Consequently, increasing attention has been given to the conservation and restoration of biodiversity in urban areas (Dearborn and Kark 2009).

Nonetheless, conserving and restoring biological diversity in urban areas is challenging (Blair 1996; McKinney 2002; Stagoll 2010), largely because green spaces, vital habitats for urban wildlife (Ikin 2013; Soga et al. 2014), are typically scarce in urbanized areas (Fuller and Gaston 2009). Rather, large portions of the landscape are dominated by artificial structures (e.g., roads, houses and high-rises; so-called “gray infrastructure”) that do not exist in natural ecosystems. This drastic land-use modification greatly alters both abiotic and biotic conditions (Gaston 2010), and makes urban landscapes a “novel ecosystem” (Hobbs et al. 2006; Faeth et al. 2011). Therefore, to successfully conserve biodiversity in urban areas, focusing on the conservation value of remaining green spaces is insufficient. However, as such a green space-based

approach has long been the standard in urban ecological studies (Alvey 2006), the potential ecological roles of artificial structures are mostly unknown.

Building gaps are common in urban environments (Moonen et al. 2012), and in Japan, their size and other attributes are often legally determined by various safety and aesthetic considerations (e.g., fire safety and shading of nearby buildings; The Building Standard Law of Japan 2013). In the city of Sapporo, the total area of building gaps (1,368 ha, calculated by multiplying the perimeter distance of all buildings by an average gap width of 0.6 m; The Geographical Survey Institute 2011; see Fig. 1) amounts to 60% of that of all public green spaces in the city. Given the spatial extent of building gaps in the urban matrix (Fig. 1), understanding their potential conservation value represents a potentially important opportunity to conserve urban biodiversity (Goddard et al. 2010). In particular, as building gaps are generally not managed after development, they are likely to act as “cryptic habitats” hidden in urban environments.

Ferns are a suitable taxon with which to investigate the ecological roles of building gaps for several reasons. First, ferns occupy even tiny microhabitats within urban areas (e.g., stone- and roadside walls; Murakami et al. 2007; Murakami and Morimoto 2008). Second, because the environmental conditions of building gaps are often similar to those of natural fern habitats (i.e., shady environments), building gaps are likely habitats for several fern species. Third, since ferns disperse efficiently via small, lightweight spores (Barrington 1993), they can colonize many potentially suitable habitats despite landscape-scale factors affecting their distributions (Faria et al. 2007).

Here, we investigated factors affecting the distribution of ferns in building gaps in

Sapporo, northern Japan. Results showed the general prevalence of ferns in building gaps and that fern distribution was influenced by a combination of local- and landscape-scale environmental factors. Based on these results, we suggest that clarifying the ecological roles of cryptic habitats hidden in urban areas would enhance our understanding of urban ecosystems and further the development of novel conservation methods.

Methods

Study area and site selection

All fieldwork was conducted in Sapporo, Hokkaido, northern Japan. Sapporo is densely populous, with nearly 2,000,000 people in an area of only 1,121 km² (Sapporo City Statistical Report 2012). Sapporo is located in southwest Hokkaido on the Ishikari Plain. Annual mean air temperature and total annual precipitation in the region are 8.5°C and 1,007 mm, respectively. A continuous forest in southwestern Sapporo accounts for 63% (706 km²) of the overall green space in the city (Greenery Promotion Department, Environmental Bureau, Sapporo 2011). Ninety fern species were found in Sapporo city including our study area and surrounding forest areas (Hara 1992). Almost all these species are forest species, and the surrounding forests can be source habitats for the habitats in the urban area.

In our study area, all residential areas were categorized into land-use districts (hereafter called district types) according to the ratio of the building footprint area to the total floor area (The Building Standard Law of Japan 2013). In Japan, district types are

normally classified into 12 types: 7 residential, 3 industrial, and 2 commercial. In this study, we randomly selected 85 study sites, each of approximately 200 m², covering as wide a range of district types as possible, and with each study site comprising one district type only (Fig. 2; Table 1).

Field surveys

Field surveys were conducted from June to August 2013. We established survey plots at all accessible building gaps, excluding those that were artificially managed. To determine whether building gaps were artificially managed, we also conducted interviews for residents. We recorded all fern species in each survey plot (i.e., building gaps) based on Asano and Kuwabara (1990) and Iwatsuki (1992) and Kurata and Nakaike (1997), excluding artificially landscaped areas. When it was difficult to identify the plant species occurring the plots, we collected specimen, and identified them in the laboratory. We also recorded two local-scale environmental factors: ground cover type and habitat age (years after building development). Ground cover was classified into one of three categories: gravel (class 1, particle size >11 mm), soil (class 2, <10 mm), and bryophytes (class 3). These categories are rough proxies for ground humidity, whereby gravel is likely to be least humid, soil is intermediate, and bryophytes are most humid. Habitat age was also classified into four categories: less than 10 years (class 1); 11-20 years (class 2); 21-30 years (class 3); and >31 years (class 4). We established survey plots so that each plot contained uniform ground cover types and habitat ages. Plot area and the number of survey plots per study site ranged from 1.0 to 27.0 m² (mean 4.7 ± 2.7 SD), and from 5 to 37 plots (mean 27.9 ± 6.3 SD, total 2,373),

respectively.

GIS analyses

We calculated the amount of solar radiation and the distance from continuous forest for each study site using Geographical Information System software [ArcGIS 10.0; Environmental Systems Research Institute (ESRI), Redlands, CA 2011]. To calculate the amount of solar radiation, we used laser profiler data provided by the Hokkaido Development Bureau (hereafter called LP data). LP data are topographical data measured by aerial laser surveys. Aerial laser surveys obtain three-dimensional spatial data by analyzing pulses emitted from an airborne laser as they reflect off the ground and return. The accuracy (standard deviation) of the original data is <25 cm horizontally. We used the original LP data without removing structures (e.g., houses, office buildings). We assumed the surface of each structure was flat, and used the building height as the maximum value of laser point. Then, we created 0.5-m resolution digital surface models (DSMs) of our survey areas. To calculate the amount of solar radiation (the sum of direct solar radiation and sky solar radiation) during the field survey, we used ArcGIS Spatial Analyst tools and our DSMs, assuming the solar radiation levels on July 1, 2013 (from 4.1 to 5829.6, mean 2459.4 ± 1160.6 SD). We defined the solar radiation of each plot as the maximum radiation value for that plot. For each survey plot, we also measured the straight-line distance from the nearest continuous forest (Fig. 2).

Statistical analyses

We examined the occurrence probabilities of four fern species found in >5% (120 plots) of all survey plots: *Equisetum arvense* L. (Fig.3a), *Matteuccia struthiopteris* (L.) Tod. (Fig.3b), *Dryopteris crassirhizoma* Nakai (Fig.3c), and *Athyrium yokoscense* (Franch. et Sav.) H. Christ (Fig.3d: see also Appendix 1). These four fern species differ markedly in their habitat preferences (*E. arvense*: roadsides, *M. struthiopteris*: grasslands, *D. crassirhizoma*: forest floors, *A. yokoscense*: forest edges; Asano and Kuwabara 1990; Iwatsuki 1992; Kurata and Nakaike 1997). Additionally, we grouped another 25 observed species into a single group (hereafter called OTHERS25, and for convenience, referred to as a fifth “collective” fern species) and examined its collective occurrence probability in later analyses. All 25 species in this group have similar woodland habitat preferences (Asano and Kuwabara 1990; Iwatsuki 1992; Kurata and Nakaike 1997).

All analyses were performed in R version 3.0.2 (R Core Team 2013). To investigate the effect of each environmental variable on the occurrence probabilities of the five fern species (four major species and OTHERS25), we used generalized linear mixed models (GLMMs) with the ‘glmer’ function in the lme4 package (Bates and Sarkar 2007). Ground cover types (classes 1-3), habitat age (classes 1-4), district types (classes 1-5; see Table 2), the amount of solar radiation, and the distance from continuous forest were used as continuous explanatory variables. To control for the effects of site-specific factors, we used site ID (85 sites) as a random effect.

In this study, survey plot size varied among the study plots (min 1.0, max 27.0 m²). Thus, even if the occurrence probability of a fern species per unit of area is

constant, the plot-level occurrence probability changes with plot area. Therefore, we assumed that the number of individuals followed a Poisson distribution and used the probability that at least one individual occurs at each survey plot (“occurrence probability” hereafter) as a response variable. We used a complementary log-log link function (c-loglog; McCullagh and Nelder 1989), with survey plot area as an offset term to account for differences in area among survey plots:

$$\text{Prob}(N_i \geq 1) = 1 - \exp[-\exp(\beta_0 + \boldsymbol{\beta} \mathbf{x}_i + \log(A_i))], \quad (\text{Equation 1})$$

where N_i is the number of individuals in plot i and $\text{Prob}(N_i \geq 1)$ is the probability that at least one individual occurs in plot i (i.e., the occurrence probability). β_0 is the model intercept, while $\mathbf{x}_i$ and $\boldsymbol{\beta}$ are covariates of plot i and their coefficients, respectively. A_i is the area of plot i and $\log(A_i)$ is an offset term, whose coefficient we fixed as 1. The random effect is not shown in this equation.

The five explanatory variables were not highly correlated with each other ($|r| < 0.31$; Appendix 2). We built full models, including all five explanatory variables (ground cover type, habitat age, district type, the amount of solar radiation, and distance from continuous forests) for each species. Using the coefficients derived from the full models, we plotted the occurrence probabilities as predicted by each of the five explanatory variables. Although ground cover type, habitat age, and district type were not **strictly** continuous values, we included their predicted curves for convenience.

Results

In 2,373 study plots (building gaps), we observed 29 fern species (mean $0.87 \pm$

0.80 SD, range: 0-8). All of them were native species in Japan, and no endangered species were included. Although there were two open-land species (*E. arvense* and *M. struthiopteris*), main habitats of the other species were forests. The four most commonly observed species were *E. arvense* (observed in 54% of our study plots), *M. struthiopteris* (8%), *D. crassirhizoma* (6%), and *A. yokoscense* (6%) (Appendix 1).

Landscape-scale environmental factors

For *D. crassirhizoma*, the highest occurrence probabilities were predicted in category 5 districts, whereas those of *E. arvense* were predicted in category 1 districts (Fig.4; Tables 1, 2). The probability of *E. arvense* occurrence increased significantly with increasing distance from continuous forest, whereas those of the other four fern species significantly decreased (Fig.4; Table 2).

Local-scale environmental factors

Ground cover types significantly affected the occurrence probabilities of all five fern species. *Equisetum arvense* occurrence probabilities were highest in gravel-covered plots, whereas those of the four other species were highest in plots with bryophyte cover (Fig.4; Table 2). Furthermore, *E. arvense* and *A. yokoscense* occurrence probabilities increased significantly with increasing habitat age (Fig.4; Table 2). *Athyrium yokoscense*, *D. crassirhizoma*, and OTHERS²⁵ occurrence probabilities were all negatively related to the amount of solar radiation (Fig.4; Table 2).

Discussion

To our knowledge, this is the first study to demonstrate the ecological importance of building gaps, which represent large portions of the urban landscape (Fig. 1). Overall, our results show that the distribution of ferns in urban building gaps was influenced by both local- and landscape-scale environmental factors. We observed 29 fern species in our field surveys, which represent 30% of all fern species previously recorded in Sapporo City (90 species; Hara 1992). Furthermore, the most common species, *E. arvense*, was found in more than half of the building gaps. These results suggest that building gaps potentially function as wildlife habitats even in highly urbanized landscapes, showing important implications for the conservation and restoration of biodiversity where most natural areas have already been lost (Fuller and Gaston 2009). Artificial structures such as building gaps have been dismissed as gray infrastructure (inhospitable habitat matrices surrounding focal green spaces), and their conservation values largely overlooked (Bengston et al. 2004). This is partly because, as the majority of building gaps fall on private property, normal statutory management options do not apply (Norton 2000). However, since creating and maintaining new green spaces in urban areas is costly (Naidoo et al. 2006), conservation programs focusing on artificial structures may represent a cost-effective and worthwhile alternative (cf. “urban reconciliation ecology”; Rosenzweig 2001; Francis and Lorimer 2011).

In this study, the occurrence probabilities of *M. struthiopteris*, *D. crassirhizoma*, *A. yokoscense*, and OTHERS25 were negatively related to their distance from continuous forest, suggesting that continuous forests surrounding urban areas act as source habitats for ferns, which is consistent with studies on other taxa (e.g., butterflies:

Soga and Koike 2013; amphibians: Fuyuki et al. 2014; birds: Natuhara and Imai 1999). On the other hand, the probability of *E. arvense* occurrence was positively related to its distance from continuous forest. This contrasting distribution of *E. arvense* can be explained by the species' ecology. Unlike other ferns, *E. arvense* is adapted to sunny and dry habitats such as agricultural or cleared lands, and roadsides (Williams 1979; Andersson and Lundegårdh 1999). In our study areas, these open lands are usually found some distance from continuous forests (K. Kajihara, unpublished data), likely explaining our result.

Fern distribution was also affected by district type. For *D. crassirhizoma*, the highest occurrence probabilities occurred in the most urbanized district type (category 5 districts). This was unexpected, since *D. crassirhizoma* is a woodland species usually found on the forest floor (Asano and Kuwabara 1990; Iwatsuki 1992, Kurata and Nakaike 1997). One potential explanation is that tall buildings acted like the forest canopy, creating a shaded microenvironment similar to the forest floor (cf. Decandido and Allen 2006).

In addition to landscape-scale environmental factors, local-scale factors (ground cover type, the amount of solar radiation, and habitat age) also affected fern distributions. The occurrence probabilities of *D. crassirhizoma*, *M. struthiopteris*, *A. yokoscense*, and OTHERS25 were higher in relatively shady plots and plots with significant bryophyte cover (i.e., more moisture; Fig.4). Bryophyte cover may help to retain ground moisture (Pharo et al. 1999), and consequently to facilitate fern growth. Solar radiation is detrimental to fern persistence because it causes habitat desiccation (Richard et al. 2000). Therefore, it is not surprising that both ground cover type and the

amount of solar radiation have strong effects on fern distribution (Fig.4).

Habitat age also influenced fern distribution patterns. The occurrence probabilities of both *E. arvense* and *A. yokoscense* were positively related to habitat age (Fig.4), suggesting that the colonization and establishment of ferns in building gaps may take considerable time, as seen in the range expansion of other exotic species (Sakai et al. 2001). This result raises the possibility that populations of some species can recover as urban ecosystems mature (cf. Yamaura et al. 2012). This is an important point, as urban biological communities are usually thought to degrade as cities age (Hahs et al. 2009; Soga et al. 2013). Urban biological communities likely have longer-term, more complex dynamics than previously thought (Ramalho and Hobbs 2012).

At present, cities around the world are expanding and becoming denser (Seto et al. 2012). Indeed, the number of mega cities (cities with more than 10 million people) has increased more than tenfold in the past 50 years (United Nations 2011), which suggests that the world's ecosystems are changing toward more human-built, modified, and engineered systems. We show that even in highly modified landscapes, artificial structures can harbor and even create suitable habitat, and that both local- and landscape-level factors affect their function. Therefore, to conserve and restore urban biodiversity, city planners and policy makers should not overlook the conservation potential of these cryptic habitats that are “hidden in plain sight.” Although we studied only ferns in building gaps, other types of artificial structures (e.g., drainage channels and stone masonry) likely act as cryptic habitats for other taxa. Clarifying the potential ecological functions of artificial structures in urban areas will lead not only to a better understanding of novel urban ecosystems (Hobbs et al. 2006), but to a novel framework

for conserving and restoring urban biodiversity.

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Figure legends

Fig. 1. The amount of solar radiation across Sapporo. Square structures and areas with low solar radiation indicate buildings and building gaps, respectively. Inserts contain detailed photographs of the study sites

Fig. 2. Study area, including the locations of the 85 study sites, and a representative photograph of a survey site.

Fig. 3. Representative habitats in Sapporo urban area for four main fern species.

(a) *Equisetum arvense* L., (b) *Matteuccia struthiopteris* (L.) Tod., (c) *Dryopteris crassirhizoma* Nakai, (d) *Athyrium yokoscense* (Franch. et Sav.) H.Christ.

Fig.4. Relationships between the occurrence probabilities of five fern species and ground cover type, habitat age, district type, solar radiation, and distance from continuous forest. Predicted lines were derived from generalized linear mixed models (GLMMs; see details in the main text). Solid and broken lines indicate significant ($P < 0.05$) and non-significant effects, respectively, of each explanatory variable. In producing these figures, we used the appropriate mean values for plot area and the environmental variables, and zero for the random effects.

Table legends

Table 1. Definitions of district types used in this study.

Table 2. Coefficients and standard errors (SEs) of five environmental variables in the generalized linear mixed models (GLMMs) for five fern species. Standard deviations of each model are also shown.

Supporting information

Appendix 1. A list of 29 fern species observed in this study.

Appendix 2. Pearson’s correlations for environmental variables (ground cover types, habitat age, district types, amount of solar radiation, and distance from continuous forest).

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Fig. 4 Relationships between the occurrence probabilities of five fern species and ground cover type, habitat age, district type, solar radiation, and distance from continuous forest.

479 **Table 1.** Definitions of district types used in this study.

Categories	Building to land ratio ¹	Floor area ratio ²	District type	# plots
1	40	80	category 1 low rise-rise exclusive residential districts, category 2 low-rise exclusive residential districts	1363
2	50	80	category 1 medium-to-high-rise exclusive residential districts, category 2 medium-to-high-rise exclusive residential districts, category 1 residential districts, category 2 residential districts, quasi-residential districts	574
3	60	200	quasi-industrial districts, industrial districts	194
4	80	200 ~ 300	neighborhood commercial districts	112
5	80	400 ~ 800	commercial districts	130

480 From the Building Standard Law of Japan

481 ¹ Proportion of the area covered by the buildings

482 ² The ratio of the area to total building floor

483

Table 2. Coefficients and standard errors (SEs) of five environmental variables in the generalized linear mixed models (GLMMs) for five fern species.

a) Parameter estimates of regression analysis						
Fixed effects:		<i>E. arvense</i>	<i>M. struthiopteris</i>	<i>D. crassirhizoma</i>	<i>A. yokoscense</i>	OTHERS25
Intercept	Estimate	-1.356	-5.239	-5.68	-5.4	-4.328
	SE	0.2011	0.4273	0.05005	0.5183	0.3878
		$p < 0.001$	$p < 0.001$	$p < 0.001$	$p < 0.001$	$p < 0.001$
Ground cover	Estimate	-0.1585	0.7574	0.9801	0.6396	0.8312
	SE	0.04822	0.09621	0.1109	0.1156	0.08834
		$p < 0.01$	$p < 0.001$	$p < 0.001$	$p < 0.001$	$p < 0.001$
Habitat age	Estimate	0.1025	0.03681	0.05118	0.2573	0.06525
	SE	0.04001	0.09629	0.1124	0.1165	0.08854
		$p < 0.05$			$p < 0.05$	
District type	Estimate	-0.4192	0.06566	0.2432	0.03334	-0.04371
	SE	0.05939	0.09281	0.1039	0.1066	0.08922
		$p < 0.001$		$p < 0.05$		
Amount of solar radiation	Estimate	0.00003898	-0.00001032	-0.0002966	-0.0002854	-0.000228
	SE	0.00003111	0.00007241	0.00009193	0.00009522	0.00006876
				$p < 0.01$	$p < 0.01$	$p < 0.001$
Distance from continuous forest	Estimate	0.00005139	-0.0001108	-0.0001432	-0.000101	-0.0001802
	SE	0.00001804	0.00003636	0.00004803	0.00004349	0.00003718
		$p < 0.01$	$p < 0.01$	$p < 0.01$	$p < 0.05$	$p < 0.001$
Random effects: site = 85	SD	0.4774	0.5792	0.6716	0.6396	0.5389

b) Ranges of environmental variables	Min	Max	Mean	SD
Area	1	27.04	4.745	2.746
Ground cover	1	3	1.521	0.727
Habitat age	1	4	2.641	0.866
District type	1	5	1.766	1.133
Amount of solar radiation	4.151	5830	2459	1160.624
Distance from continuous forest	16.6	13780	4191	3285.057

Appendix 1. A list of 29 fern species observed in this study.

No.	Family	Species	# plots ¹	Proportion ²
1	Equisetaceae	<i>Equisetum arvense</i> L.	1292	54.38
2	Athyriaceae	<i>Matteuccia struthiopteris</i> (L.) Tod.	190	8.00
3	Dryopteridaceae	<i>Dryopteris crassirhizoma</i> Nakai	143	6.12
4	Woodsiaceae	<i>Athyrium yokoscense</i> (Franch. et Sav.) H.Christ	133	5.57
5	Woodsiaceae	<i>Onoclea orientalis</i> (Hook.) Hook.	58	2.43
6	Woodsiaceae	<i>Athyrium melanolepis</i> (Franch. et Sav.) H.Christ	56	2.39
7	Equisetaceae	<i>Equisetum palustre</i> L.	33	1.38
8	Thelypteridaceae	<i>Thelypteris palustris</i> (Salisb.) Schott	28	1.17
9	Woodsiaceae	<i>Deparia conilii</i> (Franch. et Sav.) M.Kato	27	1.13
10	Woodsiaceae	<i>Athyrium vidalii</i> (Franch. et Sav.) Nakai	18	0.75
11	Woodsiaceae	<i>Athyrium deltoideofrons</i> Makino	17	0.71
12	Aspleniaceae	<i>Asplenium incisum</i> Thunb.	11	0.50
13	Dennstaedtiaceae	<i>Pteridium aquilinum</i> var. <i>latiusculum</i>	11	0.46
14	Thelypteridaceae	<i>Thelypteris phegopteris</i> (L.) Sloss. ex Rydb.	6	0.25
15	Woodsiaceae	<i>Athyrium niponicum</i> (Mett.) Hance	6	0.25
16	Dennstaedtiaceae	<i>Dennstaedtia wilfordii</i> (T.Moore) H.Christ ex C.Chr.	4	0.17
17	Dryopteridaceae	<i>Polystichum polyblepharon</i> (Roem. ex Kunze) C.Presl	4	0.17
18	Thelypteridaceae	<i>Thelypteris nipponica</i> (Franch. et Sav.) Ching	3	0.13
19	Onocleaceae	<i>Onoclea sensibilis</i> L. var. <i>interrupta</i> Maxim.	3	0.13
20	Thelypteridaceae	<i>Stegnogramma pozoi</i> (Lag.) K.Iwats. subsp. <i>mollissima</i> (Fisch. ex Kunze) K.Iwats.	3	0.13
21	Woodsiaceae	<i>Deparia pycnosora</i> var. <i>mucilagina</i>	2	0.08
22	Woodsiaceae	<i>Woodsia manchuriensis</i> Hook.	2	0.08
23	Osmundaceae	<i>Osmunda cinnamomea</i> L.	1	0.04
24	Woodsiaceae	<i>Deparia pseudoconilii</i> (Seriz.) Seriz.	1	0.04
25	Blechnaceae	<i>Blechnum niponicum</i> (Kunze) Makino	1	0.04
26	Dryopteridaceae	<i>Arachniodes standishii</i> (T.Moore) Ohwi	1	0.04

27	Woodsiaceae	<i>Athyrium x multifidum</i> Rosenst.	1	0.04
28	Woodsiaceae	<i>Cornopteris crenulatoserrulata</i> (Makino) Nakai	1	0.04
29	Lycopodiaceae	<i>Lycopodium clavatum</i> L.	1	0.04

¹ Number of plots at which each species occurred.

² Proportions of plots at which each species occurred among the 2,373 plots.

We used scientific names following “YList” <http://bean.bio.chiba-u.jp/bgplants/index.html>.

Appendix 2. Pearson's correlations for environmental variables (ground cover types, habitat age, district types, amount of solar radiation, and distance from continuous forest).

	Habitat age	Ground cover type	District type	Amount of solar radiation
Ground cover type	0.22			
District type	0.09	0.06		
Amount of solar radiation	-0.10	-0.06	-0.31	
Distance from continuous forest	-0.02	-0.10	0.09	-0.08