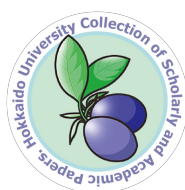




Title	Urban shade as a cryptic habitat : fern distribution in building gaps in Sapporo, northern Japan
Author(s)	Kajihara, Kazumitsu; Yamaura, Yuichi; Soga, Masashi et al.
Citation	Urban ecosystems, 19(1), 523-534 https://doi.org/10.1007/s11252-015-0499-8
Issue Date	2016-03
Doc URL	https://hdl.handle.net/2115/64616
Rights	The final publication is available at link.springer.com
Type	journal article
File Information	UE19-1_523-534.pdf



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

*Kazumitsu Kajihara¹, Yuichi Yamaura^{1, 2}, Masashi Soga¹, Yasuto Furukawa¹, Junko Morimoto¹, and Futoshi Nakamura¹

¹*Graduate School of Agriculture, Hokkaido University, 9 Kita, 9 Nishi, Kita-ku, Sapporo 060-8589, Japan*

²*Department of Forest Vegetation, Forestry and Forest Products Research Institute, 1 Matsunosato, Tsukuba, Ibaraki 305-8687, Japan*

*Corresponding author

Tel.: +81 11 706 3343.

E-mail addresses: gkbdk629@gmail.com (K. Kajihara).

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

36 **Introduction**

37 Urbanization is one of the main causes of global biodiversity decline in the 21st
38 century (McKinney 2002; Grimm et al. 2008). Although urban areas around the world
39 arguably represent the most intensive land-use type (Foley et al. 2005), they have
40 potentially high ecological value for regional biological communities (Imhoff et al.
41 2004; Yamaura et al. 2011). Indeed, the distributions of rare and endemic plants and
42 animals are often spatially overlapped with urbanized areas (e.g., Kowarik 2011). Urban
43 biodiversity is also essential for the maintenance and improvement of human well-being
44 and health (Fuller et al. 2007; Irvine et al. 2013). Even in urban areas, contact with
45 nature has a crucial role in engaging and reconnecting people with the natural world (i.e.,
46 preventing the “extinction of experience”; Miller and Hobbs 2002; Miller 2005).
47 Consequently, increasing attention has been given to the conservation and restoration of
48 biodiversity in urban areas (Dearborn and Kark 2009).

49 Nonetheless, conserving and restoring biological diversity in urban areas is
50 challenging (Blair 1996; McKinney 2002; Stagoll 2010), largely because green spaces,
51 vital habitats for urban wildlife (Ikin 2013; Soga et al. 2014), are typically scarce in
52 urbanized areas (Fuller and Gaston 2009). Rather, large portions of the landscape are
53 dominated by artificial structures (e.g., roads, houses and high-rises; so-called “gray
54 infrastructure”) that do not exist in natural ecosystems. This drastic land-use
55 modification greatly alters both abiotic and biotic conditions (Gaston 2010), and makes
56 urban landscapes a “novel ecosystem” (Hobbs et al. 2006; Faeth et al. 2011). Therefore,
57 to successfully conserve biodiversity in urban areas, focusing on the conservation value
58 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.

Acknowledgment

We are extremely grateful to the householders and landowners in Sapporo city who made their building gaps available. Thanks to M. Saitoh and Y. Shida for fern identification and K. Murakami for his helpful comments and discussion. We also thank J.T. Lundholm and an anonymous referee for their helpful comments on an earlier version of this manuscript. YY was supported by JSPS KAKENHI Grant no. 23248021 and MS partly by JSPS KAKENHI Grant no. 243222.

References

- Alvey AA (2006) Promoting and preserving biodiversity in the urban forest. *Urban Forest Urban Green* 5: 195-201.
- Andersson TN, Lundegårdh B (1999) Growth of field horsetail (*Equisetum arvense*) under low light and low nitrogen conditions. *Weed Sci* 47:41-46.
- Antrop M (2004) Landscape change and the urbanization process in Europe. *Landsc Urban Plan* 67: 9-26.
- Asano S, and Kuwabara Y (eds) (1990) The ecological encyclopedia of wild plants in Japan. Pteridophytes, Gymnosperms, and Angiosperms (Coripetalae). Zenkoku Noson Kyoiku Kyokai, Japan. [in Japanese]
- Barrington DS (1993) Ecological and historical factors in fern biogeography. *J Biogeogr* 20: 275-279.
- Baum KA, Haynes KJ, Dilleuth FP, Cronin JT (2004) The matrix enhances the effectiveness of corridors and stepping stones. *Ecology* 85: 2671-2676.
- Bengston DN, Fletcher JO, Nelson KC (2004) Public policies for managing urban growth and protecting open space: policy instruments and lessons learned in the United States. *Landsc Urban Plan* 69: 271-286.
- Blair RB (1996) Land use and avian species diversity along an urban gradient. *Ecol Appl* 6: 506-519.
- Cameron RW, Blanuša T, Taylor JE, Salisbury A, Halstead AJ, Henricot B, Thompson K (2012) The

domestic garden-Its contribution to urban green infrastructure. *Urban Forest Urban Green* 11:
129-137.

Dearborn DC, Kark S (2010) Motivations for conserving urban biodiversity. *Conserv Biol* 24: 432-440.

DeCandido R, Allen D (2006) Nocturnal hunting by peregrine falcons at the empire state building, New York City. *Wilson J Ornithol* 118: 53-58.

Faeth SH, Bang C, Saari S (2011) Urban biodiversity: patterns and mechanisms. *Ann NY Acad Sci* 1223: 69-81.

Faria D, Paciencia MLB, Dixo M, Laps RR, Baumgarten J (2007) Ferns, frogs, lizards, birds and bats in forest fragments and shade cacao plantations in two contrasting landscapes in the Atlantic forest, Brazil. *Biodivers Conserv* 16: 2335-2357.

Foley JA, DeFries R, Asner GP, Barford C, Bonan G, Carpenter SR, Chapin FS, Coe MT, Daily GC, Gibbs HK, Helkowski JH, Holloway T, Howard EA, Kucharik CJ, Monfreda C, Patz JA, Prentice IC, Ramankutty N, Snyder PK (2005) Global consequences of land use. *Science* 309: 570-574.

Francis RA, Lorimer J (2011) Urban reconciliation ecology: the potential of living roofs and walls. *J Environ Manage* 92: 1429-1437.

Fuller RA, Irvine KN, Devine-Wright P, Warren PH, Gaston KJ (2007) Psychological benefits of greenspace increase with biodiversity. *Biol Lett* 3: 390-394.

Fuller RA, Gaston KJ (2009) The scaling of green space coverage in European cities. *Biol Lett* 5: 352-355.

Fuyuki A, Yamaura Y, Nakajima Y, Ishiyama N, Akasaka T, Nakamura F (2014) Pond area and distance from continuous forests affect amphibian egg distributions in urban green spaces: A case study in Sapporo, Japan. *Urban Forest Urban Green* 13: 397-402.

Gaston KJ (eds) (2010) *Urban ecology*. Cambridge University Press.

Geographical Survey Institute (2011) Basic map information. Bigger than 1/2,500 scale maps. the outer peripheral lines constituting all buildings. [in Japanese].

Greenery Promotion Department, Environmental Bureau, Sapporo (2011) Basic Plan of Green in Sapporo. Greenery Promotion Department, Environmental Bureau, Sapporo, City of Sapporo, Hokkaido, Japan.

Goddard MA, Dougill AJ, Benton TG (2010) Scaling up from gardens: biodiversity conservation in urban environments. *Trends Ecol Evol* 25: 90-98.

Grimm NB, Faeth SH, Golubiewski NE, Redman CL, Wu J, Bai X, Briggs JM (2008) Global change and the ecology of cities. *Science* 319: 756-760.

Hahs AK, McDonnell MJ, McCarthy MA, Vesik PA, Corlett RT, Norton BA, Clemants SE, Duncan, RP, Thompson K, Schwartz MW, Williams NS (2009) A global synthesis of plant extinction

348 rates in urban areas. *Ecol Lett* 12: 1165-1173.
 349 Hara M (1992) *Flora of Sapporo*. Hokkaido University Press, Sapporo, Japan. [in Japanese].
 350 Hobbs RJ, Arico S, Aronson J, Baron JS, Bridgewater P, Cramer VA, Epstein PR, Ewel JJ, Klink CA,
 351 Lugo AE, Norton D, Ojima D, Richardson DM, Samderson EW, Valladares F, Vila M, Zamora
 352 R, Zobel M (2006) Novel ecosystems: theoretical and management aspects of the new
 353 ecological world order. *Glob Ecol Biogeogr* 15: 1-7.
 354 Ikin K, Beaty RM, Lindenmayer DB, Knight E, Fischer J, Manning AD (2013) Pocket parks in a
 355 compact city: how do birds respond to increasing residential density? *Landsc Ecol* 28: 45-56.
 356 Imhoff ML, Bounoua L, DeFries R, Lawrence WT, Stutzer D, Tucker CJ, Ricketts T (2004) The
 357 consequences of urban land transformation on net primary productivity in the United States.
 358 *Remote Sensing Environ* 89: 434-443.
 359 Irvine KN, Warber SL, Devine-Wright P, Gaston KJ (2013) Understanding urban green space as a
 360 health resource: A qualitative comparison of visit motivation and derived effects among park
 361 users in Sheffield, UK. *Int J Environ Res Public Health* 10: 417-442.
 362 Iwasa Y, Kubo T (1997) Optimal size of storage for recovery after unpredictable disturbances.
 363 *Evolutionary Ecology* 11: 41-65.
 364 Iwatsuki K (eds) (1999) *Ferns and fern allies of Japan*. Heibonsha *Ltd., Publishers*, Tokyo, Japan. [in
 365 Japanese].
 366 Kira T (1949) *Forest zones of Japan*. Ringyo Gizyutu Kyokai, Tokyo, Japan. [in Japanese].
 367 Kowarik I (2011) Novel urban ecosystems, biodiversity, and conservation. *Environ Pollut* 159: 1974-
 368 1983.
 369 Kurata S, Nakaike T (1997) *Illustrations of pteridophytes of Japan*. Vol. 1-8. Univ. of Tokyo Press.
 370 Tokyo, Japan [in Japanese].
 371 McCullagh P, Nelder JA (1989) *Generalized linear models* Second ed. CRC press, New York.
 372 McKinney ML (2002) Urbanization, Biodiversity, and Conservation The impacts of urbanization on
 373 native species are poorly studied, but educating a highly urbanized human population about
 374 these impacts can greatly improve species conservation in all ecosystems. *BioScience* 52: 883-
 375 890.
 376 Miller JR, Hobbs RJ (2002) Conservation where people live and work. *Conserv Biol* 16: 330-337.
 377 Miller JR (2005) Biodiversity conservation and the extinction of experience. *Trends Ecol Evol* 20:
 378 430-434.
 379 Moonen P, Defraeye T, Dorer V, Blocken B, Carmeliet J (2012) Urban Physics: effect of the micro-
 380 climate on comfort, health and energy demand. *Front Architect Res* 1: 197-228.
 381 Murakami K, Matsui R, Morimoto Y (2007) Northward Invasion and Range Expansion of the
 382 Invasive Fern *Thelypteris dentata* (Forssk.) St. John into the Urban Matrix of Three Prefectures
 383 in Kinki District, Japan. *Amer Fern J* 97: 186-198.

384 Murakami K, Morimoto Y (2008) Range Expansion of Two Tropical to Subtropical Ferns, Ladder
 385 Brake (*Pteris vittata* L.) and Lace Fern (*Microlepia strigosa* (Thunb. ex Murray) K. Presl.), in
 386 the Urban Osaka Bay Area, Western Japan. *Amer Fern J* 98: 171-176.
 387 Naidoo R, Balmford A, Ferraro PJ, Polasky S, Ricketts TH, Rouget M (2006) Integrating economic
 388 costs into conservation planning. *Trends Ecol Evol* 21: 681-687.
 389 Natuhara Y, Imai C (1999) Prediction of species richness of breeding birds by landscape-level
 390 factors of urban woods in Osaka Prefecture, Japan. *Biodivers Conserv* 8: 239-253.
 391 Norton DA (2000) Conservation biology and private land: shifting the focus. *Conserv Biol* 14: 1221-
 392 1223.
 393 Pharo EJ, Beattie AJ, Binns D (1999) Vascular plant diversity as a surrogate for bryophyte and lichen
 394 diversity. *Conserv Biol* 13: 282-292.
 395 Prugh LR, Hodges KE, Sinclair AR, Brashares JS (2008) Effect of habitat area and isolation on
 396 fragmented animal populations. *Proc Nat Acad Sci* 105: 20770-20775.
 397 Ramalho CE, Hobbs RJ (2012) Time for a change: dynamic urban ecology. *Trends Ecol Evol* 27:
 398 179-188.
 399 R Core Team (2013) R: A language and environment for statistical computing. R Foundation for
 400 Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>
 401 Richard M, Bernhardt T, Bell G (2000) Environmental heterogeneity and the spatial structure of fern
 402 species diversity in one hectare of old-growth forest. *Ecography* 23: 231-245.
 403 Rosenzweig ML (2001) Loss of speciation rate will impoverish future diversity. *Proc Nat Acad Sci*
 404 98: 5404-5410.
 405 Ruiters C, McKenzie B (1994) Seasonal allocation and efficiency patterns of biomass and resources
 406 in the perennial geophyte *Sparaxis grandiflora* subspecies *fimbriata* (Iridaceae) in lowland
 407 coastal fynbos, South Africa. *Ann Bot* 74: 633-646.
 408 Sakai AK, Allendorf FW, Holt JS, Lodge DM, Molofsky J, With KM, Baughman S, Cabin RJ,
 409 Cohen JE, Ellstrand NC, McCauley DE, O'Neil P, Parker IM, Thompson JN, Weller SG (2001)
 410 The population biology of invasive species. *Ann Rev Ecol Syst* 32: 305-332.
 411 Seto KC, Güneralp B, Hutrya LR (2012) Global forecasts of urban expansion to 2030 and direct
 412 impacts on biodiversity and carbon pools. *Proc Nat Acad Sci* 109: 16083-16088.
 413 Soga M, Koike S (2013) Patch isolation only matters for specialist butterflies but patch area affects
 414 both specialist and generalist species. *J For Res* 18: 270-278.
 415 Soga M, Yamaura Y, Koike S (2013) From ecological pessimism to conservation chance: reviving
 416 living dead in changing landscapes. *Anim Conserv* 16: 16-18.
 417 Soga M, Yamaura Y, Koike S, Gaston KJ (2014) Woodland remnants as an urban wildlife refuge: a
 418 cross-taxonomic assessment. *Biodivers Conserv* 23: 649-659.
 419 Stagoll K, Manning AD, Knight E, Fischer J, Lindenmayer DB (2010) Using bird-habitat

420 relationships to inform urban planning. *Landsc Urban Plan* 98: 13-25.
421 The Building Center of Japan (2013) The Building Standard Law of Japan.
422 Watling J I, Nowakowski AJ, Donnelly MA, Orrock JL (2011) Meta-analysis reveals the importance
423 of matrix composition for animals in fragmented habitat. *Glob Ecol Biogeogr* 20: 209-217.
424 Williams ED (1979) Studies on the depth distribution and on the germination and growth of
425 *Equisetum arvense* L. (field horsetail) from tubers. *Weed Res* 19: 25-32.
426 Yamaura Y, Amano T, Kusumoto Y, Nagata H, Okabe K (2011) Climate and topography drives
427 macroscale biodiversity through land-use change in a human-dominated world. *Oikos* 120: 427-
428 451
429 Yamaura Y, Oka H, Taki H, Ozaki K, Tanaka H (2012) Sustainable management of planted
430 landscapes: lessons from Japan. *Biodivers Conserv* 21: 3107-3129
431
432

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).

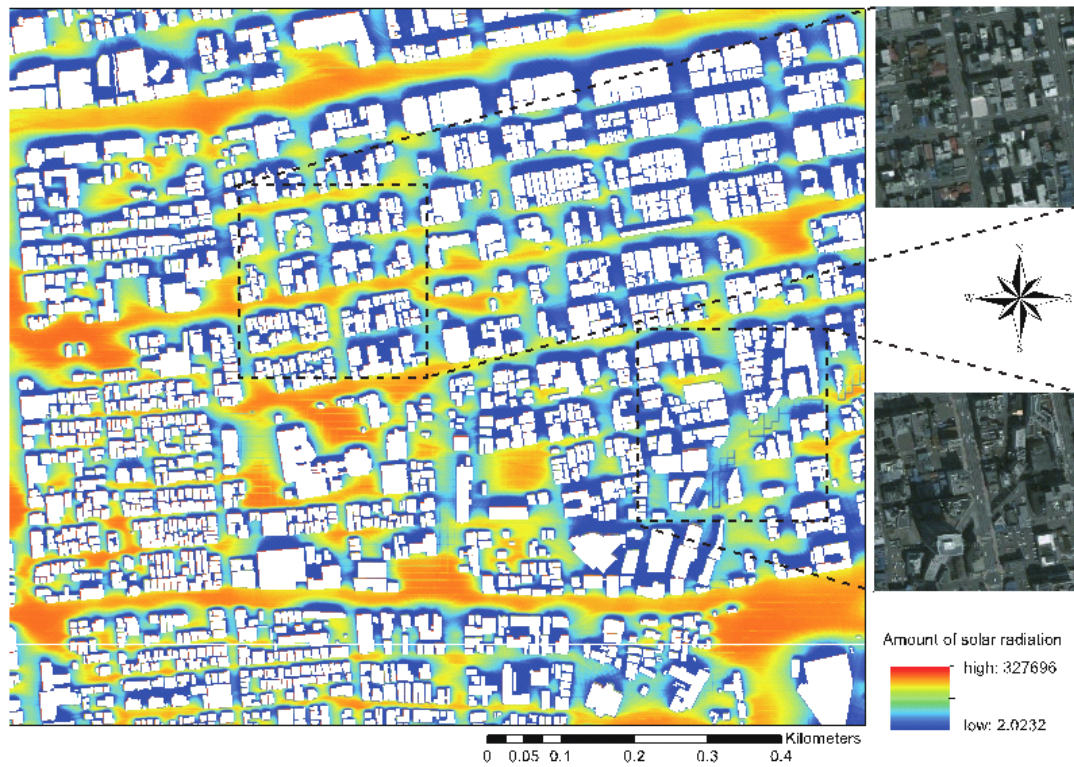


Fig. 1. The amount of solar radiation across Sapporo.

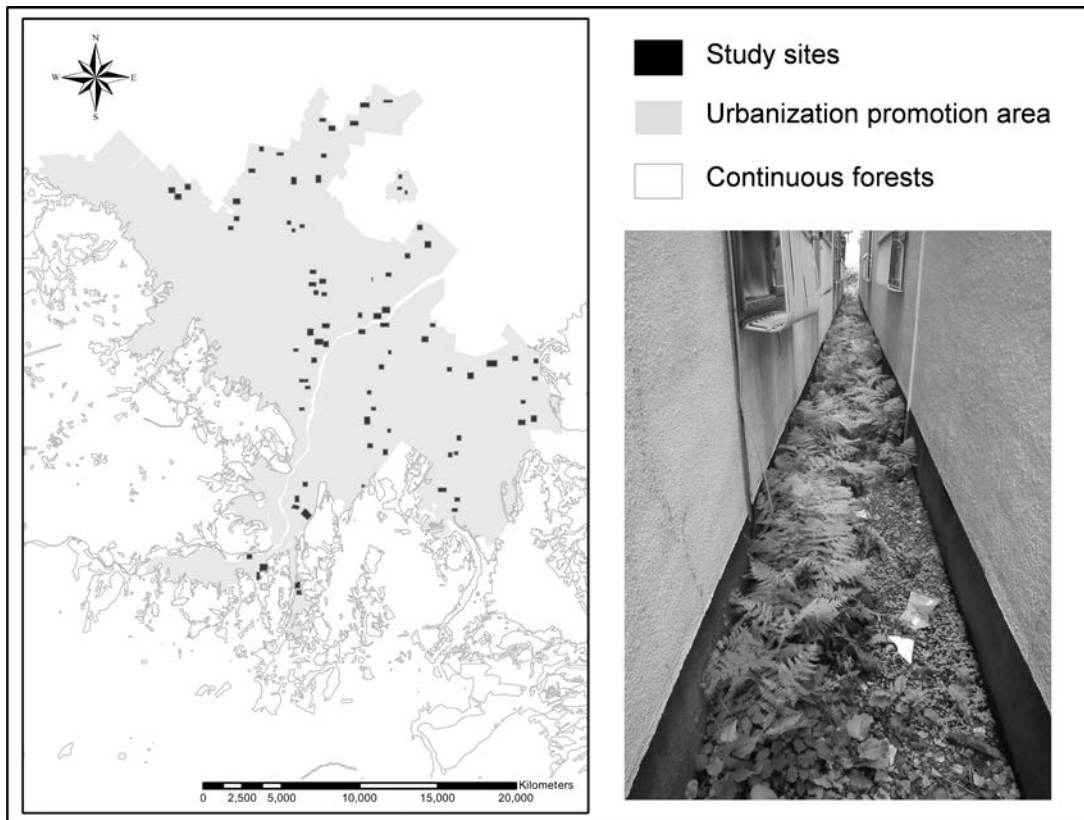


Fig. 2. Study area, including the locations of the 85 study sites, and a representative photograph of a survey site.



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.

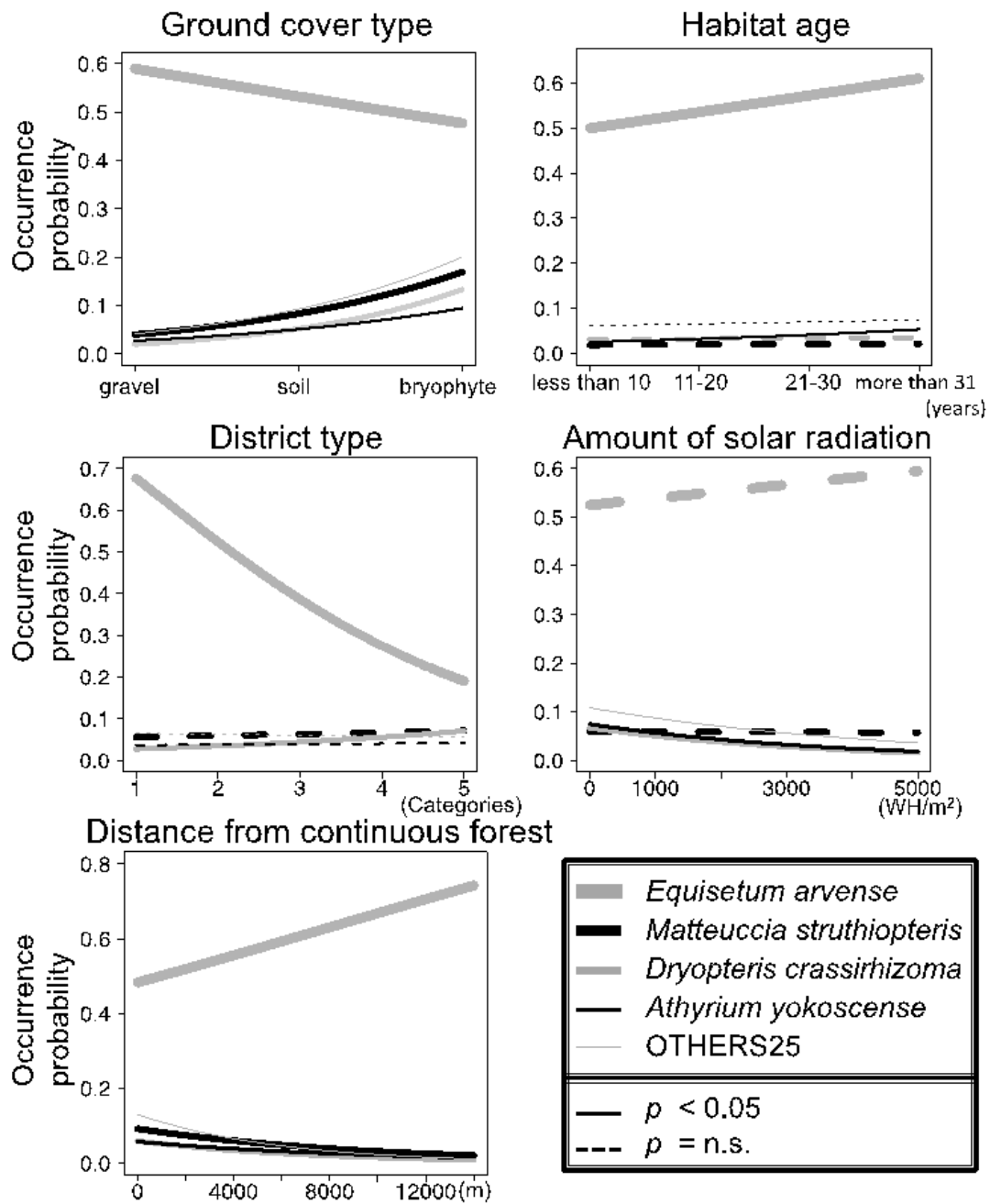


Fig. 4 Relationships between the occurrence probabilities of five fern species and ground cover type, habitat age, district type, solar radiation, and distance from continuous forest.

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 crenuloserrulata</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