



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

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12

13 **Abstract**

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

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

35

## 36 **Introduction**

37           Urbanization is one of the main causes of global biodiversity decline in the 21<sup>st</sup>  
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

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

61 Building gaps are common in urban environments (Moonen et al. 2012), and in  
62 Japan, their size and other attributes are often legally determined by various safety and  
63 aesthetic considerations (e.g., fire safety and shading of nearby buildings; The Building  
64 Standard Law of Japan 2013). In the city of Sapporo, the total area of building gaps  
65 (1,368 ha, calculated by multiplying the perimeter distance of all buildings by an  
66 average gap width of 0.6 m; The Geographical Survey Institute 2011; see Fig. 1)  
67 amounts to 60% of that of all public green spaces in the city. Given the spatial extent of  
68 building gaps in the urban matrix (Fig. 1), understanding their potential conservation  
69 value represents a potentially important opportunity to conserve urban biodiversity  
70 (Goddard et al. 2010). In particular, as building gaps are generally not managed after  
71 development, they are likely to act as “cryptic habitats” hidden in urban environments.

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

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

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

87

## 88 **Methods**

### 89 Study area and site selection

90 All fieldwork was conducted in Sapporo, Hokkaido, northern Japan. Sapporo is  
91 densely populous, with nearly 2,000,000 people in an area of only 1,121 km<sup>2</sup> (Sapporo  
92 City Statistical Report 2012). Sapporo is located in southwest Hokkaido on the Ishikari  
93 Plain. Annual mean air temperature and total annual precipitation in the region are 8.5°C  
94 and 1,007 mm, respectively. A continuous forest in southwestern Sapporo accounts for  
95 63% (706 km<sup>2</sup>) of the overall green space in the city (Greenery Promotion Department,  
96 Environmental Bureau, Sapporo 2011). *Ninety fern species were found in Sapporo city  
97 including our study area and surrounding forest areas (Hara 1992). Almost all these  
98 species are forest species, and the surrounding forests can be source habitats for the  
99 habitats in the urban area.*

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

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

107

### 108 Field surveys

109 Field surveys were conducted from June to August 2013. We established survey  
110 plots at all accessible building gaps, excluding those that were artificially managed. To  
111 determine whether building gaps were artificially managed, we also conducted  
112 interviews for residents. We recorded all fern species in each survey plot (i.e., building  
113 gaps) based on Asano and Kuwabara (1990) and Iwatsuki (1992) and Kurata and  
114 Nakaike (1997), excluding artificially landscaped areas. When it was difficult to identify  
115 the plant species occurring the plots, we collected specimen, and identified them in the  
116 laboratory. We also recorded two local-scale environmental factors: ground cover type  
117 and habitat age (years after building development). Ground cover was classified into  
118 one of three categories: gravel (class 1, particle size >11 mm), soil (class 2, <10 mm),  
119 and bryophytes (class 3). These categories are rough proxies for ground humidity,  
120 whereby gravel is likely to be least humid, soil is intermediate, and bryophytes are most  
121 humid. Habitat age was also classified into four categories: less than 10 years (class 1);  
122 11-20 years (class 2); 21-30 years (class 3); and >31 years (class 4). We established  
123 survey plots so that each plot contained uniform ground cover types and habitat ages.  
124 Plot area and the number of survey plots per study site ranged from 1.0 to 27.0 m<sup>2</sup>  
125 (mean 4.7 ± 2.7 SD), and from 5 to 37 plots (mean 27.9 ± 6.3 SD, total 2,373),

126 respectively.

127

128 GIS analyses

129 We calculated the amount of solar radiation and the distance from continuous  
130 forest for each study site using Geographical Information System software [ArcGIS  
131 10.0; Environmental Systems Research Institute (ESRI), Redlands, CA 2011]. To  
132 calculate the amount of solar radiation, we used laser profiler data provided by the  
133 Hokkaido Development Bureau (hereafter called LP data). LP data are topographical  
134 data measured by aerial laser surveys. Aerial laser surveys obtain three-dimensional  
135 spatial data by analyzing pulses emitted from an airborne laser as they reflect off the  
136 ground and return. The accuracy (standard deviation) of the original data is <25 cm  
137 horizontally. We used the original LP data without removing structures (e.g., houses,  
138 office buildings). We assumed the surface of each structure was flat, and used the  
139 building height as the maximum value of laser point. Then, we created 0.5-m resolution  
140 digital surface models (DSMs) of our survey areas. To calculate the amount of solar  
141 radiation (the sum of direct solar radiation and sky solar radiation) during the field  
142 survey, we used ArcGIS Spatial Analyst tools and our DSMs, assuming the solar  
143 radiation levels on July 1, 2013 (from 4.1 to 5829.6, mean  $2459.4 \pm 1160.6$  SD). We  
144 defined the solar radiation of each plot as the maximum radiation value for that plot. For  
145 each survey plot, we also measured the straight-line distance from the nearest  
146 continuous forest (Fig. 2).

147



148 Statistical analyses

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

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

169 In this study, survey plot size varied among the study plots (min 1.0, max 27.0  
170 m<sup>2</sup>). Thus, even if the occurrence probability of a fern species per unit of area is

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

$$177 \text{Prob}(N_i \geq 1) = 1 - \exp[-\exp(\beta_0 + \boldsymbol{\beta} \mathbf{x}_i + \log(A_i))], \quad (\text{Equation 1})$$

178 where  $N_i$  is the number of individuals in plot  $i$  and  $\text{Prob}(N_i \geq 1)$  is the probability that at  
179 least one individual occurs in plot  $i$  (i.e., the occurrence probability).  $\beta_0$  is the model  
180 intercept, while  $\mathbf{x}_i$  and  $\boldsymbol{\beta}$  are covariates of plot  $i$  and their coefficients, respectively.  $A_i$  is  
181 the area of plot  $i$  and  $\log(A_i)$  is an offset term, whose coefficient we fixed as 1. The  
182 random effect is not shown in this equation.

183 The five explanatory variables were not highly correlated with each other ( $|r| <$   
184  $0.31$ ; Appendix 2). We built full models, including all five explanatory variables  
185 (ground cover type, habitat age, district type, the amount of solar radiation, and distance  
186 from continuous forests) for each species. Using the coefficients derived from the full  
187 models, we plotted the occurrence probabilities as predicted by each of the five  
188 explanatory variables. Although ground cover type, habitat age, and district type were  
189 not **strictly** continuous values, we included their predicted curves for convenience.

190

## 191 **Results**

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

193 0.80 SD, range: 0-8). All of them were native species in Japan, and no endangered  
194 species were included. Although there were two open-land species (*E. arvense* and *M.*  
195 *struthiopteris*), main habitats of the other species were forests. The four most commonly  
196 observed species were *E. arvense* (observed in 54% of our study plots), *M.*  
197 *struthiopteris* (8%), *D. crassirhizoma* (6%), and *A. yokoscense* (6%) (Appendix 1).

198

#### 199 Landscape-scale environmental factors

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

205

#### 206 Local-scale environmental factors

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

214

215 **Discussion**

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

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

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

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

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

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

262 Habitat age also influenced fern distribution patterns. The occurrence  
263 probabilities of both *E. arvense* and *A. yokoscense* were positively related to habitat age  
264 (Fig.4), suggesting that the colonization and establishment of ferns in building gaps may  
265 take considerable time, as seen in the range expansion of other exotic species (Sakai et  
266 al. 2001). This result raises the possibility that populations of some species can recover  
267 as urban ecosystems mature (cf. Yamaura et al. 2012). This is an important point, as  
268 urban biological communities are usually thought to degrade as cities age (Hahs et al.  
269 2009; Soga et al. 2013). Urban biological communities likely have longer-term, more  
270 complex dynamics than previously thought (Ramalho and Hobbs 2012).

271 At present, cities around the world are expanding and becoming denser (Seto et al.  
272 2012). Indeed, the number of mega cities (cities with more than 10 million people) has  
273 increased more than tenfold in the past 50 years (United Nations 2011), which suggests  
274 that the world's ecosystems are changing toward more human-built, modified, and  
275 engineered systems. We show that even in highly modified landscapes, artificial  
276 structures can harbor and even create suitable habitat, and that both local- and  
277 landscape-level factors affect their function. Therefore, to conserve and restore urban  
278 biodiversity, city planners and policy makers should not overlook the conservation  
279 potential of these cryptic habitats that are "hidden in plain sight." Although we studied  
280 only ferns in building gaps, other types of artificial structures (e.g., drainage channels  
281 and stone masonry) likely act as cryptic habitats for other taxa. Clarifying the potential  
282 ecological functions of artificial structures in urban areas will lead not only to a better  
283 understanding of novel urban ecosystems (Hobbs et al. 2006), but to a novel framework

284 for conserving and restoring urban biodiversity.

285

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293

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432

433 **Figure legends**

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

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

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

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

442 **Fig.4.** Relationships between the occurrence probabilities of five fern species and  
443 ground cover type, habitat age, district type, solar radiation, and distance from  
444 continuous forest. Predicted lines were derived from generalized linear mixed models  
445 (GLMMs; see details in the main text). Solid and broken lines indicate significant ( $P <$   
446 0.05) and non-significant effects, respectively, of each explanatory variable. In  
447 producing these figures, we used the appropriate mean values for plot area and the  
448 environmental variables, and zero for the random effects.

449

450 **Table legends**

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

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

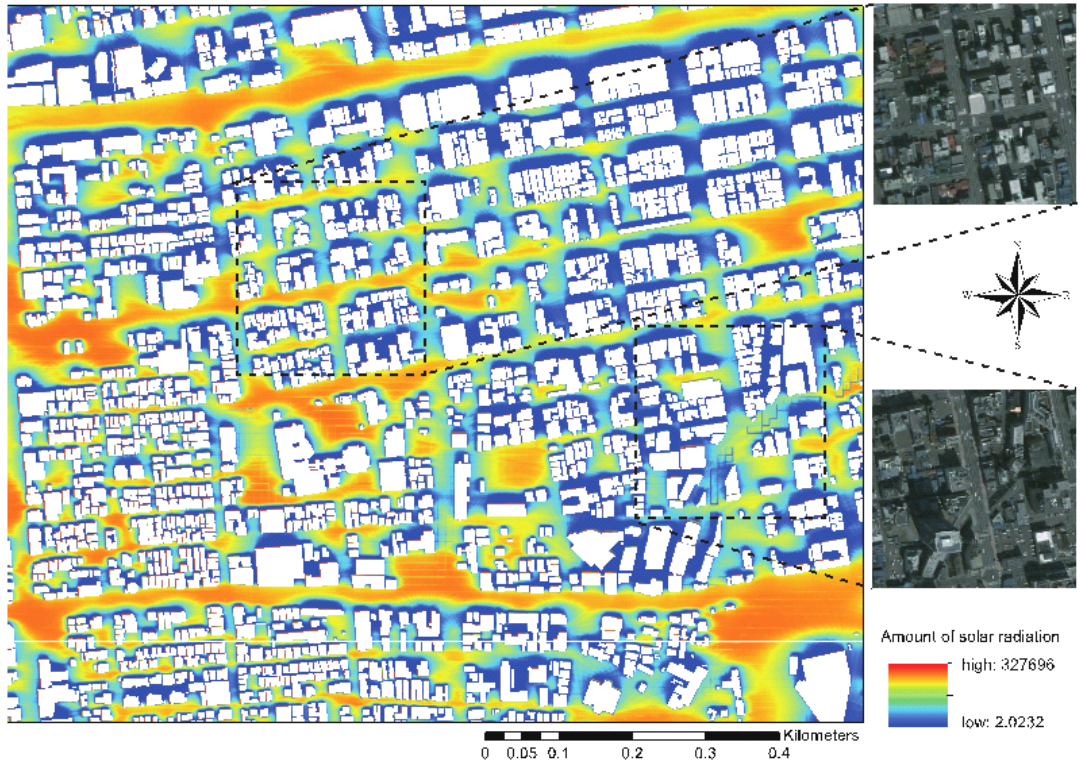
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456 **Supporting information**

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

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

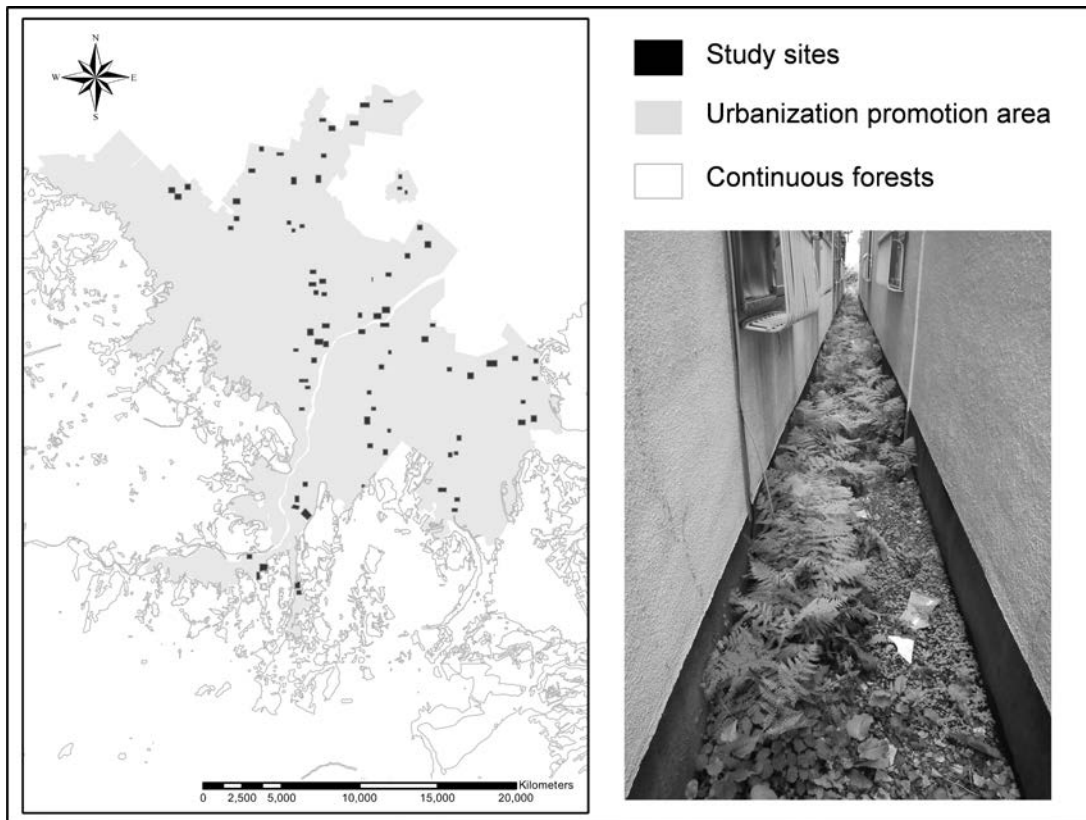
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463 Fig. 1. The amount of solar radiation across Sapporo.

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465

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

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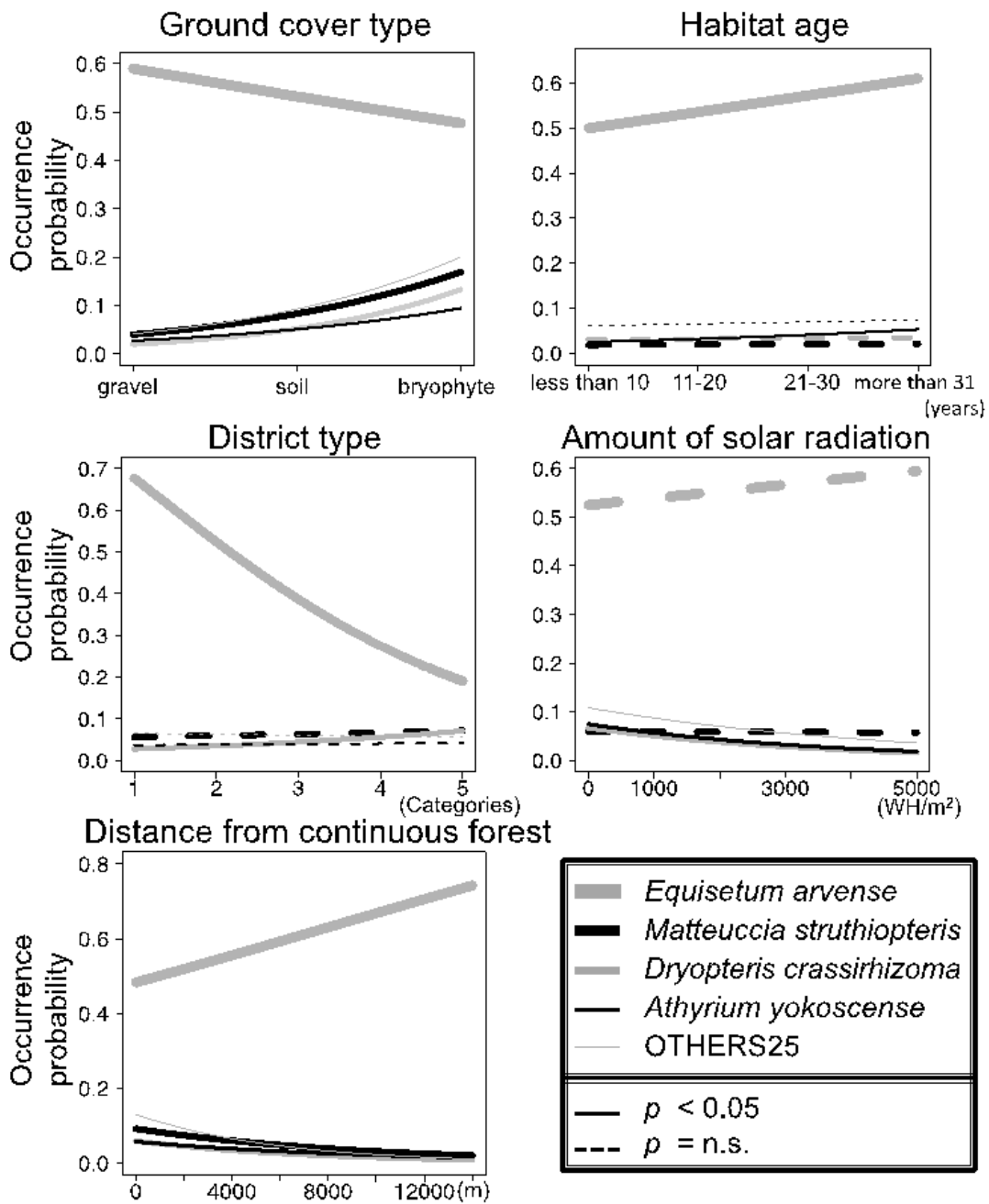
470 Fig. 3. Representative habitats in Sapporo urban area for four main fern species.

471 **(a)** *Equisetum arvense* L., **(b)** *Matteuccia struthiopteris* (L.) Tod., **(c)** *Dryopteris*

472 *crassirhizoma* Nakai, **(d)** *Athyrium yokoscense* (Franch. et Sav.) H.Christ.

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474

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

478

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

Categories	Building to land ratio <sup>1</sup>	Floor area ratio <sup>2</sup>	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 <sup>1</sup> Proportion of the area covered by the buildings

482 <sup>2</sup> 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		<i>E. arvense</i>	<i>M. struthiopteris</i>	<i>D. crassirhizoma</i>	<i>A. yokoscense</i>	OTHERS25
Fixed effects:						
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

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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

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

No.	Family	Species	# plots <sup>1</sup>	Proportion <sup>2</sup>
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

<sup>1</sup> Number of plots at which each species occurred.

<sup>2</sup> 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