RESEARCH ARTICLE

Effects of surrounding urbanization on non-native flora in small forest patches

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Abstract The purpose of our study was to compare the number, proportion, and species composition of introduced plant species in forest patches situated within predominantly forested, agricultural, and urban landscapes. A previous study suggested that agricultural landscape context does not have a large effect on the proportion of introduced species in forest patches. Therefore, our main goal was to test the hypothesis that forest patches in an urban landscape context contain larger numbers and proportions of nonnative plant species. We surveyed the vegetation in 44 small remnant forest fragments (3-7.5 ha) in the Ottawa region; 15 were situated within forested landscapes, 18 within agricultural landscapes, and 11 within urban landscapes. Forest fragments in urban landscapes had about 40% more introduced plant species and a 50% greater proportion of introduced plant species than fragments found in the other two types of landscape. There was no significant difference in the number

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Keywords Forest plants · Forest flora · Forest vegetation · Introduced species · Non-native species · Landscape context · Urbanization · Species richness · Forest patch · Forest fragmentation

Introduction

Most introduced plants are open-habitat species (Fensham and Cowie 1998; Cadotte and Lovett-Doust 2001; Weaver et al. 2001; Rubino et al. 2002; Charbonneau and Fahrig 2004; Gray 2005). Landscapes containing more open habitats should therefore contain more introduced plant species and higher abundances of introduced plant species than landscapes containing mainly forest. High abundances of introduced plants in open landscapes should produce a large influx of seeds of alien plant species into remnant forest patches within these landscapes (Boutin and Jobin 1998; Cullen et al. 2001). This should, in turn, result in more introduced plant species in forest fragments surrounded by more open landscapes than in those surrounded by high forest cover.

Charbonneau and Fahrig (2004) tested this prediction in 192 forest sites in the area around Ottawa, Canada. The forest sites were situated within landscapes that varied in open land cover from 0% to 99%. Although they did find a significant positive relationship between the proportion of introduced plant species at a site and the amount of open land cover surrounding the sites, this relationship was extremely weak, explaining only 3% of the among-site variance in proportion of introduced plant species.

The forest sites used by Charbonneau and Fahrig (2004) were chosen to represent a range in open land cover, but they explicitly avoided forest sites in urban areas. However, urban areas are known to contain many introduced species, particularly in gardens (Hodkinson and Thompson 1997; Moffatt et al. 2004). Some studies have suggested an influence of urban areas on introduced species abundance and composition in nearby forest sites (e.g., DeCandido 2004; Sullivan et al. 2005). The purpose of our study was to compare the number and proportion of introduced plant species in forest patches situated

within predominantly forested, agricultural, and urban landscapes. Based on Charbonneau and Fahrig (2004) we expected little if any difference in the proportion of introduced plant species in the patches situated in forested vs. agricultural landscapes in our area. Our main goal was therefore to test the hypothesis that forest patches in urban landscapes are subject to a higher influx of introduced plants than those in forested or agricultural landscapes.

Methods

Site selection and landscape context data

The study took place in Ontario and Quebec, Canada, within 75 km of the city of Ottawa (45°25' N-75°42' W). We selected 44 forest fragments between 3 and 7.5 ha (Fig. 1) using digital topographic maps (DMTI Spatial 2001). The digital data provided detailed topographic and geographic information derived from the 1998 1:50,000 National Topographic Data Base. We made an effort to select forest fragments that were similar in canopy tree composition. Canopy cover in most sites was dominated by deciduous trees



Fig. 1 Locations of 44 forest fragments surveyed in the Ottawa region, each surrounded by a 500 m radius buffer (landscape). Note: light grey lines and shading indicate the road network; forest cover is not shown such as Acer rubrum, Acer saccharum, Fraxinus americana, Tilia americana and Populus tremuloides. One site was dominated by Quercus rubra and Pinus barksiana, and four sites were dominated by Thuja occidentalis. There was no silvicultural activity evident in any of the fragments.

We selected the forest fragments-defined as patches of forest that were separated from other forest by at least 40 m-to represent different landscape contexts in terms of forested, agricultural, and urban landscapes. Fragments situated within urban landscapes were typically in residential areas. Fragments situated within agricultural landscapes were typically surrounded by forage crops such as alfalfa and soybean, grains such as corn and barley, and areas grazed by dairy cows. For each landscape type, we chose fragments such that the surrounding landscapes within 500 m of the fragments had the highest possible percentage of the desired land cover (forest, agriculture, or urban), given the variability available within our region. The 500 m distance was used because plant species richness has been shown to be most strongly correlated to landscape context within 200-500 m (Charbonneau and Fahrig 2004; Houlahan et al. 2006). All fragments were at least 2 km apart. We measured percent forest cover within the landscapes using the CanMap Streetfiles vegetation theme, and agricultural and urban covers using the land use theme. In the land use theme, the open area cover category was used to estimate agricultural cover and the categories commercial, government and institutional, parks and recreational, residential, and resource and industrial were merged to estimate urban cover. We conducted visual surveys around the forest fragments to ensure the map classification corresponded to what was found in the field. Fifteen fragments within forested landscapes, 18 within the agricultural landscape category, and 11 within urban landscapes were surveyed. The number of fragments was determined by a combination of fragment availability in the three landscape types, and a trade-off between sampling enough fragments to detect an effect of landscape type, and enough sample quadrats per fragment to adequately represent the vegetation in each (see Sampling design). The forested landscapes contained 3575% forest, the agricultural landscapes contained 70–100% agricultural land and the urban landscapes contained 60–95% urban land (example landscapes in Fig. 2).

Local variables

Although the fragments were selected to be as similar as possible, there were inevitably differences among fragments that could potentially affect the number of introduced species found. We measured these to control for their effects in the analysis. These variables included fragment area, canopy closure within the fragment, fragment age, and fragment heterogeneity. Charbonneau and Fahrig (2004) found a negative relationship between canopy closure and the proportion of introduced species. We expected that the number of introduced species might also be positively related to increasing fragment area, age, and heterogeneity.



Fig. 2 Examples of each of the three landscape types, showing cover types within 500 m of the sampled forest patch: black: forest cover, white: agricultural cover, grey: urban cover. The 15 forested landscapes contained 35–75% forest, the 18 agricultural landscapes contained 70–100% agricultural land and the 11 urban landscapes contained 60–95% urban land

Fragment area for each site was calculated with the Avenue script *calcapl.ave* in ArcView 3.2 (Environmental Systems Research Institute, Inc. 1999), using the digital DMTI Canmap Streetfiles (DMTI Spatial 2001). Canopy closure was estimated at every second quadrat during the second plant species inventory (see *Species richness data* below). Canopy closure was measured directly above the quadrats on a 10-point scale, 1 being between 0% and 10% canopy closure, and 10 being between 91% and 100% canopy closure. The average canopy closure for the fragment was taken as its canopy closure index.

The minimum age of the forest at each site was evaluated using time series of aerial photos and topographic maps from 1940 to 2003 (National Air Photo Library 1933–2001; Canada Surveys and Mapping Branch 1933–1968). The date of first observable forest presence was traced back and used to calculate the forest age in 2003. Forests that were present in 1940 were assigned a minimum age of 63 years (Table 1).

The difference in elevation at each site was used as a surrogate for fragment heterogeneity, on the assumption that fragments with a larger variation in elevation would contain a greater number of microhabitat types than flatter fragments. The fragment elevation differences were taken from the Ontario Base Maps (Ontario Ministry of Natural Resources 1988–1992) and Quebec topographic maps (Service de la cartographie du Québec 1983–1984).

Sampling design

Plant species richness was measured for each fragment using a grid of 1 m^2 quadrats covering the entire fragment at 50 m spacing, producing an average of 21 (s.d. 7) quadrats per forest fragment. The grid lines ran north–south and east–west, and began 50 m from the forest edges. All species of ground vegetation found in each quadrat were identified. Species identification for trees with DBH greater than or equal to 10 cm was done at every second quadrat using the point-centred quarter method (Bonham 1989). The north–south and east–west directions were used to establish four 90° sectors in which the tree closest to the quadrat centre was identified. Fragments were

surveyed twice, once between May 15th and June 21st 2003 to survey spring ephemeral species, and once between July 2nd and August 21st to survey the rest of the vegetation. Altogether this resulted in 1,902 quadrat samples and 951 point-centred quarter samples. Evidence of human use of each fragment was recorded at the same time as the vegetation surveys.

All plants were identified to species or genus and were classified as native or introduced (Gillett 1958; Fernald 1970; Niering and Olmstead 1979; Preston 1989; Gleason and Cronquist 1991; Soper and Heimburger 1982; Chambers et al. 1996). An introduced species was defined as a species that did not occur in the study area before European settlement and that arrived as a result of human activity.

Data analysis

Our response variables were the number of introduced species and the proportion of introduced species at each site. Two ANCOVA's (one for each response variable) were conducted using the categorical variable Landscape Type (with three classes: forested, agricultural and urban) and the local variables fragment area, canopy closure, forest age, and fragment heterogeneity. We did not transform the response variables because the assumptions of ANOVA were not violated; the residuals were approximately normally distributed with no apparent trends in the variance. The analyses were conducted using the GLM (general linear models) procedure in SAS (SAS Institute 1990).

We also conducted canonical correspondence analysis (CCA) (ter Braak 1986) to evaluate the response of the introduced species assemblage to landscape type. Response variables were the proportion of quadrats in each fragment containing each introduced species. In addition to our main predictor variable of interest, landscape type, we included fragment area, canopy closure, forest age, and fragment heterogeneity as covariates in the ordination to control for their effects. We evaluated the statistical significance of the relationship between the introduced species assemblage and landscape type using a Monte Carlo permutation test. The

Table 1 Attributes of small forest fragments and the numbers of p species and introduce plant species found in each fragment

Table 1 Attributes of 44small forest fragments,and the numbers of plantspecies and introduced	Landscape type	Fragment area (ha)	Canopy closure (%)	Forest age (years)	Elevation difference (m)	Total species richness	Introduced species richness
plant species found in	f	3.0	85	53	5	46	6
each fragment	f	3.7	80	63	9.5	71	9
	f	6.8	80	63	5	79	10
	f	2.7	95	63	2.5	33	2
	f	5.4	85	63	3	62	5
	f	3.3	80	43	10	73	12
	f	2.8	75	58	4	49	13
	f	4.4	90	45	3	83	4
	f	6.5	75	35	5	66	9
	f	3.7	70	63	1.5	62	7
	f	3.9	70	43	5	71	6
	f	5.7	45	63	3.5	60	2
	f	41	90	63	85	45	4
	f	73	75	63	3	51	12
	f	5.0	75	63	45	69	10
	2	6.4	85	44	10	54	10
	a	3.7	85	35	0	26	3
	a	37	75	63	0	33	4
	а Э	3.6	80	63	5	34	4
	a	2.8	90	28	5	54 46	7
	a	2.0	90 70	28 58	0	74	1
	a	2.7	70	58	0	56	4
	a	2.7	70	63	10	51	10
	a	5.2	70 80	63	10	00	10
	a	0.4	25	63	0	90 34	6
	a	0.5	33	35	0	54 61	0
	a	4.8	90	33	0	20	4
	a	5.4 2.7	80	03	0	30 24	5
	a	3.7	85	03	5	54 40	Z
	а	3.8	80	63	0	40	6
	а	/.1	80	63	2	88	7
	а	4.0	70	63	10	49	5
	а	3.6	65	63	10	53	9
See Methods for sampling	а	2.6	90	53	10	68	5
details. Landscape types:	u	5.5	75	49	3	62	7
a – agricultural	u	4.7	80	63	5	52	7
a = agricultural, f = forested u = urban	u	2.7	65	48	5	54	13
1 = 10103100, $u = u10011$	u	4.4	85	63	6	50	7
Mathada for definitions)	u	2.9	80	63	20	31	6
Note a forest age of	u	7.3	90	63	13.5	51	14
A voars represents a	u	5.4	90	63	5	47	11
by years represents a	u	5.7	60	51	1.5	55	11
Elevation difference was	u	7.3	75	63	5	58	11
Elevation difference was	u	3.0	65	56	1	41	7
fragment heterogeneity	u	4.9	75	35	2.5	54	8

CCA analyses were conducted using the vegan package in the statistical program R 2.2.

Results

Table 2 presents summary statistics for each of the three cover types surrounding the focal patch in each of the three landscape types. A total of 396 plant species were found of which 62 were introduced species. The total species richness per fragment ranged from 26 to 90 species with an average of 54.5 species, and the introduced species richness per fragment ranged from 2 to 14 with an average of 7.2 species (Table 1). Table 3 summarizes the evidence of human use

Table 2 Composition of the three landscape types

	Forested landscapes (n = 15)	Agricultural landscapes $(n = 18)$	Urban landscapes $(n = 11)$
Number of landscapes Mean forest cover (%) (s.d.) Mean agricultural cover (%) (s.d.) Mean urban cover (%) (s.d.)	15 48.4 (11.7) 39.1 (16.7) 10.7 (11.5)	18 8.4 (9.0) 86.3 (10.4) 5.1 (7.1)	11 5.7 (5.3) 13.4 (12.5) 80.8 (13.7)

Table 3 human u fragmen the three

Table 3 Evidence ofhuman use of thefragments situated withinthe three landscape types		Fragments in forested landscapes (n = 15)	Fragments in agricultural landscapes (n = 18)	Fragments in urban landscapes (n = 11)	
	Trails	1.3 (2.4)	1.8 (2.0)	10.9 (6.7)	
Values are the mean number of sightings per fragment (s.d.)	Garbage	2.9 (2.5)	2.4 (1.7)	6.5 (4.4)	
	Fire pits	0.0	0.0	0.45 (0.93)	
	Tree houses	0.33 (0.72)	0.17 (0.38)	1.1 (1.5)	
	Houses adjacent to fragment	5.3 (7.4)	1.3 (1.7)	19.1 (22.4)	

of the fragments. Characteristics of each of the 62 introduced species are shown in Table 4.

We found a marginally significant relationship between the number of introduced species and Landscape Type, and a significant relationship between the proportion of introduced species and Landscape Type (Table 5). Scheffé tests revealed that forest fragments in urban landscapes had significantly more introduced plant species than fragments in agricultural landscapes, and fragments in urban landscapes had significantly higher proportions of introduced species than fragments in either agricultural or forested landscapes. There were no significant differences in the number or proportion of introduced species in forest fragments in forested vs. agricultural landscapes. On average, there were 40% more introduced species per fragment in urban landscapes and there was a 53% higher proportion of introduced species in fragments in urban landscapes than in fragments in the other two landscape types (Fig. 3).

The type of landscape in which a forest patch was imbedded affected the introduced plant species assemblage found there (Fig. 4). Monte Carlo permutation tests confirmed the overall significance of the canonical ordination when all sites from all three landscape types were included (P = 0.0005), as well as the significance of all three pair-wise canonical ordinations where only sites from two of three landscape types were present (P < 0.05). The final column in Table 4 indicates the landscape type for the introduced species whose CCA scores were within 0.5 units (on both axes) of the centroid associated with forested, agricultural, or urban landscapes.

Discussion

Our results, in combination with those of Charbonneau and Fahrig (2004), suggest that the number of introduced species in forest patches is much more strongly affected by urban land use than by agricultural land use, at least in the region around Ottawa, Canada. Charbonneau and Fahrig (2004) did not include sites close to urban areas. They found a statistically significant but very small effect of agricultural cover (partial $R^2 = 3\%$) on the proportion of introduced species in 192 forest sites. Similarly, we found no difference between the proportion of introduced spe-

 Table 4
 Characteristics of the 62 non-native plant species found in the forest fragments

Species	Category	Lifespan	Introduction	Site type	Landscape association
Acer negundo L.	tree			I-D	•
Achillea millefolium L.	sum. herb.	р	Ι	D	f
Alliaria petiolata Bieb.	spr. herb.	b	Ν	I-D	
Arctium lappa L.	sum. herb.	b	Ν	I-D	
Arctium minus (Hill) Bernh.	sum. herb.	b	Ν	D	а
Arctium sp. L.	sum. herb.	b	Ν		u
Asparagus officinalis L.	sum. herb.	p	Ι	D	а
Barabarea vulgaris R.Br.	spr. herb.	b/p	Ν	D	f
Bromus erectus Hudson	sum. herb.	ם י	Ν	D	f
Cerastium vulgatum L.	sum. herb.	p	Ν	D	u
Chrvsanthemum leucanthemum L.	sum. herb.	p	Ν	D	
Cirsium arvense (L.) Scop.	sum. herb.	P D	N	D	
Cirsium vulgare (Savi) Tenore	sum, herb.	b	N	D	
Convallaria majalis L	spr. herb.	n	I	D	
Coronilla varia L	sum, herb.	P D	N	I-D	11
Crepis capillaris (L.) Wallr	sum herb	P a/b	N	D	
Daucus carota L.	sum, herb.	a/b	N	D	
Enipactis helleborine (L.) Crantz	sum herb	n	N	I	
Galeonsis tetrahit I	sum herb	P	N	I-D	а
Glechoma hederacea I	sum herb	n	N	D	
Hemerocallis fulva (I_) I	sum herb.	P D	I	I-D	11
Hesperis matronalis I	sum herb	p b/n	I	I-D I-D	u
Hieracium caespitosum herb Dumort	sum herb	o,p	N	П-D D	
Hieracium flagellare Wild	sum herb	p p		D	f
Hypericum perforatum I	sum herb	P D	Ν	LD	
Inspericum performum L.	tree	P	I		
Lactuca serviola I	sum herb	a/b	I N	- П	f
Lathyrus latifolius I	sum herb	a/0	I	D	1
Laonurus cardiaca I	sum herb	р р	I N	D	
Linaria vulgaris Miller	sum herb	р р	N	D	
Lithospermum officinale I	sum herb	р р	N		
Lunospermum officinute L.	sum herb	р р	I		u
Lysimuchia hummulana L. Lysimuchia salicaria I	sum herb	р р	I N		f
Medicago lupulina I	sum herb	P a/b	N	- П	1
Medicago sativa I	sum herb	a/0	I	D	u
Metalcago saliva L. Morus alba I	tree	þ	I I		a
Narcissus ionauilla I	opr harb	n	I		•
Naneta cataria I	sum herb	р р	I I		f
Pastinaca satiya I	sum herb	р b	I	ם-ו ח	f
Dhlaum protonoo I	sum horb	0	I I	D	1
Plantago major I	sum harb	p	I N	D	a
Pog grava I	sum horb	þ	N	D	
Poa pratansis I	sum herb	a	IN I		u
Polygonym gonychydyg I	sum horb	p	I N	ע-ו ת	·
Potoptilla pasta I	sum harb	a	IN N	D	•
Drunalla vulgaria I	sum horb	p	1	D	·
Fruneita Vulgaris L.	suill. liefb.	р	T		•
Pyrus maius L.	tree		I N	I-D	•
Ranunculus acris L.	sum. nero.	р	IN T	I-D	•
Rhamhus cainartica L.	tree		I T	I-D	•
Knamnus frangula L.	tree	•	I T	I-D 1	•
<i>Kibes sativum</i> Sime.	snrub	•	1 N	I	u
Suene vulgaris (Moench) Garcke.	sum. herb.	р	N	D	I
Solanum dulcamara L.	sum. herb.	р	N		
Taraxacum officinale Weber	spr. herb.	р	N	I-D	
Trifolium pratense L.	sum. herb.	р	I T	D	
Irifolium repens L.	sum. herb.	р	1	D	

Table 4 continued

Species	Category	Lifespan	Introduction	Site type	Landscape association
Tussilago farfara L.	sum. herb.	р	Ν	D	а
Urtica dioica var. dioica L.	sum. herb.	p		Ι	а
Verbascum thapsus L.	sum. herb.	b	Ν	D	
Veronica officinalis L.	sum. herb.	р	Ν	I-D	
Viburnum opulus var. opulus L.	shrub		Ι	Ι	
Vicia cracca L.	sum. herb.	р	Ν	D	•

"Category": tree, shrub, sum. herb. = summer-flowering herbaceous plant, spr. herb. = spring-flowering herbaceous plant. Lifespan: p = perennial, b = biennial, a = annual. Introduction: I = intentionally introduced, N = non-intentionally introduced (Rousseau 1971). Site type: I = intact sites (forest, open woods, streams, wetlands), D = disturbed sites (fields, pastures, roadsides, ditches, train tracks, urban sites) (Rousseau 1968; Gleason and Cronquist 1991; Marie-Victorin 1995). Landscape association: species strongly associated with sites in one of the three landscape types, f (forested), a (agricultural), or u (urban), where strong association was indicated when a species' CCA score was within 0.5 units (on both axes) of the centroid for the sites in that landscape type (Fig. 4)

Table 5 ANOVA tables for analyses relating (a) the number, and (b) the proportion of introduced species in remnant forest fragments to the landscape type surrounding the fragments (forested, agricultural, or urban)

Source	(a) Response variable: number of introduced plant species				(b) Response variable: proportion of introduced species			
	DF	Type III SS	F	Р	DF	Type III SS	F	Р
Landscape type	2	42.4	2.6	0.09	2	0.0229	3.9	0.03
Fragment area	1	55.9	6.8	0.01	1	0.0021	0.72	0.40
Canopy closure	1	1.75	0.21	0.64	1	0.002	0.69	0.41
Fragment age	1	4.03	0.49	0.49	1	0.0000	0.00	0.98
Fragment heterogeneity	1	29.4	3.4	0.07	1	0.01	3.38	0.07
	Corrected total SS = 463.7 (n = 44 forest fragments); Model R^2 = 35%				Corrected total SS = 0.156 (<i>n</i> = 44 forest fragments); Model $R^2 = 30\%$			

Fragment area, mean canopy closure within the fragment, fragment age, and fragment heterogeneity (approximated as elevation difference) were included to control for possible local effects

cies in fragments within agricultural landscapes and fragments in forested landscapes. However, we found about 40% more introduced species in the fragments in urban landscapes than in the other two landscape types and about a 50% higher proportion of introduced species in forest fragments in urban landscapes than in the other two landscape types (Fig. 3). The importance of urbanization is also implicated in a study by McKinney (2004), who found a significant positive association between exotic plant species richness of an area and the human population size of that area. A study of introduced species to Taiwan (Wu et al. 2004) suggested that nonnative species introduced as ornamental plants are more likely to become common or invasive than non-native species introduced as forage plants, also indirectly suggesting that residential areas may be important foci for plant species introductions.

The large effect of urban context on the number and proportion of introduced species that we found is somewhat at odds with the emphasis in the current literature. We conducted a systematic literature search of papers on nonnative (or "alien" or "introduced" or "invasive") plant species (or "flora" or "vegetation") in either agricultural (or "crop" or "farmland") settings or urban (or "city") settings, using the Web of Science database. We found 131 studies in agricultural settings and 41 studies in urban settings. It is difficult to say whether this bias towards agricultural settings is appropriate. In most regions there are many more forested



Fig. 3 Mean number (*upper panel*) and proportion (*lower panel*) of introduced species per forest fragment (\pm s.e.) in different landscape types: n = 15 forested, 18 agricultural, and 11 urban landscapes

patches imbedded within agricultural landscapes than within urban landscapes. Therefore, even if, on the scale of a single forest patch, the effect of urban context is much greater than the effect of



Fig. 4 CCA biplot. Δ : sites in forested landscapes. •: sites in agricultural landscapes. *: sites in urban landscapes. Large symbols show the centroids of the sites in each landscape type. Eigenvalues are 0.21 for CCA1 and 0.18 for CCA2

agricultural context, when summed over a whole region the overall influence of agricultural context could be greater, simply because there is more agricultural land. In any case, our results support previous studies suggesting that urban and suburban areas may be important foci for spread of introduced plant species (Arevalo et al. 2005; Smith et al. 2006).

Our study was not designed to determine the mechanism(s) through which introduced species enter forest fragments in urban landscapes. However, we can suggest several possibilities. First, the non-native species could be remnants from past gardens in the fragments within urban landscapes. However, our observations do not support this explanation; while abandoned houses were found in two of the fragments in agricultural landscapes and two of the fragments in forested landscapes, there were no abandoned houses found in any of the fragments in urban landscapes. Also, of the species strongly associated with sites in particular landscape types, the proportion that were intentionally introduced was not higher for those associated with sites in urban landscapes (2 of 8) than for those associated with sites in agricultural landscapes (3 of 6) or forested landscapes (3 of 8) (Table 4). Second, the forest fragments in urban landscapes may be currently more heavily used by people. This is supported by our data; fragments in urban landscapes contained more trails, garbage, fire pits, and tree houses than did the fragments in forested and agricultural landscapes (Table 3). There were also more houses directly adjacent to the fragments in the urban landscapes (Table 3). This higher use of the fragments in urban landscapes could result in importation of seeds of non-native plants carried by people (e.g., on their boots) using the sites. It is also possible that disturbances to the soil caused by this human activity could favour germination and growth of introduced species, which are often disturbance-adapted (Table 4; see also Rodgers and Parker 2003; Beckstead and Augspurger 2004; Hager 2004; Kim 2005; Setterfield et al. 2005; Sanz-Elorza et al. 2006; but see Leishman and Thomson 2005). Finally, it is possible that the larger number of introduced species in urban sites is due to an influx of seeds through ordinary seed dispersal, from the surrounding urban landscapes. Of course, more than one of these mechanisms could be operating simultaneously.

The number of introduced species increased with fragment area as expected, and both the number and proportion of introduced species had marginally significant (positive) relationships to fragment heterogeneity, measured as elevation difference. Unlike Charbonneau and Fahrig (2004) we found no effect of canopy closure on the number or proportion of introduced species. This is not surprising. Since we selected our fragments to be as similar as possible (see Methods), the variation in canopy closure values among our sites (Table 1) was much smaller than in Charbonneau and Fahrig (2004).

Finally, we note that the increase in introduced species in forest patches within urban landscapes does not necessarily imply that these forest sites are unimportant for conservation of biodiversity. Houlahan and Findlay (2004) surveyed the literature and found no evidence for a negative correlation between the number of introduced and native species. Our data are consistent with this; the correlation between native and introduced species richness in our sites was extremely low (r = -0.02, p = 0.92, n = 44). Houlahan and Findlay concluded that a much larger threat to biodiversity is site dominance by one or a few species; such species can be either native or introduced.

In conclusion, our results suggest that landscape context does have a substantial effect on the number, proportion, and type of introduced plant species in forest fragments. Forest fragments situated in urban landscapes had about 40% more introduced species and a 50% greater proportion of introduced species over forest fragments in agricultural or forested landscapes. Further research would be needed to determine the primary mechanisms through which these introduced species enter forest fragments in urban landscapes, and to determine whether this influx is a significant concern for conservation.

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