

Landscape effects of forest loss in a pollination system

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Received: 24 February 2007 / Accepted: 13 August 2007 / Published online: 6 September 2007
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Abstract Forest loss has been invoked as a cause for changes in the reproductive success of animal-pollinated woodland plants, associated with changes in their pollinators. To analyze such effects, it is important to include all of the three key players: landscapes, pollinators and a plant. We investigated effects of forest loss on an insect-pollinated plant through landscapes in forested ecosystems to pollinator communities and plant populations. Then we questioned if abundance and species richness in pollinator communities decrease as forest loss increases, and this in turn leads to a decrease in reproductive output of an insect-pollinated plant. We

made a study with 12 populations of the bee pollinated herb, *Erythronium americanum*, in a landscape characterized by scattered fragments of deciduous forest within intensively managed agricultural fields. We also sampled bees as the potential pollinators by pan traps. We quantified the study landscapes using the amount of forest cover and the length of forest edge within each of the six radii (250, 500, 750, 1,000, 1,250 and 1,500 m). Regression analyses showed that the abundance and species richness of all collected bees were positively related to only the forest cover at the radius of 750 m. We also found the positive relationships for the seed set of *E. americanum* when the forest cover at the same radius and abundance of all collected bees were used as the predictor variables. These results indicate that forest loss causes negative impacts on potential pollinator communities and seed sets of some woodland herbs.

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Keywords Apiformes · Apoidea ·
Carolinian forest · Forested ecosystem ·
Fragmentation · Habitat loss · Spring ephemeral

Introduction

Habitat loss is a current major threat to biodiversity, and the losses occurring within landscape scales could result in habitat fragmentation (Fahrig 2003; Ewers and Didham 2006). Landscape changes lead

to alterations in the inter-specific interactions of organisms, such as plants and pollinators (Didham et al. 1996; Tscharntke and Brandl 2004; Aguilar et al. 2006). Plant-pollinator interactions are one of the critical services for sustainable ecosystems, so that loss of the function provided by such services can lead to extirpations and potentially to extinctions (Rathcke and Jules 1993; Buchmann and Nabhan 1996; Allen-Wardell et al. 1998; Kearns et al. 1998; Kevan 1999; Biesmeijer et al. 2006).

Several studies showed that such habitat disturbances, including both loss and fragmentation, negatively affect the sexual reproductive success of plants in forest environments (Aizen and Feinsinger 1994a; Cunningham 2000a, b; Parra-Tabla et al. 2000; Rocha and Aguilar 2001; Aguilar and Galetto 2004; Kolb 2005). Moreover, such changes in the reproductive success of plants have been shown to be accompanied by changes in the communities of their mutualistic partner, pollinators (Aizen and Feinsinger 1994b; Steffan-Dewenter and Tscharntke 1999; Steffan-Dewenter et al. 2001; Donaldson et al. 2002; Ghazoul and McLeish 2002; Murren 2002; Quesada et al. 2004). Those studies suggest that it is important to include all of the three key players: landscapes, pollinators and plants.

For such ecological studies on landscape-scale, one of these three factors, technological developments of geographic information systems (GIS), have been contributing (Turner et al. 2001), and there are few studies on pollination systems including the landscape aspect. In this study, we quantify each of the three factors within forest environments to analyze the landscape consequences of forest loss to insect pollinator communities and woodland plant populations with the aid of GIS. The main questions we asked in this study are if abundance and species richness in pollinator communities decrease as forest loss increases, and this in turn leads to a decrease in reproductive output of an insect-pollinated plant. Landscape values to represent forest loss were quantified by the amount of forest cover, simply caused by loss of forest area, and the amount of forest edge associated with forest fragmentation caused by loss of forest area. Additionally, we investigated the relationship, if any, between forest loss and flowering density of study plant populations, and between the flowering density and seed set.

Methods

Study region

Our study was made in Norfolk County, Ontario, Canada (42°37'–42°48' N, 80°25'–80°39' W) in the Carolinian forest region of southern Ontario's deciduous forest zone, an ecosystem of limited distribution in Canada (Allen et al. 1990). The chosen landscape is rather flat and homogeneous with scattered fragments of forest patches within intensively managed agricultural fields of annual crops, mainly tobacco, corn and soybean. There are few covered by other vegetation types such as orchard fields, grazed grasslands and weedy verges. It follows that after intensive agricultural development, which started in the late 18th century, plant species found in the Carolinian forest have decreased and have been identified as being of high priority for conservation within Canada (Argus 1992; Waldron 2003).

Study plant

We selected *Erythronium americanum* Ker. (Liliaceae) as our model plant species. This species is bulbous, perennial, a common vernal woodland herb, widely distributed in Eastern North American forests (Gleason and Cronquist 1963). It is known as a spring ephemeral, which takes advantage of phenology including flower bloom for the high light intensities in the early spring before leaf-out of canopy trees shading the forest understory (Holland 1974; Muller 1978; Lapointe and Lerat 2006). Sexually mature, two-leaved, plants produce a single, yellow, perfect flower.

Flowers of *E. americanum* are visited by numerous insect species, of which various bees are considered the potential main pollinator assemblages. These reported bee species include *Osmia atriventris* Cresson, *Osmia lignaria* Say, *Lasioglossum (Dialictus) coeruleum* (Robertson), *Andrena arabis* Robertson, *Andrena carlini* Cockerell, *Andrena erigeniae* Robertson, *Andrena erythronii* Robertson, *Andrena forbesii* Robertson, *Andrena tridens* Robertson, *Apis mellifera* L., *Bombus bimaculatus* Cresson, and *Nomada* species (cleptoparasites of *Andrena* species) (Blanchan 1916; Michener and Rettenmeyer 1956; Bernhardt 1977; Krombein et al. 1979; Harder et al.

1985, 1993). Our preliminary insect samples from the flowers in the study region included some of these reported species, as well as *Lasioglossum (Lasioglossum) paraforbesii* McGinley, *Andrena vicina* Smith, *Bombus vegans* Smith, *Ceratina calcarata* Robertson (Taki and Kevan 2007).

Among these reported and sampled bee species, we especially focused on the following three *Andrena* species: *A. erythronii*, *A. carlini* and *A. vicina* for our species-level analysis. *A. erythronii* is known as the specialist bee species of *Erythronium* (Michener and Rettenmeyer 1956). *Andrena carlini* is a comparably large andrenid bee and has been indicated as the primarily pollinator species of *E. americanum* by Harder et al. (1985, 1993). It was considered that *A. vicina* could also be a primarily pollinator for *E. americanum* because both large andrenid bees in the same subgenus *Melandrena* are morphologically and ecologically similar.

Study sites

In April 2005, we selected 12 populations of *E. americanum* in 12 different sites surrounded by varying amounts of forest cover, all in a 67,500 ha area of Norfolk County (Fig. 1). The criteria for accepting a site included a distance of at least 3,000 m from any other study populations, ensured by use of ArcView (version 3.3, ESRI, Redlands, Calif.) and global positioning system (GPS) (Garmin International, Olathe, Kan.). The geospatial data of forest cover were obtained from aerial photography (1:30,000 and 1:50,000) and the Ontario Base Map Series by the Ontario Ministry of Natural Resources, Peterborough, Ontario, Canada in 2003.

On the maps, we created a circle with six radii (250, 500, 750, 1,000, 1,250 and 1,500 m) on an *E. americanum* population, which was projected by ArcView and used to measure the amount of forest cover (m^2) at each of the 12 selected site. These scales of radii were selected as being relevant to foraging distance of and landscape-scale response of bee communities (Gathmann and Tscharrntke 2002; Steffan-Dewenter et al. 2002; Winfree et al. 2007). In addition to the forest cover, another landscape effect, the amount of forest edge represented by the total length (m) within the same six radii (250, 500, 750, 1,000, 1,250 and 1,500 m) was measured, using

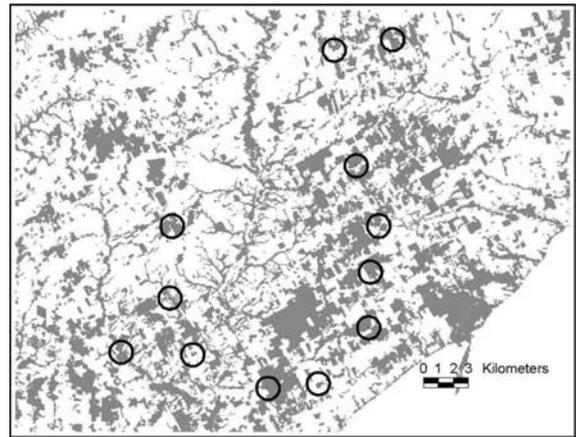


Fig. 1 Twelve study sites of *E. americanum* with 750-m radius used to obtain the forested landscape values, amount of forest cover and length of forest edge, in Norfolk County of Ontario, Canada. Shaded areas indicate forests. The geospatial data were obtained from the Ontario Base Map Series in 2003 (Ontario Ministry of Natural Resources, Peterborough, Ontario, Canada)

ArcView. We then investigated if there were any edge effects.

Furthermore, to see the effects of forest cover on flowering density of *E. americanum*, and later to check on the effects of the plant density on seed set, flowering heads within a 10-m radius from the central point of the population were counted at each of the 12 sites on 4 and 5 May.

Sampling of bees

Three yellow bowl pan traps (diameter = 15 cm top × 6.5 cm base; 7 cm deep) with approximately 200 ml of soapy water were used to collect the potential bee pollinator species (Potts et al. 2005). They were set out within the *E. americanum* populations at each of the 12 sites. The three traps for each site were randomly placed 5 m apart on the ground. To prevent possible disturbances by mammals and birds, all the pans were covered with metal mesh fence (1-inch chicken wire) supported by twigs. The spacing in the mesh was large enough for even the largest bees in the region (bumble bee queens) to pass through. The traps were deployed for a total of 72 h from 4 to 7 May on sunny days during the blooming of *E. americanum*. Placement of and collecting from

the traps were done in the evenings from 18:00 to 21:00.

Different bee species and sexes within species are attracted to different colors and shapes of pan traps (Leong and Thorp 1999; Cane et al. 2000; Toler et al. 2005). It was recognized that the results may be biased through the pan traps, but the bias would be consistent among the 12 study sites.

Trapped bees were taken to the laboratory to be pinned and labeled. Specimens were identified by John Ascher and Sam Droege using standard references, reference collections at the American Museum of Natural History and the Smithsonian, and online keys available at www.discoverlife.org. Vouchers are deposited in the Department of Environmental Biology, University of Guelph. As well as analyses of all collected bees (non-cleptoparasitic females and males, and cleptoparasites), analyses of pollen-foraging bees (non-cleptoparasitic females), which were likely more important pollinators, were made. Moreover, as indicated above, analyses on *A. erythronii*, *A. carlini* and *A. vicina* alone were attempted for our species level analysis.

Seed set

For each of the 12 populations, we randomly selected 17 individual stalks, at least 30 cm from each other, of *E. americanum* with buds on 24 and 25 April. After blooming on 15 May, the stalks with open flowers were covered by polypropylene 3-mm-square mesh bags (product number ON-6200, InterNet, Minneapolis, Minn.) to prevent possible damage by herbivorous mammals and birds.

In addition to those open pollinated flowers, 17 individual flowering stalks were randomly selected at each site for hand self-pollinations to check for self-compatibility in each population (Sage et al. 2005). Stalks with buds were covered with paper bags on the same days the buds were selected on 24 and 25 April. Each recipient flower's bag was opened and the flower pollinated by dusting its stigma with pollen from its own anthers by use of a wooden tooth pick. The flowers were then re-bagged. This was done 1 or 2 days after anthesis, following the protocol of Harder et al. (1985).

On 24 May, all of the swollen fruits were taken to the laboratory where they were dissected and the

developed and undeveloped seeds (the latter from unfertilized ovules or aborted seeds) were counted using Wolfe's (1983) criteria. The mean percentage of seeds set was obtained by comparing the ratios of developed to aborted seeds for each of the 17 fruits for each site.

Statistical analyses

First, we made simple linear regression analyses to see effects of forest cover amount (m^2) on abundance and species richness of all collected bees and of pollen-foraging bees alone, where each of the forest covers within the six radii (250, 500, 750, 1,000, 1,250 and 1,500 m) was used as the predictor variable. Similarly, for the species level analyses on our selected *Andrena*, we made linear regression analyses on abundance of each species, where each of the forest covers within the six radii was used as the predictor variable. These and following statistical computations were done by PROC GLM of SAS (version 8.2, SAS Institute, Cary, N.C.), and a type I error rate of 0.05 was set for all of the analyses.

Second, to see if there were any edge effects, we used simple linear regression analyses to test for abundance and species richness of all collected bees and of pollen-foraging bees alone, where the amount forest edge represented by the length (m) was used as the predictor variable. Similarly, for the species-level analyses on our selected *Andrena*, we made linear regression analyses on abundance of each species, where each of the forest edge lengths within the six radii was used as the predictor variable.

Third, we made linear regression analyses for the seed set in *E. americanum*. Simple linear regression analyses were made to test for the seed set in *E. americanum*, where the amount of forest cover and length forest edge were analyzed at the six radii. We also made multiple regression analyses, where both landscape values (the amount of forest cover and the length forest edge) and bee abundances were used as the predictor variables. To select the predictor variables, we used the results from the analyses of bee community and species on the amount of forest cover and length of forest edge.

Additionally, we made regression analyses to examine the relationship, if any, between forest cover and/or forest edge and flowering density of

E. americanum, and between the flowering density and seed set. To select the radii to measure characteristics of forested landscape, we referred the results of the radii obtained from the analyses of bee community and species on the amount of forest cover and length of forest edge.

Results

Bees

In total, 564 bee individuals were collected from the 12 study sites. Ten bees had to be excluded from analysis of species richness because they could not be identified. Of the remaining 554 individuals, 46 species were found in the families Colletidae, Megachilidae, Halictidae, Andrenidae and Apidae (Table 1). Among the 564 individuals, 208 (36.9% of total individuals) were pollen-foraging female bees represented by 32 (69.6% of total species) species of the families Colletidae, Halictidae, Andrenidae and Apidae (Table 1).

The regression analyses indicated significant positive relationships with the highest R^2 value between the forest cover within 750 m radius and abundance of all bees and their species richness, but no significant relationships were found from the forest covers within the other five radii (250, 500, 1,000, 1,250 and 1,500 m) (Table 2). The analysis also indicated a significant positive relationship with the highest R^2 value between the forest cover at 750 m radius and abundance of pollen-foraging bees (Table 3). However, no significant relationships were detected between forest cover at the other five radii and abundance of pollen-foraging bees, and between forest covers at any of the six radii and species richness of pollen-foraging bees (Table 3).

No significances were indicated when the regression analyses were made on the abundance and species richness of both all bees and pollen-foraging bees in relation to the length of forest edge within any of the six radii (Tables 4, 5).

For the species level analysis, because we collected only seven individuals of *A. erythronii*, the further analysis on the species was not made on this species. We collected 240 *A. carlini* and 99 *A. vicina* individuals. The regression analyses on the abundances on these two species showed no significances

in relation to both the amount of forest cover and the length of forest edge within the six radii (Tables 6, 7).

Seed set

From the 204 hand self-pollinated flowers of *E. americanum*, we found no stalks with fruits expressing developed seed in any of the 12 sites.

Using the data on the open pollinated flowers, we found a significant positive relationship with the highest R^2 value between the seed set and forest cover within 750 m radius, but no significant relationships were found from the forest covers within the other five radii (250, 500, 1,000, 1,250 and 1,500 m) (Table 8). The analyses indicated no significances when lengths of forest edge with any of the six radii were used for the predictor of the seed set (Table 8).

Multiple leaner regression analyses for the seed set of the open pollinated flowers indicated significant positive relationships, when abundance of all bees alone, and when both forest cover and abundance of all bees together were used as the predictor variables for the seed set (Table 9). However, significant relationships were not indicated when the abundance of pollen-foraging bees was included as the predictor variable for the seed set (Table 9).

Additionally, either significant positive or negative relationships were not indicated between the number of flowering stalks and forest cover at 750 m radius ($R^2 = 0.001$, $F_{1,10} = 0.01$, $P = 0.917$) and between the seed set and the number of flowering stalks in a population ($R^2 = 0.091$, $F_{1,10} = 1.00$, $P = 0.341$).

Discussion

An assessment of all of the bees sampled by pan trap indicated that abundance and species richness were positively related to forest cover. However, the results of species richness of pollen-foraging (non-cleptoparasitic female) bees and the abundance of two *Andrena* species, *A. carlini* and *A. vicina*, suggest that they are not affected by forest loss. None of our bee assemblages and species was affected by the effects of forest edge amount. It is still premature to conclude that forest loss adversely affects whole bee

Table 1 Bee species and their abundance collected by yellow pan traps in Norfolk County of Ontario, Canada. Numbers and C within brackets indicate the abundance of female pollen-foraging individuals and cleptoparasitic species, respectively

Family	Species	No. of individuals	
Colletidae	<i>Colletes inaequalis</i> Say	3 (3)	
Megachilidae	<i>Osmia atriventris</i> Cresson	1 (0)	
Halictidae	<i>Augochlorella aurata</i> (Smith)	1 (1)	
	<i>Halictus confusus</i> Smith	2 (2)	
	<i>Halictus rubicundus</i> (Christ)	1 (1)	
	<i>Lasioglossum (Lasioglossum) coriaceum</i> (Smith)	5 (5)	
	<i>Lasioglossum (Lasioglossum) paraforbesii</i> McGinley	3 (3)	
	<i>Lasioglossum (Dialictus) coeruleum</i> (Robertson)	3 (3)	
	<i>Lasioglossum (Dialictus) cressonii</i> (Robertson)	1 (1)	
	<i>Lasioglossum (Dialictus) foxii</i> (Robertson)	4 (4)	
	<i>Lasioglossum (Dialictus) laevisimum</i> (Smith)	18 (18)	
	<i>Lasioglossum (Dialictus) lineatulum</i> (Crawford)	7 (7)	
	<i>Lasioglossum (Dialictus) nigroviride</i> (Graenicher)	1 (1)	
	<i>Lasioglossum (Dialictus) oblongum</i> (Lovell)	8 (8)	
	<i>Lasioglossum (Dialictus) perpunctatum</i> (Ellis)	1 (1)	
	<i>Lasioglossum (Dialictus) pilosum</i> (Smith)	3 (3)	
	<i>Lasioglossum (Dialictus) versans</i> (Lovell)	4 (4)	
	<i>Lasioglossum (Dialictus) sp. 1</i>	1 (1)	
	Unidentified <i>Lasioglossum (Dialictus)</i>	2 (2)	
	Andrenidae	<i>Andrena barbilabris</i> (Kirby)	3 (3)
		<i>Andrena bisalicis</i> Viereck	2 (0)
		<i>Andrena carlini</i> Cockerell	240 (61)
<i>Andrena dunningi</i> Cockerell		6 (3)	
<i>Andrena erythrogaster</i> (Ashmead)		2 (0)	
<i>Andrena erythronii</i> Robertson		7 (7)	
<i>Andrena forbesii</i> Robertson		6 (0)	
<i>Andrena frigida</i> Smith		2 (2)	
<i>Andrena geranii</i> Robertson		3 (3)	
<i>Andrena imitatrix</i> Cresson		1 (0)	
<i>Andrena milwaukeeensis</i> Graenicher		6 (0)	
<i>Andrena miserabilis</i> Cresson		6 (4)	
<i>Andrena nasonii</i> Robertson		29 (8)	
<i>Andrena nigrihirta</i> (Ashmead)		1 (0)	
<i>Andrena rugosa</i> Robertson		5 (5)	
<i>Andrena sigmundi</i> Cockerell		1 (0)	
<i>Andrena tridens</i> Robertson		16 (16)	
<i>Andrena vicina</i> Smith		99 (22)	
Unidentified <i>Andrena</i>		3 (2)	
Apidae		<i>Apis mellifera</i> Linnaeus	2 (2)
	<i>Bombus bimaculatus</i> Cresson	1 (1)	
	<i>Ceratina calcarata</i> Robertson	9 (1)	
	<i>Nomada cressonii</i> Robertson	2 (C)	
	<i>Nomada illinoensis</i> Robertson	1 (C)	
	<i>Nomada luteoloides</i> Robertson	11 (C)	

Table 1 continued

Family	Species	No. of individuals
	<i>Nomada maculata</i> Cresson	21 (C)
	<i>Nomada pygmaea</i> Cresson	1 (C)
	<i>Nomada sayi</i> Robertson	3 (C)
	<i>Nomada</i> sp 1	1 (C)
	Unidentified <i>Nomada</i>	5 (C)

communities in our study region in Ontario (see Cane 2001): the sampling time was limited to the vernal flowering period and the trapping may have been biased. However, the potential functional effects of the representationally collected bees in pollination of *E. americanum* would be clear because our sampling was made during its blooming duration.

Winfree et al. (2007) found that abundance and species richness of bee community in southern New Jersey decrease as forest cover increase. One of the possible explanations for the differences between their results and ours is seasonal difference of the diverse forested ecosystems. Although they sampled bees from spring to summer (April–August), our study in a deciduous forest was made in only spring (beginning of May), which is before the leaf-out of the forest canopy. Understory conditions in temperate deciduous forests dramatically change from season to

season (Barnes et al. 1998; Kimmins 2004): ecosystems of deciduous forest understory in different seasons are almost different ecosystems. For example, many of forest understory herbs and shrubs bloom in spring. Many of our collected bees would be depending upon these vernal flower resources in forest.

No seed set occurred on plants with flowers retained in bags and hand self-pollinated. Studies suggest that the ratio of self-incompatibility to self-compatibility of *E. americanum* varies (0–33.3% of fruit set success), depending on population and location (Bernhardt 1977; Harder et al. 1985, 1993). The populations of *E. americanum* investigated seem to be self-incompatible, so out crossing followed by insect pollination would be essential for seed set.

The results from open pollinated flowers showed a significant positive relationship of forest cover at

Table 2 Relationships between the amounts of forest cover (m²) within the six radii (250, 500, 750, 1,000, 1,250, 1,500 m) and all collected bees in Norfolk County of Ontario, Canada

Radius (m)	<i>a</i>	<i>b</i>	<i>R</i> ²	<i>F</i>	<i>P</i>
<i>Abundance</i>					
250	23.707	0.0001753	0.106	1.18	0.302
500	21.194	0.0000576	0.222	2.86	0.122
750	14.196	0.0000357	0.374	5.97	0.035
1,000	14.437	0.0000213	0.300	4.28	0.066
1,250	17.406	0.0000136	0.196	2.44	0.149
1,500	21.737	0.0000087	0.123	1.41	0.263
<i>Species richness</i>					
250	8.527	0.0000274	0.063	0.67	0.433
500	6.312	0.0000131	0.277	3.84	0.079
750	5.619	0.0000071	0.361	5.65	0.039
1,000	5.424	0.0000044	0.311	4.52	0.059
1,250	5.872	0.0000029	0.215	2.74	0.129
1,500	7.224	0.0000017	0.114	1.29	0.282

Simple linear regressions for the abundance and for the species richness of all collected bees are shown. *a* and *b* are regression parameters

Table 3 Relationships between the amounts of forest covers (m²) within the six radii (250, 500, 750, 1,000, 1,250, 1,500 m) and pollen-foraging bees in Norfolk County of Ontario, Canada

Radius (m)	<i>a</i>	<i>b</i>	<i>R</i> ²	<i>F</i>	<i>P</i>
<i>Abundance</i>					
250	5.856	0.0000864	0.214	2.72	0.130
500	6.594	0.0000240	0.320	4.71	0.055
750	5.863	0.0000125	0.380	6.13	0.033
1,000	5.752	0.0000076	0.315	4.60	0.058
1,250	7.150	0.0000047	0.193	2.40	0.153
1,500	9.308	0.0000028	0.103	1.15	0.308
<i>Species richness</i>					
250	5.406	0.0000227	0.077	0.83	0.382
500	4.552	0.0000086	0.217	2.77	0.127
750	4.774	0.0000040	0.201	2.51	0.144
1,000	4.902	0.0000023	0.152	1.79	0.210
1,250	4.872	0.0000016	0.123	1.40	0.265
1,500	5.111	0.0000011	0.092	1.01	0.338

Simple linear regressions for the abundance and for the species richness of pollen-foraging bees are shown. *a* and *b* are regression parameters

750 m radius on the seed set in *E. americanum*. The self-incompatible populations in our study sites of *E. americanum* follow the trend found by the recent review of plant reproductive susceptibility by Aguilar et al. (2006), where they found that self-incompatible species are in fact more susceptible to reproductive

impairment due to habitat loss because they are highly dependent on animal pollinators. In fact, we found significant positive relationships on the seed set of *E. americanum* when abundance of all collected bees alone and both the abundance and forest cover were used as the predictors. Although there is no

Table 4 Relationships between the amounts of forest edge, measured by length (m), within the six radii (250, 500, 750, 1,000, 1,250, 1,500 m) and all collected bees in Norfolk County of Ontario, Canada

Radius (m)	<i>a</i>	<i>b</i>	<i>R</i> ²	<i>F</i>	<i>P</i>
<i>Abundance</i>					
250	35.812	0.00946	0.068	0.73	0.412
500	31.372	0.00402	0.117	1.33	0.276
750	34.674	0.00151	0.050	0.53	0.485
1,000	37.617	0.00066	0.022	0.23	0.644
1,250	43.161	0.00017	0.002	0.02	0.883
1,500	41.130	0.00019	0.003	0.03	0.866
<i>Species richness</i>					
250	11.822	0.00029	0.002	0.02	0.903
500	8.941	0.00083	0.121	1.38	0.268
750	9.253	0.00036	0.068	0.73	0.414
1,000	9.809	0.00016	0.034	0.35	0.566
1,250	8.947	0.00014	0.039	0.41	0.539
1,500	7.606	0.00014	0.044	0.46	0.514

Simple linear regressions for the abundance and for the species richness all collected bees are shown. *a* and *b* are regression parameters

Table 5 Relationships between the amounts of forest edge, measured by length (m), within the six radii (250, 500, 750, 1,000, 1,250, 1,500 m) and pollen-foraging bees in Norfolk County of Ontario, Canada

Radius (m)	<i>a</i>	<i>b</i>	<i>R</i> ²	<i>F</i>	<i>P</i>
<i>Abundance</i>					
250	15.199	0.00181	0.021	0.21	0.656
500	11.214	0.00157	0.149	1.76	0.215
750	11.922	0.00066	0.080	0.87	0.373
1,000	12.576	0.00033	0.047	0.5	0.496
1,250	12.088	0.00024	0.035	0.37	0.558
1,500	11.014	0.00020	0.029	0.3	0.598
<i>Species richness</i>					
250	7.196	0.00103	0.035	0.37	0.558
500	4.838	0.00092	0.267	3.65	0.085
750	5.066	0.00041	0.161	1.92	0.196
1,000	5.250	0.00022	0.110	1.24	0.292
1,250	4.119	0.00019	0.125	1.42	0.260
1,500	1.838	0.00021	0.164	1.96	0.192

Simple linear regressions for the abundance and for the species richness pollen-foraging bees are shown. *a* and *b* are regression parameters

statistical power to disentangle cause and effect among the values and similarly no manipulative experiments (like pollen hand supplementation vs. open treatment in each site) in this study, the results are nevertheless consistent with there having been an effect of forest loss on the bee abundance, which then had consequences for the seed set.

No significant relationship was however found when we used abundance of pollen-foraging bees, a subset of all collected bees to predict the seed set. More trapping methods, including pans of other colors, and direct observations on the abundance, species richness and behaviors (e.g., pollen versus nectar foraging) of flower visiting bees (e.g. Frankie

Table 6 Relationships between the amounts of forest covers (m²) within the six radii (250, 500, 750, 1,000, 1,250, 1,500 m) and the abundance two bee species, *Andrena carlini* and *Andrena vicina*, in Norfolk County of Ontario, Canada

Radius (m)	<i>a</i>	<i>b</i>	<i>R</i> ²	<i>F</i>	<i>P</i>
<i>Andrena carlini</i>					
250	9.035	0.0000825	0.061	0.65	0.437
500	9.203	0.0000241	0.102	1.13	0.312
750	6.531	0.0000147	0.165	1.98	0.190
1,000	6.667	0.0000087	0.132	1.51	0.247
1,250	6.696	0.0000061	0.104	1.16	0.307
1,500	10.602	0.0000032	0.045	0.47	0.510
<i>Andrena vicina</i>					
250	5.846	0.0000181	0.011	0.11	0.751
500	4.820	0.0000077	0.037	0.38	0.551
750	2.481	0.0000063	0.108	1.21	0.297
1,000	2.845	0.0000035	0.077	0.84	0.382
1,250	3.720	0.0000021	0.043	0.45	0.518
1,500	2.426	0.0000020	0.061	0.65	0.438

Simple linear regressions for each of the species are shown. *a* and *b* are regression parameters

Table 7 Relationships between the amounts of forest edge, measured by length (m), within the six radii (250, 500, 750, 1,000, 1,250, 1,500 m) and the abundance two bee species, *Andrena carlini* and *Andrena vicina*, in Norfolk County of Ontario, Canada

Radius (m)	<i>a</i>	<i>b</i>	R^2	<i>F</i>	<i>P</i>
<i>Andrena carlini</i>					
250	20.789	-0.00067	0.001	0.01	0.927
500	21.076	-0.00028	0.001	0.01	0.906
750	25.922	-0.00072	0.030	0.31	0.589
1,000	30.351	-0.00072	0.071	0.76	0.403
1,250	35.579	-0.00070	0.098	1.09	0.321
1,500	41.987	-0.00069	0.110	1.24	0.292
<i>Andrena vicina</i>					
250	1.925	0.00535	0.204	2.56	0.141
500	3.095	0.00133	0.119	1.35	0.272
750	2.628	0.00069	0.097	1.08	0.324
1,000	1.219	0.00049	0.117	1.32	0.278
1,250	3.704	0.00020	0.030	0.31	0.591
1,500	0.911	0.00023	0.044	0.46	0.514

Simple linear regressions for each of the species are shown. *a* and *b* are regression parameters

et al. 1997; Klein et al. 2002, 2003a, b; Cairns et al. 2005; Hines and Hendrix 2005) would reveal more completely representative of the entire functional group (Kevan et al. 1997; Belaussoff et al. 2003). However, our results suggest that diverse insect species including male and cleptoparasitic (non-pollen-foraging) bees seem to be effective pollinators

for *E. americanum* as indicated by the results of regression analyses with and without these bees.

The effects of each of our collected bee species on the pollination mechanisms of *E. americanum* were not considered in the detailed analyses on the pollination mechanisms. Different pollinator species vary in their pollination effectiveness. For instance,

Table 8 Relationships between seed set of *E. americanum* and both the amount of forest covers (m²) and the length of forest edge (m) within the six radii (250, 500, 750, 1,000, 1,250, 1,500 m) and in Norfolk County of Ontario, Canada

Radius (m)	<i>a</i>	<i>b</i>	R^2	<i>F</i>	<i>P</i>
<i>Amount of forest cover</i>					
250	15.405	0.0000617	0.087	0.95	0.352
500	11.841	0.0000263	0.306	4.42	0.062
750	10.118	0.0000147	0.419	7.22	0.023
1,000	10.478	0.0000086	0.323	4.77	0.054
1,250	12.019	0.0000053	0.200	2.49	0.145
1,500	15.564	0.0000028	0.083	0.90	0.364
<i>Length of forest edge</i>					
250	19.060	0.00384	0.075	0.81	0.390
500	20.125	0.00089	0.038	0.40	0.541
750	21.274	0.00028	0.012	0.12	0.737
1,000	20.164	0.00024	0.020	0.20	0.663
1,250	23.039	0.00003	0.0003	0.00	0.956
1,500	27.184	-0.00011	0.007	0.07	0.790

a and *b* are regression parameters

Table 9 Linear regressions using the forest cover (X_{forest}) within 750 m radius and the abundance of all bees (X_{abee}) and pollen-foraging bees (X_{pfbee}) as the predictor variables of the seed set of *E. americanum* (Y_{seed})

Model	a	b_1	b_2	R^2	F	P
$Y_{\text{seed}} = a + b_1 X_{\text{abee}}$	11.442	0.259		0.444	8.00	0.018
$Y_{\text{seed}} = a + b_1 X_{\text{abee}} + b_2 X_{\text{forest}}$	7.735	0.168	0.0000087	0.536	5.20	0.032
$Y_{\text{seed}} = a + b_1 X_{\text{pfbee}}$	13.744	0.569		0.258	3.48	0.092
$Y_{\text{seed}} = a + b_1 X_{\text{pfbee}} + b_2 X_{\text{forest}}$	8.964	0.197	0.0000122	0.438	3.51	0.075

a , b_1 and b_2 are regression parameters

the gynodioecious herb *Knautia arvensis* (L.) Coult. (Dipsacaceae) in Sweden is visited by both generalist and specialist flower visitors, but the specialist bee *Andrena hattorfiana* (Fabricius) is a more effective pollinator than are generalist visitors (Larsson 2005). Like *K. arvensis*, *E. americanum* is visited by diverse bee species, including a specialist, *A. erythronii* (Michener and Rettenmeyer 1956), and numerous generalists (Blanchan 1916; Bernhardt 1977; Krombein et al. 1979; Harder et al. 1985, 1993). This suggests that although only seven *A. erythronii* individuals were found, indicating that it may not be playing the most important role in pollinating *E. americanum*, in our study region, it would be interesting to investigate the populations of *A. erythronii* and their pollination effectiveness for *E. americanum*.

We found, regardless of forest cover, seed set was not influenced by density of flowering stalks of *E. americanum*, which was also uninfluenced by forest cover at the radius of 750 m. Other researchers have found the seed sets of self-incompatible plants are affected positively and negatively or not affected by population densities and sizes (e.g., Agren 1996; Kunin 1997; Molano-Flores and Hendrix 1999; Forsyth 2003; Waites and Agren 2004; Kirchner et al. 2005). Their results, and the findings, suggest that the landscapes surrounding each population are more important than plant density or size, or both of insect pollinated-plants in influencing seed set. Our analyses indicate that forest loss has significantly negative impacts on bee communities (i.e., the potential pollinators) and seed sets in populations of self-incompatible populations of *E. americanum*, which potentially could lead to local extirpation of sensitive bee species and the plant. Although the population densities of the study plants presently are unaffected by landscape change, it is suggested that

over time a senescing and obligately out-crossing population with diminished sexual reproductive output would be in jeopardy.

Acknowledgements We thank Long Point Conservation Authority, M. Armstrong, J. DeCloet and J. Knack for access to the study sites. We also thank B. Viana, F. Silva, J. Trevors and G. Umphrey for discussion, A. Pawlowski, K. Ferguson and R. Barbero for their assistance with the field and laboratory work, A. Manceur and V. MacPhail for their assistance with the field sampling, A. Serafin for supplying plant mesh covering, C. Connell and Q. Shirk-Luckett for GIS support and S. Droege for identifying *Lasioglossum* (*Dialictus*) bees. This work was supported by a scholarship from the Rotary Foundation to H. Taki and a grant from the Natural Sciences and Engineering Research Council of Canada to P.G. Kevan.

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