

The effects of urbanization on ant communities and myrmecochory in Manitoba, Canada

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Abstract With the increase in urbanization globally, there is an increased need to understand the ecology of forest fragments in urban and urbanizing landscapes. Although urban forests are known to be relatively lacking in plants whose seeds are dispersed by ants, little is known about the effects of urbanization on the community composition and behaviour of forest dwelling ants. Ant communities in forest fragments along an urban–rural gradient were described using a rapid quadrat search technique and multivariate analysis. Interactions between the ants and seeds of the myrmecochorous *Viola pubescens* within a subset of these forests were described using a series of cafeteria experiments. Urbanization was found to be associated with changes in microhabitat characteristics and a concomitant simplification of the ant community. Despite this, the removal rate of *V. pubescens* seeds actually increased in urban forests, which may be a result of the foraging behaviour of the remaining species.

Keywords Ant communities · Habitat fragmentation · Land use · Myrmecochory · Seed dispersal · Riparian forest

Introduction

As landscapes across the globe are progressively urbanized, conservation of extant natural habitat becomes increasingly important (McDonnell and Pickett 1990; McKinney 2002).

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Forests in urban areas are under particular stress and studies have identified many urban-associated changes in communities of birds (e.g., Bolger et al. 1997; Parody et al. 2001), small vertebrates (e.g., Dickman 1987; Germaine and Wakeling 2001) and insects (e.g., Bolger et al. 2000; Gibb and Hochuli 2002; Shochat et al. 2004).

In addition, comparisons of plant communities in urban and non-urban forests on Staten Island (Robinson et al. 1994), in Wisconsin (Hoehne 1981) and in Manitoba (Moffatt et al. 2004) found urban communities to exhibit significant changes, including a decline in the abundance and diversity of native species and an increase in the abundance and diversity of non-natives. These studies, from various parts of North America have found similar patterns in plant response to urbanization. Generally species whose seeds are dispersed by birds, such as *Rhamnus cathartica* or *Prunus virginiana* exhibit relative increases in urban areas, while species whose seeds are dispersed by ants, such as *Viola* spp. exhibit relative decreases in urban areas (Robinson et al. 1994; Hoehne 1981; Moffatt et al. 2004).

Many spring-flowering plants in eastern North America, including several species of *Viola*, benefit from enhanced seed dispersal as part of a mutualistic relationship with ants. Seeds of such myrmecochorous plants bear a sugar and lipid rich body called an elaiosome, which acts as food sources for ant colonies (e.g., Petal 1978; Beattie 1985). Foraging ants collect and transport these elaiosome-bearing seeds to nests, where the elaiosome is consumed and the seed is discarded either in unused galleries or in areas adjacent to the nest (Beattie 1985). These seeds may benefit from decreased competition (Culver and Beattie 1980; Pudlo et al. 1980; Beattie 1985), deposition in beneficial micro-sites (Beattie and Culver 1983; Beattie 1985), or increased dispersal distance (Pudlo et al. 1980; Beattie 1985). Thus, *Viola* seeds, which may be explosively dispersed up to 4 m, can be dispersed over 10 m by ants (e.g., Willson 1993; Pudlo et al. 1980).

In addition to the effects on plant communities, urbanization may also affect the composition or behaviour of forest-dwelling ant communities. For example, urban habitat fragments in both California and Quebec exhibited an alteration in ant species assemblages, including a decrease in species richness, a decrease in the number of habitat specialists and an increase in the relative abundance of non-native ant fauna, associated with urbanization (Suarez et al. 1998; Lessard and Buddle 2005). Although little is known about the interaction between ants and seeds in urban areas, habitat disturbance has been associated with disruption of the seed dispersal mutualism (e.g., Pudlo et al. 1980; Andersen and Morrison 1998). In temperate deciduous forests this has included a decrease in both the rate and distance of seed dispersal by ants (Pudlo et al. 1980).

Effective conservation of plant diversity in extant urban forests requires an increased understanding of the impacts of land use on ecological processes, including seed dispersal mutualisms. The purpose of this study is to describe the changes in ant community composition and rate of seed removal by ants in temperate deciduous forests along an urban-rural gradient.

Materials and methods

Site description

This study was conducted in riparian forests along the Assiniboine River in southeastern Manitoba, Canada (49°46' N, 97°9' W). These forests are dominated by *Fraxinus pennsylvanica*, *Quercus macrocarpa* and *Acer negundo*. Dominant understorey species

include *Rhus radicans*, *Aralia nudicaulis*, *Matteuccia struthiopteris*, *Laportea canadensis*, and *Thalictrum venulosum*. Myrmecochorous plants in this system include *Trillium cernuum*, *Viola pubescens* and *Viola canadensis* (Moffatt 2001).

A previous study in this system classified riparian forests along the Assiniboine River into urban, suburban, and rural land use types according to their location and a qualitative analysis of surrounding land use. Forests were classified as ‘urban’ if they were situated in the city centre, with a local landscape dominated by industrial or multiple resident housing; ‘suburban’ if situated away from the city centre and surrounded by single family residences; or ‘rural’ if situated outside the city limits, and surrounded by farmland. Five forests of each land use type were randomly selected from those described previously (Moffatt et al. 2004) to study the impacts of urbanization on ant communities.

Ant community description

Nesting habitat preferences and impacts of land use were studied using a quadrat sampling method between June and August 2002. Five 5×5 m quadrats were randomly placed within each of the 15 forest sites. Searching was limited to mornings between approximately 0800 and 1100, as initial investigation suggested ant activity was highest during that time period. Preliminary results also indicated that 5×5 m quadrats were optimal; no additional species were found when size was increased to 10×10 m, although species were lost when quadrats were reduced to 2×2 m (Thompson 2003). Ants were collected by crawling through the quadrat, overturning objects, removing litter, breaking open detritus and aspirating samples from all ant nests.

Within each 5×5 m quadrat the number of recreation trails, the depth of leaf litter, the percent cover of coarse woody debris (>1 cm diameter), and the canopy cover of over-, mid-, and understorey was estimated. The canopy layer above 2 m was defined as overstorey, that between 0.5 and 2 m was defined as midstorey and any canopy below 0.5 m was defined as understorey. In addition, ground moisture was categorized as wet (i.e., standing water at least part of the summer), mesic (i.e., visibly moist 24 h after precipitation) or dry (i.e., no discernable soil moisture 24 h after precipitation). Forest patches were digitized and forest area and perimeter-to-area ratio were calculated using aerial photos taken in 1994 (Linnet 1994).

All ants were stored in 90% ethanol and identified using Wheeler and Wheeler (1963; 1977) and François (1973) and names were updated using Bolton (1995). Voucher specimens were deposited at the Department of Entomology, University of Manitoba.

Cafeteria experiments

Relative impacts of seed dispersing ants and vertebrate seed harvesters in two urban and two rural reference forests were studied using commercially provided *V. pubescens* seeds in unsupervised cafeteria-style experiments in July 2001 and 2002. At this time, seeds of resident populations of *V. pubescens* were maturing and seed pods dehiscent. Seed depot sets were randomly located at eight sites within each forest. Each set consisted of three depots 1-m apart. Debris was cleared and soil flattened in a 25 cm diameter circle around each depot. One depot was treated as an arthropod enclosure, one as a vertebrate enclosure, and the last as a no-enclosure control. The arthropod enclosure consisted of an aluminium

pie plate (22 cm diameter) the edge and lip of which were painted with sticky non-drying resin (Tanglefoot) to prevent arthropod entry. The vertebrate enclosure consisted of a cage (30×30×30 cm) with 1 cm wire mesh covering the sides and top, and fixed into the ground to prevent vertebrate foraging. The third depot allowed access by both arthropods and vertebrates. Twenty-four hours after creation of the depots five seeds were piled on the natural substrate or aluminium plate at each of the depots.

Seeds in each pile were counted and replaced after 12, 24, 36 and 48 h. Evidence of mastication by seed-eating arthropods at each of the depots was monitored. Evidence of mastication included the presence of empty seed coats and broken seeds. Any missing seeds that were not masticated on site were assumed to have been removed by ants (*sensu* Smith et al. 1989).

Although seed removal tests were conducted using seeds of *V. pubescens*, paired depot sets ($n=4$) were also conducted using the myrmecochorous *T. cernuum* in order to assess if seed removal were purely a species-based response. *Trillium cernuum* occurred in one urban and both rural sites. Similarly, paired tests ($n=4$) were also conducted on seeds of the non-myrmecochorous *Anemone canadensis* to determine if elaiosome and non-elaiosome bearing seeds were differentially removed. Finally, two cafeterias were situated in each of the rural forests within 1 m of an existing population of *V. pubescens*.

Data analysis

To examine the similarity of ant species composition among sites and land use types, we calculated the Euclidean distance between each pair of sites. The significance of the difference between ant species assemblages in the three land use classes was tested with an analysis of similarity (ANOSIM; Clarke 1993). Permutation tests ($n=1000$) were used to examine the efficiency of the classifications by randomly assigning data points to classes.

Relationships between ant nest density and environmental variables were described using stepwise multiple regression with backward elimination (SAS Institute 1988). Data were averaged per forest and log-transformed to meet the assumptions of normality (Zar 1974). Nest density for all species combined, nest density for each species, and overall species richness were regressed against land use (coded with dummy variables for ‘urban,’ ‘suburban’ and ‘rural’), wetness, trail density, and depth of leaf litter, CWD, and over, mid- and understorey canopies. A sequential Bonferroni adjustment was applied to the results of the regressions to avoid a group-wide type I error (Rice 1989).

Relative removal rates of *V. pubescens* seeds from enclosure treatments and the two land use types were characterized using two-factor ANOVA (SAS Institute 1988). Number of seeds removed during the 12, 24, 36 and 48-h period at each depot were averaged prior to ANOVA to avoid pseudoreplication. All data were log transformed prior to analysis in order to meet the assumptions of the ANOVA model and untransformed data are presented (Zar 1974). Orthogonal contrasts were used to compare removal rate by ants in urban and rural forests (SAS Institute 1988). Rate of removal of *V. pubescens* seeds from depots within 1 m of existing *V. pubescens* population with depots at least 30 m from any evident populations were tested with a Student’s *t*-test (SAS Institute 1988). Rate of removal of *T. cernuum*, and *A. canadensis* seeds were also compared to the removal rates of *V. pubescens* seeds using a Student’s *t*-test.

Table 1 Number of ant nests per 5 m² quadrat in forests of three land use intensities. Data are reported as mean (standard error)

	Urban	Suburban	Rural
<i>Camponotus noveboracensis</i>	0	0.8 (0.4)	0.12 (0.05)
<i>Camponotus pennsylvanicus</i>	0.4 (0.4)	0	0.4 (0.4)
<i>Formica aserva</i>	0	0	0.08 (0.08)
<i>Formica glacialis</i>	0.12 (0.07)	0.5 (0.2)	0.16 (0.07)
<i>Formica subaenescens</i>	0	0	0.04 (0.04)
<i>Lasius pallitarsis</i>	0.9 (0.1)	0.08 (0.04)	0.4 (0.1)
<i>Leptothorax muscorum</i>	0	0.04 (0.04)	0
<i>Myrmica detritinodis</i>	0	0.2 (0.1)	0.2 (0.1)
<i>Polyergus breviceps</i>	0	0	0.04 (0.04)
<i>Tapinoma sessile</i>	0	0.08 (0.04)	0

Results

Effects of land use on ant community composition

Fewer ant species occur in urban areas, and urban forests exhibit less within-class variation in ant community composition than forests in rural or suburban areas (Table 1). Although *Lasius pallitarsis* and *Leptothorax muscorum* were the only species that individually responded significantly ($p < 0.001$ and $p = 0.0009$, respectively) to land use, overall community composition varied significantly (ANOSIM $R = 0.4622$, $p < 0.001$) between the

Table 2 Influence and significance of land use (urban, suburban, rural) and habitat characteristics on ant nest density as identified by stepwise multiple regression with backward selection

	Landuse	wetness	trail density	leaf litter depth	coarse woody debris	mid-storey	under-storey	over-storey
Nest density	ns	**(-)	**(+)	ns	ns	ns	ns	ns
Species richness	ns	***(-)	*(+)	**(+)	ns	ns	ns	ns
<i>Camponotus noveboracensis</i>	ns	ns	ns	ns	ns	ns	ns	ns
<i>Camponotus pennsylvanicus</i>	ns	ns	ns	ns	ns	ns	ns	ns
<i>Formica aserva</i>	ns	ns	ns	ns	ns	ns	ns	ns
<i>Formica glacialis</i>	ns	**(-)	ns	ns	ns	ns	ns	ns
<i>Formica subaenescens</i>	ns	ns	ns	ns	ns	ns	ns	ns
<i>Lasius pallitarsis</i>	***	ns	ns	ns	ns	ns	ns	*(-)
<i>Leptothorax muscorum</i>	**	**(-)	ns	***(+)	**(+)	**(+)	ns	ns
<i>Myrmica detritinodis</i>	ns	**(-)	**(+)	***(+)	ns	ns	ns	ns
<i>Polyergus breviceps</i>	ns	ns	ns	ns	ns	ns	ns	ns
<i>Tapinoma sessile</i>	ns	ns	ns	ns	ns	ns	ns	ns

Significance levels: ns non significant, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Trends: (+) positive, (-) negative

Table 3 Removal rate of *Viola pubescens* seeds over a 12-h period from depots with exclosures. Data are reported as mean (standard error)

	Rural	Urban
No exclosure	1.9 (0.3)	3.3 (0.3)
Vertebrate exclosure	1.5 (0.2)	2.8 (0.3)
Invertebrate exclosure	1.3 (0.3)	0.8 (0.3)

three land use categories. When rural and suburban forests were considered separately, no significant difference was found in species composition (ANOSIM $R=0.272$, $p=0.057$).

Although there was no significant response to land use by either nest density or species richness, ants were significantly associated with selected environmental variables (Table 2). Soil wetness was negatively associated with ant nest density ($p=0.0066$) and species richness ($p=0.0005$), as well as the density of several individual species, and trail density positively associated with nest density ($p=0.0084$) and species richness ($p=0.0110$). Leaf litter depth was positively associated with species richness ($p=0.0023$) and the densities of the litter dwelling *Myrmica detritinodis*¹ ($p=0.003$) and *L. muscorum* ($p=0.0002$), as was CWD ($p=0.0016$) in the case of *L. muscorum*. Litter depth, in turn, was significantly negatively associated with urbanization ($F_{2,12}=4.20$, $p=0.0413$). *L. muscorum* also responded positively ($p=0.0015$) to midstorey canopy, while *L. pallitarsis* responded negatively ($p=0.0477$) to overstorey canopy.

Seed removal

Land use and exclosure type had a significant ($F_{5,59}=6.8$, $p<0.0001$) overall effect on *V. pubescens* seed removal rates. Although there were no differences between removal rates of seeds from the arthropod exclosures among forests, removal rates from the vertebrate exclosures in urban forests were significantly ($p=0.0308$) greater than in rural forests (Table 3). Seeds deposited within 1 m of mature seed-bearing *V. pubescens* were not removed significantly ($t_6=0.81$, $p=0.4479$) more rapidly than those deposited more than 30 m from any evident populations of *V. pubescens*. Similarly, there was no significant difference between removal rates of *V. pubescens* and *T. cernuum* ($F_{3,11}=2.06$, $p=0.1836$). However, *V. pubescens* had a significantly ($t_6=-7.50$, $p=0.0003$) greater removal rate than did the non-elaisome bearing *A. canadensis*; indeed, none of the *A. canadensis* seeds were removed from the vertebrate exclosures.

Discussion

Urbanization is significantly associated with habitat fragmentation and changes in extant habitat in these systems. Urban forests are significantly smaller, more isolated, and exhibit greater edge-to-area ratios than other forests. These forests also tend to have a lower vascular plant species richness and a greater proportion of exotic species in the flora

¹ Although *M. detritinodis* is considered to be a defunct species name (Bolton 1995), this name is expected to be resurrected in an upcoming revision of the genus (*A. Francoeur, personal communication*) Specimens were identified as *M. detritinodis* using these newly identified characteristics.

(Moffatt et al. 2004). Studies of microhabitat features within quadrats have also found that urban forests have significantly less accumulated leaf litter and significantly more canopy cover at the upper canopy layer. The combination of landscape-level and habitat-level changes in forest communities associated with urbanization may explain, in part, the observed changes in ant community composition.

Forest-dwelling ant communities are often structured based on factors such as physiography, microclimate and vegetation structure. Variation in factors such as soil moisture, canopy cover, and forest community composition have been shown to be associated with changes in ant diversity and community composition (e.g., Levings 1983; Wang et al. 2001). In Manitoba's riparian forests, canopy cover at the overstorey and midstorey, as well as the presence and abundance of coarse woody debris, leaf litter and recreational trails affected the presence and density of ant nests of various species. Disturbance of forests by activities such as commercial forestry, farming, as well as grazing or trampling by livestock have been associated with a loss of habitat diversity and vegetative cover. These alterations to forest habitat have been translated into changes in forest-dwelling ant communities, including in some cases, a drastic loss of species (e.g., Greenslade and Greenslade 1977; Punttila et al. 1991; Abensperg-Traun et al. 1996; Bestelmeyer and Wiens 2001). The disturbance of urban forests in Manitoba, including a loss in litter depth, may help explain the relative lack of ant diversity in these forests and the resultant significant differences in the ant community.

Ants remaining in urban forests (i.e., *Formica glacialis*, *L. pallitarsis*, and *Camponotus pennsylvanicus*) are habitat generalists, and can adapt to a greater range of environmental conditions (Wheeler and Wheeler 1963), and thus are able to persist in these highly degraded environments. Although *L. pallitarsis* prefer moist, shaded forests, they are able to adapt to heavily degraded or edge-dominated habitat (Wilson 1955). For example, although they were commonly found nesting in decaying oaks in rural forests, in urban forests, *L. pallitarsis* were observed nesting under cement blocks. There was also a strong negative association between the congeners *Camponotus novaboracensis* and *C. pennsylvanicus* in this area. Both nest in wood and have similar life histories (Sanders 1964). However, there was a change in dominance from *C. novaboracensis* to *C. pennsylvanicus* with increasing urban land use. Other studies (e.g., Sanders 1964) have also shown that *C. novaboracensis* tends to be restricted to large and undisturbed forests.

In addition to the effects of loss of habitat heterogeneity, flooding may also play an important role in determining ant composition in urban forests. Urban riparian forests tend to be smaller than suburban or rural riparian forests, thus spring flooding would have an impact on a larger proportion of the forest. As density of ant nests tends to decrease with soil moisture, annual flooding may have eliminated ants from a larger proportion of urban forests each spring.

Forests in suburban areas supported a greater variety of ant species, including the relatively uncommon *Tapinoma sessile* and *L. muscorum*. Although these forests are currently rich in ant species, suburban development and increasing use of suburban forests may be expected to cause increasing stresses on these forests in the future (Moffatt et al. 2004). As use increases, trail density may increase, and the amount of leaf litter and, potentially, mid- and understorey canopy may decrease (e.g., Cole 1993), thus leading to a possible decrease in ant species in suburban forests.

Variation or changes in ant communities can often be associated with variation or changes in the rate of seed dispersal. Thus, the species composition and activity rate in forest-dwelling ant communities can act as an effective predictor of the number of myrmecochorous plants in a given habitat (Beattie and Culver 1981). Studies in other

disturbed forests have found relationships between changes in ant assemblages and seed dispersal rates. Savannahs in Australia experiencing relatively low levels of disturbance support a more diverse ant community than undisturbed savannahs. These more diverse communities also exhibit seed dispersal distances that can double that found in undisturbed habitats. In heavily disturbed ecosystems however, ant species richness is much simpler, and seed dispersal is essentially non-existent (Andersen and Morrison 1998). In temperate deciduous forests in West Virginia, anthropogenic disturbance is associated with a decline in the richness of the ant community and a drastic reduction of the rate and distance of seed dispersal (Pudlo et al. 1980).

Despite the loss of ant species in urban forests, the removal rate of seeds *V. pubescens* actually increased in the current study. These differences may be explained, at least in part, in terms of the foraging behaviour of the species remaining in urban forests. Many of the ants in this region are potential seed dispersers. *L. pallitarsis*, *F. glacialis* and *M. detritinodis* were all observed removing seeds, while *C. pennsylvanicus* and *T. sessile* have been reported to disperse *Viola* seeds elsewhere (Culver and Beattie 1978; Pudlo et al. 1980).

Of the species found in this system, those remaining in urban forests tend to be the most competitively dominant (Fellers 1987; Gorb and Gorb 1999). Furthermore, members of the *Formica fusca* group (which includes *F. glacialis* and *F. subaenescens*) exhibit competitive release when interference at food resources from superior competitors is removed (Savolainen and Vepsäläinen 1988), and can also become more effective competitors when numerically superior (Fellers 1987). Not only will the behaviour of the *F. fusca* group at food resources change in a different competitive environment; but they tend to be among the most effective foragers of the forest-dwelling ants found in Manitoba. Although smaller species such as *T. sessile* and *M. detritinodis* typically find food depots more quickly, larger ants such as *Camponotus* spp. and *Formica* spp. generally have higher per capita seed removal rates (Fellers 1987; Gorb and Gorb 1999). Within *F. fusca*–*Camponotus*–*Lasius* habitat, seed removal rate is often greatest, not only due to greater average body size and behavioural release, but because *F. fusca*, as effective scavengers, are often “parasitized” by the other two genera. Both *Camponotus* and *Lasius* may use *F. fusca* to find food resources—due to their greater foraging ability and chemosensory perception—and then remove food from depots found by this species (Carroll and Janzen 1973; Stradling 1987). Increases in seed removal rate in urban forests may be, at least in part, associated with these changes in competitive environment.

To a certain extent, the composition of the plant community can affect seed removal rates as well. When encountering a choice of foods, ants may opt to remove the novel food more rapidly than a commonly available food source (e.g., Heithaus 1986). However this preference for exotic foods seems to hold only when the common food is fairly dense (Smith et al. 1989). It is possible that the significant increase in seed removal observed in urban riparian forests reflects the relative rarity of *Viola* seeds as a food source in these habitats, and a relative satiation in rural forests. Although they are quite rare in urban forests (less than 0.1% of the herbaceous cover in the study forests; S. Moffatt, unpublished data), they are also relatively rare in rural forests (approximately 3% of the herbaceous cover in the study forests; S. Moffatt, unpublished data). In addition, seeds placed within 1 m of existing seed-bearing *V. pubescens* in rural forests were not removed at a rate significantly different than those placed more than 30 m from existing populations.

Despite the rapid removal of seeds in urban forests they remain depauperate in myrmecochorous plants. Low connectivity of within this landscape might compromise dispersal among fragments. The average distance of seed dispersal by the myrmecochorous

ants remaining in these urban forests ranges from 0.72 to 12 m (Gómez and Espadaler 1998)—still several orders of magnitude less than average inter-patch distance in this system (Moffatt et al. 2004). However, results from this study suggest that the ant–plant mutualism is a relatively robust one, able to persist despite changes in site- and landscape-level habitat characteristics. This suggests the reintroduction of myrmecochorous plants into isolated forests to overcome their natural dispersal limitation might be an effective method of initiating local reproduction and dispersal.

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