

Does forest loss affect the communities of trap-nesting wasps (Hymenoptera: Aculeata) in forests? Landscape vs. local habitat conditions

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Abstract We investigated changes in the communities of trap-nesting Hymenoptera in forests in relation to forest loss on a landscape scale and understory conditions on a local habitat scale. Two specific questions were addressed. (1) Do the communities change with degrees of forest loss? (2) Do the communities change with varying local environmental conditions of understory habitats? The study was made in a landscape characterized by distributed forest patches within intensively managed agricultural surroundings. We deployed trap-nests at eight randomly selected sites in forests in summer. To quantify forest loss, the amount of forest coverage was calculated using GIS. To indicate local habitat conditions, the species richness of understory flowering plants was used. All together, 12 species of wasps and no bees were captured. Regression analyses showed that both abundance and species richness of the wasps were not significantly related to forest coverage. However, abundance of trap-nesting wasps was significantly

related to species richness of understory plants, but species richness of the wasps was not significantly related to the plants. These results suggest that communities of trap-nesting wasps in forests are influenced more by the local habitat conditions than by forest loss.

Keywords Carolinian zone · Cavity-nesting · Fragmentation · Habitat loss · Local characteristics

Introduction

Habitat loss is a current major threat to biodiversity (e.g. Findlay and Houlihan 1997; Debinski and Holt 2000; Gurd et al. 2001), and losses occurring within landscapes result in habitat fragmentation (Fahrig 2003; Ewers and Didham 2006). Our study attempts to quantify loss of deciduous forests and to analyze the effects by focusing on trap-nesting forest species (Hymenoptera: Aculeata) that use tunnels in tree trunks, branches, and logs. These insects, because of their reliance on availability of nest sites and materials, would be sensitive to forest loss. Changes in their diversity and abundance could affect overall ecosystem relationships through their roles as predators and pollinators.

Studies at landscape scales show habitat loss negatively affects both abundance and species richness of trap-nesting bees and wasps (Steffan-Dewenter 2002, 2003). Other investigators have also shown that surrounding landscapes significantly influence communities of various insect groups, such as ants, flies, beetles and Lepidoptera (Ricketts 2001; Ricketts et al. 2001; Soderstrom et al. 2001; Perfecto and Vandermeer 2002; Jeanneret et al. 2003; Kruess 2003). Nevertheless,

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there are studies that show local habitat conditions have more influence than landscape features on insect communities (Collinge et al. 2003; Summerville and Crist 2004). Both sets of findings imply that factors of both landscape and local habitat affect communities differently, depending on the organisms, seasons, ecosystems and the complex interactions among them (Stoner and Joern 2004; Tschardt et al. 2005).

The use of trap-nests is a valuable tool for environmental assessment (Tschardt et al. 1998). For example, by using the populations and communities of trap-nesting Hymenoptera, several researchers have investigated and discussed the effects of competitive non-native species on native species (Frankie et al. 1998), of different ecosystems on the diversity and abundance (Buschini 2006) and of various types and levels of land uses on the diversity and abundance (Fye 1972; Gathmann et al. 1994; Klein et al. 2002; Kruess and Tschardt 2002; Tylianakis et al. 2005).

The main purpose of our study was to investigate changes in the communities of trap-nesting Hymenoptera that could potentially be affected by forest loss on a landscape scale or as related to understory conditions of the local habitat, or both. In this study we address two specific questions. (1) Do the communities (abundance and species richness) of trap-nesters change with varying degrees of landscape scale forest loss? (2) Do their communities (abundance and species richness) change with local habitat conditions? These questions lead to the following null hypotheses, respectively. (1) There is no relationship between the communities of trap-nesters and forest loss (landscape condition). (2) There is no relationship between the communities of trap-nesters and local habitat condition.

Methods

Study sites

The study was made in Norfolk County of southern Ontario, Canada. Numerous high priority conservation plant species are known to occur in this deciduous forest zone (Allen et al. 1990; Argus 1992; Waldron 2003). The landscape is rather flat, characterized by distributed fragments of forest patches within intensively managed agricultural fields of crops, such as corn, soybean and tobacco. Eight forest sites, separated by a distance of at least 4 km were selected. Site selection of the eight sites was determined using randomized geographical points of latitudes and longitudes with the aid of ArcView (version 3.3, ESRI,

Redlands, California, USA) and global positioning system (GPS) (Garmin International, Olathe, Kansas, USA). The geospatial data of forest coverage was 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.

Trap-nests

At each of the eight sites, six trap-nest boxes (Fig. 1) were attached horizontally to trees about 1–1.5 m above the ground at the corners of an equilateral hexagonal array and 50 m from the randomly selected centre point. Consequently, neighbouring trap-nests were 50 m apart. The orientation of the nest entrances for each box was randomly selected. Each nest box was constructed from a 2-l milk carton ($9.5 \times 9.5 \times 16.5$ cm) with a polystyrene piece. Each box contained 36 cardboard trap-tubes; nine of each 3, 5, 7 and 9 mm internal diameters \times 15 cm length (Custom Paper Tubes Inc., Cleveland, Ohio, USA) to give hymenopteran species of different sizes access to the trap-tubes to make their nests (Potts et al. 2005). The trap-tubes were supported by holes in the polystyrene plug.

Each site contained two forms of the nest boxes, as three boxes were artificially covered and three were left un-covered. As reported by Taki et al. (2004), these two types were included to see if the covering technique would provide more opportunities for insects to colonize the trap-nests. However, since the same numbers of trap types were set at all of the eight sites, and because the goal of this study was comparisons among



Fig. 1 Nest box constructed from a 2-l milk carton ($9.5 \times 9.5 \times 16.5$ cm³) with a polystyrene piece. Each box contained 36 cardboard trap-tubes; nine of each 3, 5, 7 and 9 mm internal diameters \times 15 cm length

the sites, we did not include the covered and uncovered effects in our analyses. The data from both types of traps were therefore combined and treated as one for each site.

Insect collection

The setting and collecting of traps were at two-week intervals from 10 June to 20 August, 2003. At each time, trap-tubes were checked and collected if their ends were closed with soil or plant materials indicating completed nest construction (Krombein 1967). Collected nests were replaced immediately with new, empty ones and taken to the laboratory.

The individual trap-tubes were then placed into a larger plastic tube (12 mm ϕ \times 17 cm length \times 2 mm wall thickness) with both ends covered by metal mesh. All these plastic tubes were kept outside at the University of Guelph campus, Guelph, Ontario, Canada (42°31' N, 80°13' W) to allow for the newly laid Hymenoptera and their parasites, if present, to develop and emerge as adults. The tubes were checked for signs of emergence at least three times a week from June to November in 2003 and at least once a week from May to November in 2004. During the winter, the tubes were checked from time to time, but no insects emerged.

All insects taken from their tubes were pinned and labeled. The specimens were identified by M. Buck and the vouchers are deposited in the University of Guelph Insect Collection. The number of trap-tubes with any emerged insects was used for the analyses of their abundance, because it was expected that multiple individuals would emerge from a single host and a single individual would emerge from multiple hosts in some parasites (Krombein 1967).

Landscape and local conditions

To quantify amount of forest coverage as the landscape condition, circles of various radii (250, 500, 750 and 1,000 m) were created, using ArcView, on maps around each of the trap-nest locations. The scale for these circles was chosen from known scale-dependent effects and foraging ranges of Aculeata (Steffan-Dewenter et al. 2001, 2002; Gathmann and Tscharrntke 2002).

To indicate and quantify the understory condition, we used species richness of the flowering plants. Plant species in bloom at each of the eight sites were recorded once a month in June, July and August. A belt-transect (1-m wide) method was used and followed the perimeter of hexagons 20-m on a side with the

same centre (concentric) as was used for placement of the trap-nest boxes. The perimeter was walked and any plants in bloom in the belt were recorded. Upon each plant sighting, one specimen of that species was brought back to the laboratory at the University of Guelph to confirm field identification.

Data analysis

To test the relationships between abundance and species richness of trap-nest catches and forest loss (landscape scale) and the plant richness of the understory (local habitat scale), simple linear regression analyses were made. The statistical computations for the analyses were made by PROC GLM of SAS (version 8.2, SAS Institute, Cary, North Carolina, USA). The presence of outliers was examined by a studentized residuals' test with Lund's critical values (Lund 1975) and Cook's *D* statistic (Bowley 1999). A Type I error rate of 0.05 was set for all the statistical analyses.

To test the effects of forest loss at the level of the landscape, the abundance and the species richness of trap-nesting Hymenoptera were set as the dependant variables of the regression analysis. The percentage of forest coverage, obtained from the amount of forested areas within a circle, at each of the radii 250, 500, 750 and 1,000 m was set as the independent variable for the regression analysis. The null hypothesis of the tests is that there is no relationship between the communities (abundance and species richness) of trap-nesting Hymenoptera and the forest coverage within circles.

To test the effects of understory condition (local habitat), the abundance and the species richness of trap-nesting Hymenoptera were set as the dependant variables, and the species richness of understory plants was set as the independent variable. The null hypothesis of the tests is that there is no relationship between the communities (abundance and species richness) of trap-nesting Hymenoptera and the species richness of understory plants. Additionally, to check, if there were any relationships between forest loss and the species richness of understory plants, simple linear regression analyses were made using forest coverage at the radii of 250, 500, 750 and 1,000 m as the independent variable.

To see if there were the effects of the distance from the forest edge, we tested the null hypothesis that there is no relationship between plant species richness, abundance and species richness of trap-nesting Hymenoptera in the individual sites and their distances from the nearest forest edge by simple linear regression analyses. The plant species richness, abundance and species richness of trap-nesting Hymenoptera were

set as the dependant variables, and the distance from the nearest forest edge was set as the independent variable.

Results

A total of 612 trap-tubes with emerged insects were collected. Altogether, 12 species of trap-nesting wasps, including *Ancistrocerus adiabatatus*, *A. antilope*, *A. campestris*, *Euodynerus foraminatus*, *Symmorphus canadensis* and *S. cristatus* (Vespidae: Eumeninae), *Trypoxylon frigidum* and *T. lactitarse* (Crabronidae), *Isodontia mexicana* (Sphecidae), *Auplopus mellipes*, *Dipogon sayi sayi*, and *D. papago anomalus* (Pompilidae). Also, their parasites, including two species of wasps, *Chrysis coeruleans* and *C. nitidula* (Chrysididae), and flies in the genus *Amobia* (Sarcophagidae) were collected.

In total, 25 species of blooming flowering plants in the belt transects were recorded from all of the eight sites in June, July and August. Species richness of blooming plants at each site ranged from one to 15. The relationships for forest loss and species richness of blooming understory plants were not significant at any of the radii, 250, 500, 750 and 1,000 m ($P > 0.05$) (Table 1).

There were no outliers detected ($P > 0.05$). In relation to forest loss, both abundance (number of trap-tubes) (Table 2) and species richness of the trap-nesting wasps (Table 3) were not significantly related to forest coverage at any of the four radii (250, 500, 750 and 1,000 m) ($P > 0.05$). However, the wasp abundance was significantly related to the species richness of blooming plants observed in the understory ($P = 0.035$) (Fig. 2a), but no significance was indicated for species richness of wasps in relation to the understory plants ($P > 0.05$) (Fig. 2b).

We found no significant relationship between plant species richness ($R^2 = 0.026$; $F_{1,6} = 0.16$; $P = 0.70$),

Table 1 Results of simple linear regression analyses (R^2 , $F_{1,6}$ and P) between species richness of understory plants (Y) and forest coverage (X) at the four radii (250, 400, 750 and 1,000 m) in Norfolk County of Ontario, Canada

Radius (m)	a	b	R^2	F	P
250	6.74	-0.019	0.012	0.07	0.798
500	8.18	-0.045	0.071	0.46	0.524
750	8.35	-0.055	0.067	0.43	0.537
1,000	7.49	-0.043	0.022	0.13	0.728

The forest coverage (%) was calculated from the amount of forested areas within circles at each of the four radii. a and b are regression parameters ($Y = a + bX$)

Table 2 Results of simple linear regression analyses (R^2 , $F_{1,6}$ and P) between the abundance of trap-nest wasps (Y) and forest coverage (X) at the four radii (250, 400, 750 and 1,000 m) in Norfolk County of Ontario, Canada

Radius (m)	a	b	R^2	F	P
250	119.28	-0.59	0.082	0.58	0.492
500	121.72	-0.73	0.132	0.91	0.377
750	118.89	-0.78	0.096	0.63	0.456
1,000	104.08	-0.57	0.026	0.16	0.702

The abundance of trap-nesting wasps was obtained from the number of trap-nest tubes closed with soil or plant materials. The forest coverage (%) was calculated from the amount of forested areas within the circles at each of the four radii. a and b are regression parameters ($Y = a + bX$)

Table 3 Results of simple linear regression analyses (R^2 , $F_{1,6}$ and P) between the species richness of trap-nest wasps (Y) and forest coverage (X) at the four radii (250, 400, 750 and 1,000 m) in Norfolk County of Ontario, Canada

Radius (m)	a	b	R^2	F	P
250	6.90	-0.021	0.183	1.34	0.290
500	7.19	-0.029	0.374	3.59	0.107
750	7.31	-0.036	0.351	3.24	0.122
1,000	7.40	-0.041	0.249	1.99	0.208

The forest coverage (%) was calculated from the amount of forested areas within the circles at each of the four radii. a and b are regression parameters ($Y = a + bX$)

wasp abundance ($R^2 = 0.13$; $F_{1,6} = 0.88$; $P = 0.38$), and wasp species richness ($R^2 = 0.16$; $F_{1,6} = 1.16$; $P = 0.32$) in the individual sites and their distances from the nearest forest edge.

Discussion

Linear regression analyses show that habitat loss at landscape scales negatively affects both abundance and species richness of trap-nesting Hymenoptera and their natural enemies (Steffan-Dewenter 2002, 2003). However, our results show that communities of trap-nesting wasps were not affected by forest loss. We found that the communities of trap-nesting wasps were affected by local habitat complexity, indicated by species richness of flowering plants, rather than by loss of forest. Micro-environments influence insect communities in the understory of forests. For example, canopy gaps provide light to the forest understory and positively affect communities of Homoptera (Gorham et al. 2002), Diptera and other insect groups (Horn et al. 2005) there. Additionally, Fye (1972) reports that abundance and species richness of wasps and bees are higher in disturbed forest sites which had more light and cover of understory plants.

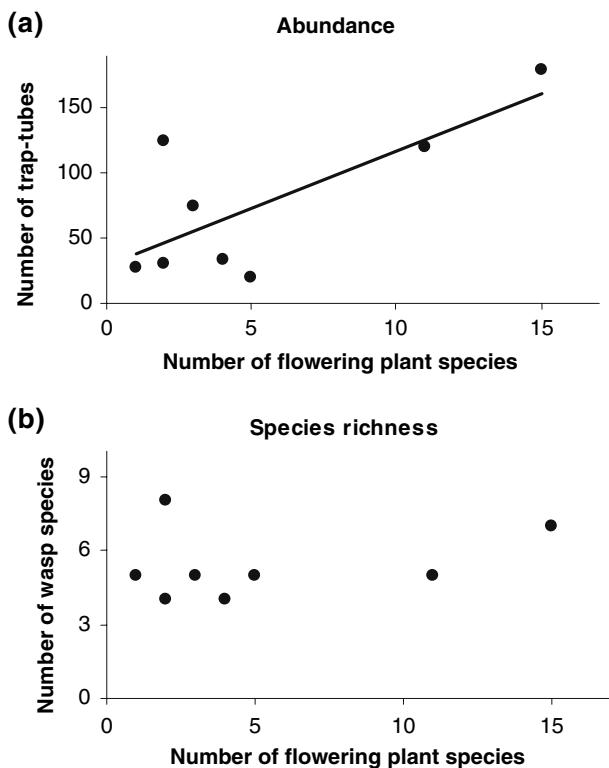


Fig. 2 Relationships between the species richness of understory plant and community of trap-nesting wasps in Norfolk County of Ontario, Canada. Simple linear regression analyses for the abundance (a) is $Y = 29.219 + 8.797X$, $R^2 = 0.550$, $F_{1,6} = 7.33$, $P = 0.035$, and for the species richness of trap-nesting wasps (b) is $R^2 = 0.080$, $F_{1,6} = 0.52$, $P = 0.498$. The abundance of trap-nest wasps was obtained from the number of trap-nest tubes closed with soil or plant materials

The 12 captured species prey upon various arthropods for provisioning their brood (Krombein 1967; Krombein et al. 1979). *Ancistrocerus diabatus*, *A. antilope*, *A. campestris*, *Euodynerus foraminatus*, *Symmorphus canadensis* (Vespididae: Eumeninae) hunt caterpillars (Lepidoptera) (Collins and Jennings 1987; McKenna et al. 2001). *Symmorphus canadensis* (Vespididae: Eumeninae) hunts grubs of leaf-mining beetles (Coleoptera) and caterpillars (Krombein 1967; Krombein et al. 1979), and *S. cristatus* is a leaf-beetle (grub) hunting wasp (Sears et al. 2001). *Isodontia mexicana* (Sphecidae) is a cricket (Orthoptera) hunting wasp (O'Neill and O'Neill 2003). *Trypoxylon frigidum* and *T. lactitarse* (Crabronidae) and *Auplopus mellipes*, *Dipogon sayi sayi*, and *D. papago anomalus* (Pompilidae) hunt spiders (Araneae) (Kurczewski and Spofford 1986; Jennings and Parker 1987; Kurczewski 1989; Camillo and Brescovit 1999; Culin and Robertson 2003). Adults of all the wasps presumably feed on floral and extra-floral nectar (Kevan and Baker 1983, 1999).

Vegetatively rich environments in the forest understory could provide more food resources, both of prey and nectar, for the wasps.

We analyzed the numbers of trap-tubes with nests, rather than the numbers of individuals we reared, to measure abundance. This measure avoids the complexity of dealing with parasite numbers from species that produce many offspring from a single host and species that a single parasite parasitizes multiple numbers of hosts, and it can include the abundance data of parasitized trap-nesting wasps. The collected parasites *C. coeruleans*, *C. nitidula* and *Amobia* attack a broad range of hosts. Krombein (1967) reported that both cuckoo wasps, *C. coeruleans* and *C. nitidula*, parasitize various wasp species of Vespididae, producing a single adult per host insect. *Amobia* parasitizes species of Vespididae, Crabronidae, and Sphecidae, but it is uncertain if only one adult *Amobia* emerges per host insect; for instance, they may invade adjacent cells from their original in order to obtain enough food (Krombein 1967), resulting in fewer surviving adults of trap-nesting wasps from the original tube occupants.

The species richness of understory flowering plants was used to indicate the conditions of the local habitats. These conditions of micro-environments include various factors, such as presence of other organisms, soil type and canopy density, which alters light penetration, temperature and moisture. However, vegetation must reflect these biotic and abiotic factors, which act together in setting the stage of an environment (Hardtle et al. 2003), and therefore is simpler to use as an indicator.

The focus of this study is habitat loss rather than habitat fragmentation. Habitat fragmentation is different from habitat loss. It has to be treated as a process in which a large expanse of habitat is transformed into a number of smaller patches that not only have reduced total area, but are also isolated from one another by a matrix of habitats unlike the original (Wilcove et al. 1986). Habitat fragmentation is thus next stage of the study. For instance, edge effects must be considered in studies of habitat fragmentation. More edges are created by fragmentation rather than by the loss of habitat per se (Debinski and Holt 2000). For edge effects, both increases and decreases in species richness and abundance, and reproductive success in plants (Chen et al. 1992; Jules and Rathcke 1999; Tomimatsu and Ohara 2004; Bach et al. 2005; Burgess et al. 2006) and animals (Paton 1994; Donovan et al. 1997; Driscoll and Donovan 2004) have been reported. Those complexities associated with edge effects may also affect the micro-environments of habitats.

Our results suggest that the communities of trap-nesting wasps within forests could be influenced more by the local habitat conditions than by the forest loss per se, but we conceded that our results may reflect our limited sampling season (i.e. excluding spring and autumn). Understory conditions in deciduous forests dramatically change in the short vernal period preceding canopy closure and during autumnal leaf-fall (Anderson 1964; Barnes et al. 1998). Therefore, it would be interesting to investigate the dynamics of the communities of trap-nesting wasps throughout a complete season in relation to landscapes and to local habitat conditions, and with respect to considering fragmentation itself.

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