Research Article

Edge Effects on Community and Social Structure of Northern Temperate Deciduous Forest Ants

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Determining how ant communities are impacted by challenges from habitat fragmentation, such as edge effects, will help us understand how ants may be used as a bioindicator taxon. To assess the impacts of edge effects upon the ant community in a northern temperate deciduous forest, we studied edge and interior sites in Jericho, VT, USA. The edges we focused upon were created by recreational trails. We censused the ants at these sites for two consecutive growing seasons using pitfall traps and litter plot excavations. We also collected nests of the most common ant species at our study sites, *Aphaenogaster rudis*, for study of colony demography. Significantly greater total numbers of ants and ant nests were found in the edge sites compared to the interior sites but rarefaction analysis showed no significant difference in species richness. *Aphaenogaster rudis* was the numerically dominant ant in the habitats sampled but had a greater relative abundance in the interior sites than in the edge sites both in pitfall and litter plot data. Queen number of *A. rudis* significantly differed between the nests collected in the edge versus the interior sites. Habitat-dependent changes in social structure of ants represent another possible indicator of ecosystem health.

1. Introduction

Data on the response of ant communities to disturbance of temperate forests in the United States are scant, despite calls to action to find indicator groups for temperate forest biodiversity conservation [1, 2]. Many of the existing studies of temperate deciduous forest ant communities in the US have been done in southern forests [3, 4]. For northern forests, studies have surveyed species diversity of ant communities, for example, for the northeastern USA [5–9], but the response of ant communities to disturbance of these north temperate deciduous forests has not been well explored. The northern forests of the eastern United States are increasingly subject to land development as 76% of northeastern forest is privately owned [10]. In Vermont, much of the forest was cleared for agriculture by the early 1800s. However, in the last century, reforestation has been extensive, as agriculture has declined, and percentage forest cover in Vermont has increased from 40% in the 1840s to 78% in 2010; the result is a landscape of highly fragmented secondary forests

[11]. What impacts do that fragmentation and resultant abundance of edge habitats have on ant communities?

Habitat fragmentation, a major force decreasing biodiversity, produces landscapes with many edges, sharp boundaries between distinct patches of habitat [12]. Habitat fragmentation increases the amount of edge relative to the area of the interior of patches. Despite the facts that habitat fragmentation has greatly increased, worldwide, and that ecological edge effects have attracted much study by ecologists (e.g., [12]), our broader understanding of edge effects is still limited as studies have produced results that appear to be idiosyncratic based upon the differing ecological phenomena at work [13]. In eight studies of edge effects upon terrestrial invertebrates reviewed in Ries et al. [13], species richness/diversity increased in one study was unaffected in three studies and showed mixed responses at edges in four studies.

With respect to ground-dwelling insects, some studies of edge effects have demonstrated the importance of edge effects with respect to conservation and land management.

Golden and Crist [14] experimentally untangled two key issues related to habitat fragmentation: decreased patch sizes and increased edge, demonstrating that edge effects were more pronounced than effects of patch area on ground-dwelling rove beetle and ant species richness in old fields. Edges may be problematic because organisms living there are potentially exposed to variability in wind and weather conditions, invasive competitor species, and increased levels of anthropogenic disturbance [15, 16]. In areas with invasive ant species, the negative effects of habitat edge are clear as invaders are able to exploit the disturbed edges more readily than native competitor species [16–18]. Increased edge can lead to a reduction in biological diversity within a region, reviewed in Saunders et al. [19], and edge effects may pose a bigger challenge for insect populations than patch size.

Ant species, such as leaf-cutters or myrmecochorous species, that are highly reliant on particular plant species have been hypothesized to be particularly susceptible to negative edge effects. However, the results of studies addressing this question have been mixed. Falcão et al. [20] found significant restriction of dietary composition in leaf-cutter ant colonies living in human-created edges of Neotropical rainforest habitat in Brazil. But in a southern Appalachian highland deciduous forest, Mitchell et al. [4] found the myrmecochorous ant species, *Aphaenogaster rudis*, to be more common in small patches of forest with a history of human disturbance than in larger, less disturbed patches, perhaps due to the beneficial microclimate (warmer temperatures created by opening of canopy receive more penetrating sunlight) created by past disturbance. The presence of edge habitats increases microclimatic diversity and contributes to landscape-level heterogeneity, potentially promoting increased species richness, for mobile invertebrates (e.g., butterflies [21]).

Understanding the impacts of habitat edge on ant community structure could inform our use of ants as a bioindicator taxon. In the present study we asked: How do ant communities differ between edge and interior habitats within northern temperate deciduous forests? Furthermore, we examined colony demography and social structure of the ecologically dominant ant species, *Aphaenogaster rudis*, to determine whether social behavior of this important member of the ant community varied in edge versus interior habitats following the work of Herbers and Banschbach [22] which experimentally demonstrated the impact of food availability on social structure in the ant *Myrmica punctiventris*. We discuss our results making reference to the conceptual framework for edge effects provided by Ries et al. [13].

2. Methods

2.1. Study Area. We worked in deciduous, hardwood forest at the Mills Riverside Park in Jericho, VT, USA (44°30′N, 72°66′W; sites ranging from 244 to 410 m elevation). The Mills Riverside Park is a multiple-use conservation area with trails for hiking, mountain biking, and horseback riding winding through the forests. The park contains 66.4 hectares of conserved forest. It is adjacent to privately owned land

that is currently forested, and next to a busy highway, agricultural land and the Browns River. The upper reaches of the park (northern hardwood forest type) contain a stand of American beech important for the local black bear population. All of the forest is secondary, but a small number of older "witness" trees (>100 years old) remain, spared from logging for use as markers of property boundaries [23]. Since the recreational use of this island of forest is heavy, edge habitats (adjacent to trails) are subject to regular human disturbance as well as physical edge effects.

During May through July of 2003 and in the same months of 2004, we censused ants and other invertebrates in three different forest types: a mixed woodlot, a sugar maple forest, and a northern hardwood forest, defined by stand analysis done by consulting foresters for the Jericho Underhill Land Trust (full description in Appendix [23]). In each forest type, we sampled in an edge and an interior location, matched for elevation ±10 m. Edge habitat was defined as a site within 30 m of a recreational trail; in two edge sites, the trails creating the edge also delineated a park boundary. All edge sites included in this study were in forested areas of the park and edges separated patches of forested land from other patches of forested land, park-owned or privately owned. We did not work at any edges separating forested land from agricultural land, grassland or any other habitat type. Interior sites were at least 100 m from a trail or apparent habitat boundary. Since the Mills Riverside Park is a relatively small land area, centered on a hill, we used only two distance categories in relation to edge (i) within 30 meters from the edge; (ii) greater than 100 m from the edge), while matching our study sites for elevation and forest types.

2.2. Pitfall Sampling. To determine the species composition and abundance of ants in the edge and interior forest sites, we conducted pitfall trapping using centrifuge tubes (50 mL size) half-filled with a 1 : 1 Sierra antifreeze/tap water mixture as pitfall traps. In the summer of 2003, we placed 50 traps per 40 m transect along four transects, two edge and two interior, in the sugar maple forest of the park. The transects were aligned parallel to the edge, within the 30 m zone without being so close to the trail as to be subject to human disturbance of the traps. Individual traps were arranged in squares around points on the transect, with one trap centered on a point on the transect itself and the four others at each corner of a square centered on that point but one meter diagonally away from the point. We collected the 200 traps three times, at two-week intervals, for a total of 600 trap collections during the summer of 2003. During the summer of 2004, we sampled in all three forest types of the park: mixed woodlot, sugar maple, and northern hardwood. We placed two 40 m transects in each of the three forest types, with 25 traps per transect, one transect in the interior and one at the edge of each of the three forest habitats. Again, transects were aligned parallel to the edge and traps were arranged in large squares centered on the transect, as described above. We collected the 150 traps two times, at two-week intervals, for a total of 300 trap collections, in 2004. All ants collected in traps were identified to species
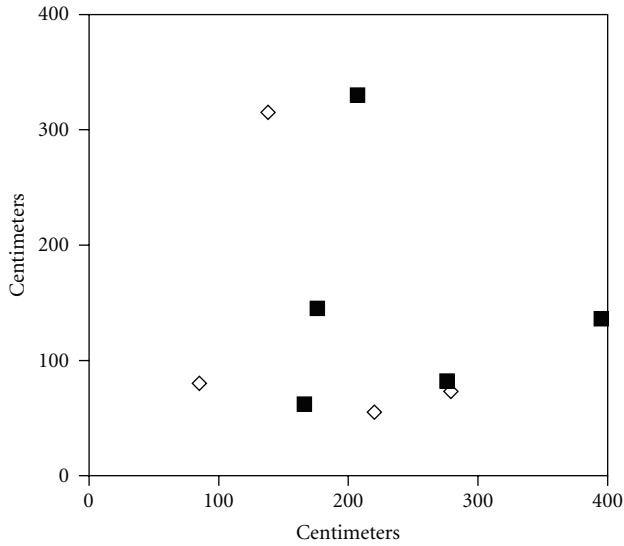
FIGURE 1: Example litter plot excavated in edge habitat. Each symbol represents an ant nest (defined as consisting of at least two workers and some brood) that was found. Filled squares represent *Aphaenogaster rudis* nests and open diamonds denote nests of *Stenamma diecki*. Individual ants walking through the leaf litter were not mapped.

with verification by S. Cover, Curatorial Assistant, Museum of Comparative Zoology, Harvard University.

2.3. Litter Plot Sampling. We excavated litter plots to estimate abundance of ant colonies to supplement the measure of individual ant abundance and diversity provided by pitfall sampling [7]. Furthermore, litter plot sampling allowed us to collect ant nests for the study of colony social structure, as in [24, 25]. To excavate litter plots, we marked off 4×4 m square plots of forest and searched the leaf litter for ant nests. We sampled one 16 m^2 plot in the interior and at the edge of each of the three forest types, mixed woodlot, sugar maple, and northern hardwood, during early June of 2004. Because of the high abundance of ants in the northern hardwood forest plots, we excavated two additional plots in that forest habitat: one plot was located in the interior and one was located at the edge, in mid-June of 2004. In total, eight 16 m^2 plots were surveyed. When nests were found, we mapped their locations on the plots (e.g., Figure 1). We collected nests of ants found in preformed cavities such as acorns, beech nuts, logs, and hollow sticks for laboratory censuses.

2.4. Colony Demography. To examine colony social structure of the most common ant species in both habitats, *Aphaenogaster rudis*, we transported nests excavated from litter plots in 2004 to the laboratory in plastic bags, and housed colonies in plastic boxes, providing glass tubing for nesting material. These colonies were maintained in the laboratory on a standard ant diet [26] and dead fruit flies. We censused the number of queens, workers, eggs, larvae, pupae, and alates in these colonies within a week of field collection.
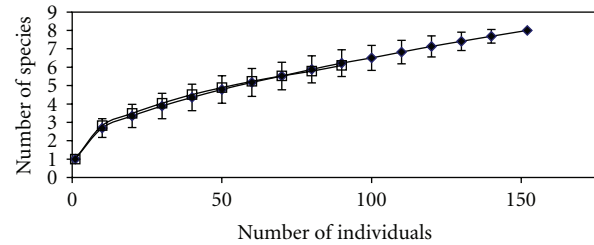

FIGURE 2: Rarefaction analysis. Expected species richness for given numbers of individuals collected in each habitat type, generated using EcoSim software [28]. Filled diamonds represent edge habitat, while open squares are for interior habitat. The 95% confidence intervals shown were generated using the edge site data.

3. Results

3.1. Species Composition and Abundance. We found 10 species of ants in the Mills Riverside Park forest sites (Table 1); pitfall samples contained 9 of the 10 species found, while litter plot excavations produced nests of 5 species including 1 species not found in pitfall traps. Nine ant species were collected in the edge sites, 7 in the interior sites. Significantly more individual ants were found in edge site pitfall traps than in interior traps (152 versus 90 individuals; $\chi^2 = 16.4$, df $= 1$, $P < 0.0001$), and significantly more ant nests were found in edge site litter plots than on interior site litter plots (61 versus 25 nests; $\chi^2 = 15.6$, df $= 1$, $P = 0.0001$) (Table 1). *Aphaenogaster rudis* (morphological form of the *Aphaenogaster fulva-rudis-texana* complex delineated by Umphrey [27]) was the most common ant overall, in terms of both frequency in samples and relative abundance (Table 1). However, the relative abundance of *Aphaenogaster rudis* was higher in interior forest habitats than in edge habitats in both pitfall data and litter plot data (Table 1).

Rarefaction analysis via simulation performed using EcoSim software [28] showed that edge and interior sites did not differ substantially in terms of ant species richness (Figure 2). The rarefaction curves in Figure 2 show the expected species richness for a given number of randomly sampled individuals in a simulation based upon our data, as described in [29, 30]. The rarefaction curves for the interior and edge sites were very similar; the interior curve lies well within the 95% confidence intervals for the edge data.

3.2. Colony Demography of Aphaenogaster rudis. Queen state of *A. rudis* nests collected from litter plots in 2004 significantly differed depending upon whether the nests were from edge or interior sites (Figure 3; Mann-Whitney U test statistic, $W = 216$, $N = 12$; 13, $P < 0.0035$); most edge nests contained a single queen, while most interior nests were queenless. Worker numbers in *A. rudis* nests from the edge sites compared to those from the interior were not significantly different (Mann-Whitney U test, $W = 185.0$, $N = 12$; 13, $P = 0.399$).

TABLE 1: Species composition, frequency, and relative abundance of ants. Frequency is the proportion of samples that contained individuals (in pitfall traps) or nests (on litter plots) of the species. Relative abundance is the proportion of individuals (in pitfall traps) or nests (on litter plots) of the total individuals (*n*) or nests collected (*n*). Species that were present in at least 20% of the plots or pitfall samples at either site are highlighted in bold type. In 2003, sampling was conducted on 3 dates, 1 site per date. In 2004, sampling was conducted on 2 dates, 3 sites per date.

| Ant species	Interior forest sites				Edge forest sites			
	Pitfall	Pitfall	Plot	Plot	Pitfall	Pitfall	Plot	Plot
	Freq.	Rel. Ab.	Freq.	Rel. Ab.	Freq.	Rel. Ab.	Freq.	Rel. Ab.
Sample sizes	450 traps	90 ants	4 plots	25 nests	450 traps	152 ants	4 plots	61 nests
Aphaenogaster rudis	**0.44**	**0.38**	**0.75**	**0.56**	**0.67**	**0.28**	**0.75**	**0.21**
Camponotus herculeanus	0.00	0.00	0.00	0.00	0.11	0.01	0.00	0.00
Camponotus nearcticus	0.00	0.00	0.00	0.00	0.11	0.01	0.00	0.00
Camponotus noveboracensis	0.00	0.00	0.00	0.00	0.11	0.01	0.00	0.00
Camponotus pennsylvanicus	**0.22**	**0.02**	**0.00**	**0.00**	**0.11**	**0.64**	**0.00**	**0.00**
Lasius alienus	**0.22**	**0.52**	**0.25**	**0.12**	**0.22**	**0.04**	**0.25**	**0.07**
Lasius nearcticus	0.11	0.01	0.00	0.00	0.00	0.00	0.00	0.00
Myrmica punctiventris	**0.22**	**0.01**	**0.00**	**0.00**	**0.22**	**0.01**	**0.25**	**0.02**
Stenamma diecki	**0.22**	**0.04**	**0.50**	**0.12**	**0.11**	**0.01**	**0.50**	**0.57**
Temnothorax longispinosus	**0.00**	**0.00**	**0.50**	**0.20**	**0.00**	**0.00**	**0.50**	**0.13**
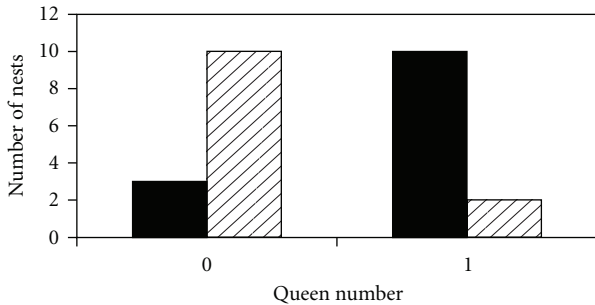
FIGURE 3: Queen number in *Aphaenogaster rudis* nests. Nests were collected in edge (solid bars) and interior habitat litter plots (diagonal hatched bars). Sample sizes were *n* = 13 edge nests and *n* = 12 interior nests.

4. Discussion

The edges we investigated were ones presenting a steep gradient in the main environmental variable (forest cover) defining the boundary, as the edges were created by the trails running through the park, forming linear gaps in the forest cover. The trails were mostly only two to three meters wide, but the traffic and maintenance activities associated with the trails create a much broader zone of disturbance. Given the size scale that is relevant to ants, we predicted that these edges would be meaningful enough to be impactful, despite the fact that the larger habitat patches on either side of the edge zone consisted of quite similar forest types. We found that ant species richness was not significantly different between our edge and interior sites, but abundance of individual ants and ant nests differed significantly, with more individual ants and ant nests in edge habitat.

Ries et al. [13] developed a predictive model of edge effects based upon ecological flows of light, heat, moisture, wind, as well as species interactions, species distribution and resource distribution. The Ries et al. [13] model predicts negative impacts of edge when edges separate a higher-quality habitat from one that is degraded or of lower resource quality, positive impacts of edges when edges separate patches that provide complementary resources or when edge habitat leads to a concentration of resources, and neutral impacts of edge when the edges separate patches of similar resource levels. In our case, the edges studied separate larger patches of similar resource levels (forested land of similar specific forest types) but also created a small zone of highly concentrated resources (e.g., dead wood leftover from trail maintenance activities).

Our results may be in accord with the Ries et al. [13] model in two ways. First, we saw no impact on ant species richness, likely due to the fact that our edges separated larger patches of similar resources with similar species richness. Second, our finding that abundance of both individual ants and ant nests were greater in edge habitats also is in accord with the idea that concentrated resources at the edges would have a positive impact, particularly for species that can utilize the particular resources predominant at edges [13]. Although we did not quantitatively characterize the habitat features, an abundance of downed wood was an obvious resource difference at edges compared to interior habitats (Banschbach, pers. obs.) that would have ramifications for ant abundance.

The dominant ant species at our study site is the myr-mecochorous ant *Aphaenogaster rudis*. Other ant species appeared more frequently in the edge (e.g., *Camponotus pennsylvanicus*) decreasing the relative abundance of *A. rudis* in the edge, but the frequency of *A. rudis* was highest in edge habitat. One important kind of food for *A. rudis* is

the seeds of perennial herbs [31–33]. Ness and Morin [32] suggest that in edge forest habitats seed-eating rodents are more prevalent, out competing *A. rudis* for that food source, leading to a habitat preference for interior versus edge plots but we did not find clear support for that as the frequency of *A. rudis* workers in edge habitats was greater than in interior habitats. Our results are more similar to those of Mitchell et al. [4] who found both *A. rudis* and *Camponotus* spp. to be more frequent at baits in smaller habitat patches (which would have greater edge to volume ratios than larger patches) in southern Appalachian highland temperate forests.

We employed both pitfall trapping and litter plot excavations to census the ant community. Mitchell et al. [4] and Ness and Morin [32] relied upon bait attendance to census ant communities. Pitfall trapping provides an estimate of ant diversity and abundance but can be biased by the nonrandom movement patterns of individual ants and the patchy distribution of ant nest sites [34, 35]. Nevertheless, in an assessment of the efficacy of different sampling methods for assessing ant species richness and community structure, Tista and Fielder [36] concluded that pitfall trapping produced the greatest species numbers in temperate montane and floodplain European sites. Our litter plot results were in accord with our pitfall data, but the wide ranging, large individual, and colony-sized *Camponotus* spp. was found only in pitfall traps and not as nests on litter plots (Table 1). Furthermore, we collected more of the small, preformed cavity (e.g., acorn) nesting species *Temnothorax longispinosus* via nests we excavated from litter plots rather than by individual ants falling into pitfall traps (Table 1). With such low ant species richness overall, multiple methods were important to use.

The ant species richness in our pitfall trapping and litter plot collections was low (10 total species) but in keeping with other surveys of the Vermont ant fauna in second-growth hardwood forests [5, 7, 37]. Additional data we collected using food baits did not add any species to the sample (Yeamans, unpublished data). Nevertheless, greater ant species richness has been found in other habitats in Vermont such as sandplain forest [38] and lowland forests adjacent to bogs [6]. Jenkins et al. [39] found temperature to be of key importance in predicting ant species density globally. The climate in Vermont is a northern temperate climate, with an average minimum temperature of 1.8 degrees Celsius in Burlington, VT, the nearest weather monitoring station to our study site (http://www.erh.noaa.gov/btv/climo/BTV/monthly_totals/avgmin.shtml) and a very short active season for ants. Majer et al. [40] suggest that one reason for the paucity of studies on the use of ants as bioindicators in the temperate regions of Europe and North America is the relatively low species richness of ants in these world regions. For using ants as an indicator taxon for biodiversity in this habitat (using as surrogates for diversity across other taxa, McGeoch [41]), it would be challenging to correlate ant species richness with that of other taxa given the low overall richness for the ants.

Since *Aphaenogaster rudis* is such a dominant ant in our study sites and throughout temperate deciduous forests in the USA, our data regarding differences in social structure in edge versus interior habitats have some interesting possible ramifications. We found that almost none of the nests we excavated from litter plots in the interior forest contained queens, while the reverse was true of the nests we collected in the edge habitats of the forest. Since we excavated litter plots down to bare earth, we are certain that we removed all ants and brood present on these plots and did not leave any queens behind. *A. rudis* has been described as a monogynous ant species [31, 42], but other details of colony social structure and reproduction are less certain [43]. The Mediterranean *Aphaenogaster senilis* is a related monogynous species that reproduces exclusively by colony fission [44]. If this colony fission process is the main reproductive means for *A. rudis*, then the lack of queens found in the nests in our interior forest plots could be attributed to fission events occurring in advance of the production of new gynes. Boulay et al. [45] experimented with *A. senilis* and demonstrated with microsatellite analysis that after the reproductive season, many colonies were headed by a young queen who was not the mother of the workers in the colony. Since we censused ants prior to the alate production season in Vermont (late summer, early Fall), we may have detected the early evidence of the colony fission events. Resources for *A. rudis* may be more plentiful in the interior than the edge, at least in terms of reduced competition with rodents for seeds of perennial herbs [32], or perhaps general foraging competition with *Camponotus* spp.; therefore, colonies were able to fission sooner, having acquired the resources necessary to reach sufficient size to do so. Boulay et al. [45] found that *A. senilis* colonies adjust the timing of their fission events in response to competition and, therefore, resource availability.

Many studies of social structure in other ant species have documented the importance of resource availability to queen number in temperate or boreal forest ants (*Formica* spp., [46]; *Myrmica punctiventris*, [22]; *Temnothorax longispinosus* [47]). We think that future study of the genetic structure of *Aphaenogaster rudis* colonies in different habitat types could provide support for the idea that edge habitats disadvantage *A. rudis* colonies, delaying the time to fission. Because of *A. rudis*' important role as a disperser of perennial herb seeds [33], this edge effect has ramifications for the forest plant community and the forest ecosystem overall. More generally, further studies of edge effects that quantify resource availability in relation to patterns of ant diversity and abundance could substantiate the idea that edges creating a concentration of certain resources lead to increased abundance of species utilizing those particular resources.

Appendix

Description of our forest habitats in the Mills Riverside Park. This information was taken from the forest stand analysis generated by Kara Wires and Scott Moreau for the Jericho Land Trust, in 2000 [23].

Mixed Woodlot. 38% red maple, 16% white pine, 16% red spruce, 13% sugar maple, 12% black cherry and fewer ash,

aspen, paper birch and yellow birch. The approximate stand age ranged from 30 to 70 years, at the time of our study. Elevation ranges from 220 m to 280 m.

Sugar Maple Forest. 64% sugar maple and fewer ash, paper birch, red maple, red oak, red spruce, aspen, yellow birch, beech, and hop hornbeam. The approximate stand age ranged from 60 to 80 years, at the time of our study. Elevation ranges from 287 m to 384 m.

Northern Hardwood Forest. 60% sugar maple, 21% yellow birch, 16% red maple, and fewer beech, paper birch, and red spruce. The approximate stand age ranged from 30 to 70 years, at the time of our study. Elevation ranges from 299 m to 408 m.

Acknowledgments

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