



Ski trail effects on a beetle (Coleoptera: Carabidae, Elateridae) community in Vermont

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Abstract

Beetle diversity and species composition were studied using pitfall traps placed along three parallel transects that extended from the center of a downhill ski trail, 100 m into a large, unfragmented spruce-fir forest on Mount Mansfield State Park, VT, USA. Groups of beetles showed associations with three distinct habitats: ski trail openings (*Agonum cupripenne*, *Amara* spp., *Poecilus lucublandus*, *Hypnoidus bicolor*, and *H. abbreviatus*), edge (*Pterostichus coracinus*, *Agonum retractum*, *Sphaeroderus canadensis*, and *Calathus ingratus*), and forest (*Pterostichus adstrictus*, *P. punctatissimus*, *P. brevicornis*, *Platynus decentis*, *Trechus apicalis*, *T. crassiscapus*, and *Eanus maculipennis*). Consequently, carabid and elaterid species composition in the ski trail, edge, and 5 m into the unfragmented forest showed nearly complete turnover. Most beetles within the ski trail were colonizers from lower elevations; however, one species, *H. bicolor*, was a tundra species that appeared to have colonized lower elevations along the ski trail opening. Of "forest" beetles, only 2 of 540 individuals (< 0.5%) were collected in the ski trail opening. Thus, ski trails are strong barriers to dispersal for forest beetles, several of which are flightless or dimorphic and primarily short-winged. Consequently, fragmentation of mountain slopes by ski trails, especially those that run perpendicular to the climatic gradient, may put isolated populations at a greater risk of local extirpation.

Introduction

High elevation forest ecosystems are considered to be vulnerable to perturbation because of their shallow soils, low nutrient availability, poor buffering capacity, and short growing seasons. However, their scenic value, unique vegetation, and low human population densities have made high elevation forests important recreational areas for hiking, climbing, birding, and photography. In the northeastern U.S., skiing is an important recreational industry within these high elevation ecosystems, but one with potentially significant effects on ecosystem function. Erosion, modification of hydrological patterns, loss of fish and wildlife habitat, and forest clearing for ski trails and associated infrastructure have led to myriad ecologi-

cal impacts (Molles and Gosz 1980; Watson 1985; Haslett 1991; Illich and Haslett 1994; Tsuyuzaki 1994; Morrison et al. 1995; Ries 1996). Despite these potentially significant impacts, relatively few studies have investigated the direct effects of ski area development on high elevation fauna.

In the northeastern U.S., few mountain peaks rise above tree line; therefore, cleared ski trails create strong habitat discontinuities and sharply delineated edges in forested ecosystems. These edges may have substantial effects on species' distributions by differentially altering movement patterns, competitive interactions, and demographic parameters (Fagan et al. 1999). However, the effects of edges on high elevation vertebrate fauna may be difficult to detect because of their relatively low species richness. In con-

trast, beetles (Coleoptera) are a useful taxon for assessing the effects of these habitat modifications because of their high species diversity, ease of sampling, and diverse habitat use patterns (Maelfait et al. 1990; Dufrêne et al. 1990; Eyre et al. 1996). Several studies have shown that ground beetles (Coleoptera: Carabidae) show strong (but not necessarily predictable) responses to forest edges (Davies and Margules 1998; Didham et al. 1998) and that strong habitat discontinuities consistently act as dispersal barriers for species with poor gap-crossing abilities (Frampton et al. 1995).

Although the effects of habitat discontinuities created by roads (Plat et al. 1995; Haskell 2000), clearcuts (Lenski 1982; Jennings et al. 1986; Heliölä et al. 2001), hedgerows (Burel 1992; Petit and Burel 1998), agricultural fields (Klein 1989), and riparian or roadside buffer strips (Vermeulen 1994; Major et al. 1999) on beetle species diversity and composition have been investigated, there has been little study of the effects of ski trail edges. As high elevation forests frequently support unique natural communities, there is a critical need to understand the effects of ski area development on the distribution and abundance patterns of high elevation fauna. In this study, we examined community composition, community similarity, species richness, and species diversity across transects extending from a ski trail opening into unfragmented forest for a portion of the epigeic beetle community (Coleoptera: Carabidae, Elateridae). We hypothesized we would find strong edge effects, with at least some forest species avoiding edges and more generalist open field species extending their range into forested habitat. We also predicted that species diversity would be greatest along ski trail edges, as this community would support species from both forest and open habitats (e.g., Didham (1997a)), but that the edge community would not be comprised of a distinct subset of species (e.g., Spence et al. (1996) and Heliölä et al. (2001)).

Methods

We collected beetles from the Stowe Mountain Ski Resort in Stowe, Vermont, USA, in the Mt. Mansfield State Park (44°32.6' N, 72°48.7' W), along an east-facing slope, ranging in elevation from 1019 m to 1097 m. The forest was dominated by balsam fir (*Abies balsamea*), with paper birch (*Betula papyrifera*), red spruce (*Picea rubra*), and speckled alder

(*Alnus rugosa*) present but less common. Ground cover was dominated by *Dryopteris spinulosa*, *Lycopodium lucidulum*, *Oxalis montana*, *Coptis groenlandica*, and *Cornus canadensis*. The ski trail (19–22 m in width) was created in 1968 and was dominated by grasses and forbs with occasional shrubs. The trail was mowed irregularly (≤ 1 mowing/year) to prevent establishment of woody vegetation and maintain a permanent opening for skiing. The edge boundary was maintained at the outer tips of the horizontal branches of the canopy trees (canopy dripline edge); however, there was some mortality of canopy trees along the edge, such that regenerating vegetation (primarily balsam fir) graded into the ski trail at the edge boundary (advancing edge; Ranney et al. (1981) and Murcia (1995)).

We established three parallel transects that extended 100 m into the forest from the edge of the northernmost ski trail (Gondolier) on the Stowe ski area. The three transects were extended perpendicular to the ski trail, also roughly perpendicular to the elevational gradient, at 1019 m, 1050 m, and 1072 m elevation (on the ski trail) and were separated by 100 m. On each transect, we sampled at seven locations: the center of the ski trail, the edge of the ski trail, but under the canopy of the adjacent woody vegetation (edge), and 5, 10, 25, 50, and 100 m from the ski trail-forest edge. Although the sampling design could be construed as pseudoreplication, we contend that these sites were representative of landscape of this ski development. Further, ground beetle home ranges are quite small (Riecken and Raths 1996; Charrier et al. 1997; Vermeulen 1994) such that it is unlikely an individual's home range would intersect more than one transect. Additionally, ground beetle species composition changes over an elevational gradient (Hosoda 1999), such that our three transects sampled at least somewhat different communities.

Beetles were collected using pitfall traps filled with approximately 75 ml of a 0.1% formalin solution to deter mammalian predators and to prevent beetle decomposition. The pitfall traps were 296 ml plastic cups (7.3 cm at the opening, 10.0 cm deep) placed so that the opening was flush with the ground surface. A second cup was placed within the exterior cup to minimize disturbance to the forest floor during collections. Each cup was covered loosely with the bark of paper birch to prevent overflow from rain. At each sampling location, five pitfall traps were placed at 1-m intervals perpendicular to the transects. Thus, a total of 35 pitfall traps were operated on each transect

($n = 105$ in total). Traps were set out on 9 June 2000, and the contents were collected at 10-day intervals, 6 times during the field season with the final collection on 8 August 2000. Upon returning to the lab, carabids and elaterids were placed in 70% ethanol/1% glycerol solution, and identified to species (carabids: Laroche (1976), elaterids: Dietrich (1945)).

Data analysis

We pooled captures from the 5 traps at each location. Additionally, for carabid diversity analyses, we treated the 6 sampling dates as replicates as there was no significant date \times distance ($F = 1.053$, $P = 0.417$, $df = 30$ and 70) or date \times transect ($F = 0.489$, $P = 0.859$, $df = 10$ and 90) interaction (one-way repeated measures ANOVA).

We used the Shannon-Wiener diversity index to compare diversity across elevation for carabids, however, our sample sizes for elaterids were too small to calculate meaningful diversity indices (88 of 126 samples had 0 individuals). We used Morisita's similarity index to numerically compare carabid and elaterid communities among sampling locations (Magurran 1988), eliminating species that were represented by only a single individual. To compare the communities graphically, we used Detrended Correspondence Analysis (DCA), which is an eigen value-based ordination technique that uses detrending to counteract the arch effect, a limitation of correspondence analysis (Hill and Gauch 1980). Species represented by a single individual were also excluded from the DCA. We conducted G -tests to assess whether use of particular sampling locations was greater than or less than expected. As all species with adequate sample sizes (expected value ≥ 35 ; 5 individuals/distance category) showed non-random distributions, we pooled sampling locations into ski trail, edge, and forest to further evaluate habitat use vs. availability. Thus, expected proportions for these three habitat types were 0.143 (1/7), 0.143 (1/7), and 0.714 (5/7), respectively. We derived simultaneous 95% confidence intervals around each observed proportion using the Bailey and Goodman method, which showed overall type I error rates of $< 5\%$ in simulation trials (Cherry 1996). If the expected value was above, below, or within the confidence interval of observed use, the species was considered to use that habitat less than expected, greater than expected, or as expected, respectively. All analyses were conducted with SYSTAT 10.0, with the exception of DCA, which was

Table 1. Results of a two-way ANOVA showing a significant effect of elevation (transect), but no effect of distance from the ski trail on carabid diversity indices. See Figure 1 for graphical presentation of the data.

Source	df	Mean square	F	P
Elevation ^a	2	1.121	3.98	0.022
Distance ^b	6	0.439	1.56	0.167
E \times D	12	0.298	1.06	0.404
Error	105	0.282		

^a Three parallel transects at initial elevations of 1019 m, 1050 m, and 1072 m. ^b Carabids were collected in pitfall traps in the ski trail, at the ski trail edge, and 5, 10, 25, 50, and 100 m into the unfragmented forest.

conducted with PC-ORD (McCune and Meford 1999).

Results

Species richness and diversity

We collected 933 individuals of 37 species of Carabidae and 102 individuals of 20 species of Elateridae. Carabid diversity varied among the three transects (Table 1, Figure 1a) and was significantly greater on the low elevation transect than the middle elevation transect. We found no indication of an elevation \times distance interaction. Carabid diversity showed no variation from the ski trail to 100 m into the forest (Figure 1b), although species richness was somewhat greater in the ski trail (22 species) than in the edge or various forest sites (12–16 species). We collected more carabids from the high elevation transect (393 vs. 198 and 342 for the medium and low transects, respectively), however, approximately 62% of all individuals on the high elevation transect were *Pterostichus brevicornis*. Species richness did not vary appreciably among transects (26, 26, and 23 species on the low, middle, and high elevation transects, respectively). For the elaterids, we found a noticeable decrease in species richness from the ski trail (11 species) to the edge (8 species) to the forested sites (2–4 species), but little variation across transects (10 or 11 species).

Community patterns

Despite the lack of variation in diversity from the ski trail to the forest interior, we found a nearly complete turnover in carabid species composition. While simi-

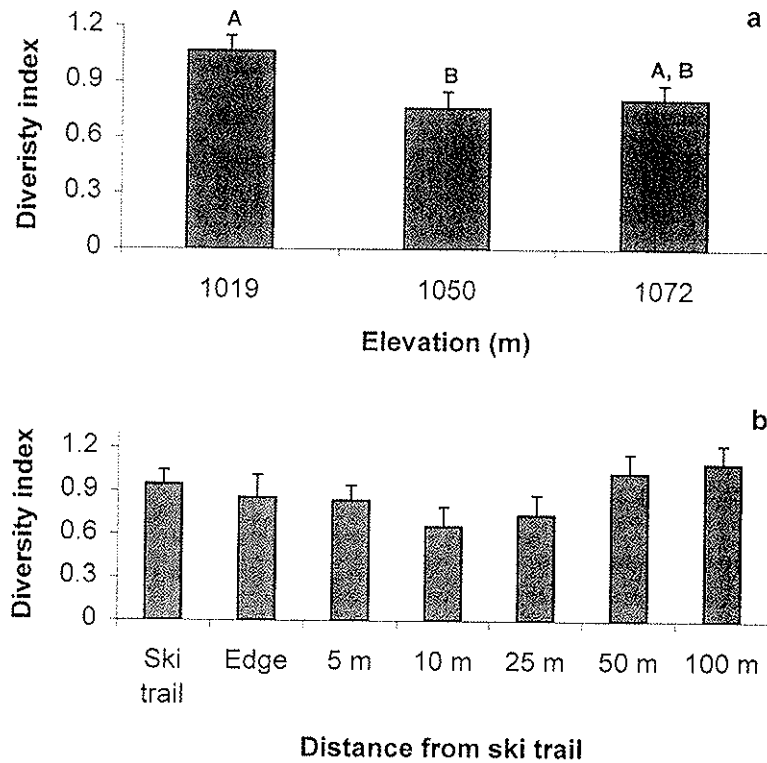


Figure 1. Mean carabid diversity across three transects (a) and varying distances from a ski trail on Mount Mansfield, VT, June–August, 2000. Means (\pm SE) with the same letter are not significantly different. Carabid diversity was significantly greater on the low elevation transect (a). However, there was no significant variation among distances from the ski trail (b).

larity indices ranged from 0.72 to 0.99 for all forest sampling locations (Table 2), the greatest similarity value between the ski trail and a forest site was 0.04 (50 m), and the greatest similarity index value between the edge and forest sites was 0.42 (50 m). Further, the ski trail and edge communities were quite distinct, with a similarity index of 0.11. Using DCA, the first (68.4%) and second (6.4%) axes explained 74.8% of the variation in the model, and suggested three general groups, ski trail, edge, and all forested sites (Figure 2). As with the similarity indices, edge and forested sites were more similar than forest and ski trail sites.

The pattern was similar for the elaterids, despite the smaller sample size (Table 2), with the five forested sites showing the greatest similarity, and ski trail and forest sites showing extreme divergence. Of the five species for which we collected greater than five individuals, no species was found in both the forested sites and the ski trail and only one species was found both in the ski trail and the edge sites. For elaterids, the axis 1 (54.1%) and axis 2 (11.9%) explained 66% of the variation in the model. As with

Table 2. Matrix of Morisita's similarity indices for carabid (below the diagonal) and elaterid (above the diagonal) fauna from Mount Mansfield, 2000.

	Ski trail	Edge	5 m	10 m	25 m	50 m	100 m
Ski trail	-----	0.08	0.00	0.00	0.00	0.00	0.00
Edge	0.11	-----	0.72	0.48	0.54	0.75	0.16
5 m	0.04	0.32	-----	0.47	0.58	0.75	0.60
10 m	0.03	0.28	0.99	-----	0.77	0.62	0.82
25 m	0.02	0.17	0.94	0.95	-----	0.63	0.86
50 m	0.04	0.42	0.92	0.93	0.87	-----	0.85
100 m	0.04	0.42	0.75	0.75	0.72	0.91	-----

carabids, ski trail sites separated from all other sites, with edge sites tending to group closer to forest sites (Figure 3).

Individual patterns

The community patterns were mirrored by the distributional patterns of individual species. None of the species with sample sizes > 35 were randomly dis-

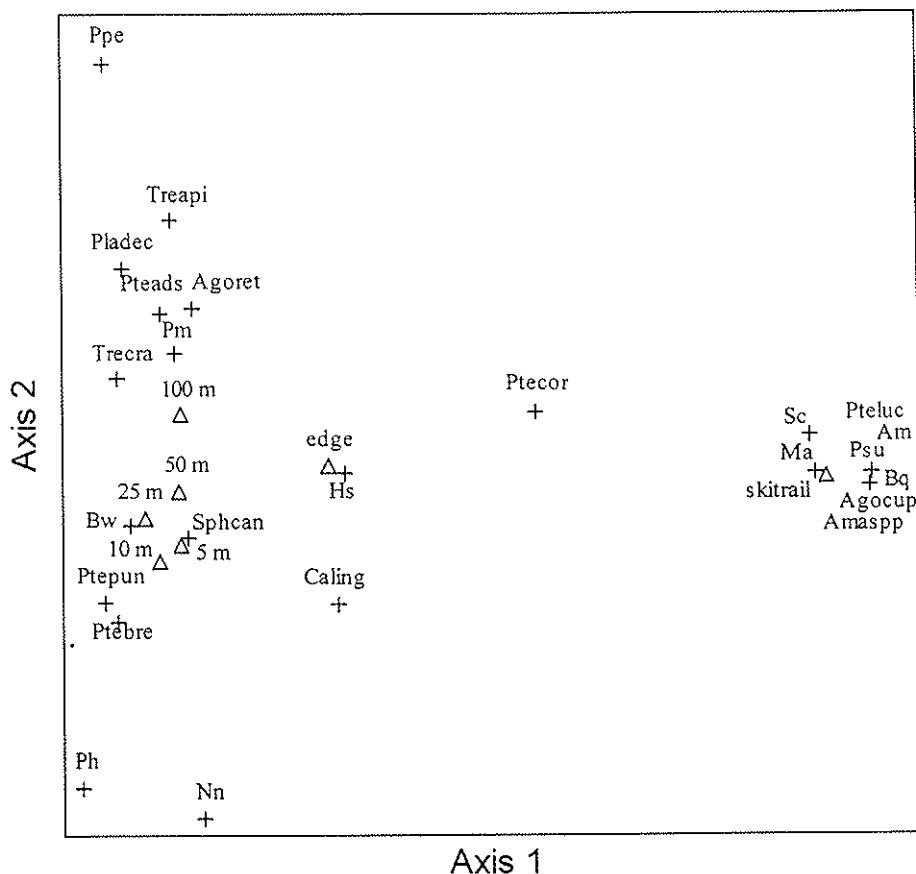


Figure 2. Detrended correspondence analysis of carabids species collected using pitfall traps across transects from a ski trail to 100 m into unfragmented forest on Mt. Mansfield, VT, June–August, 2000. Open triangles represent sample locations (ski trail opening, edge, and 5, 10, 25, 50, and 100 m into the unfragmented forest). "+" represent species distributions. Species with six letters represent those with adequate sample sizes to use in more detailed analyses; those with two or three letters are represented by 2–11 individuals. Am = *Agonum muelleri*. Amaspp = *Amara* spp., Agocup = *Agonum cupripenne*, Agoret = *A. retractorum*, Bq = *Bembidion quadrimaculatum*, Bw = *B. wingatei*, Caling = *Calathus ingratus*, Hs = *Harpalus somnulentus*, Ma = *Metabletus americanus*, Nn = *Notiophilus nemoralis*, Ph = *Pterostichus honestus*, Pladec = *Platynus decentis*, Pm = *P. mannerheimi*, Ppe = *Pterostichus pensylvanicus*, Psu = *Pseudamara arenaria*, Pteads = *Pterostichus adstrictus*, Ptebre = *P. brevicornis*, Ptecor = *P. coracinus*, Pteluc = *Poecilus lucublandus*, Ptepun = *Pterostichus punctatissimus*, Sc = *Stenolophus comma*, Sphcan = *Sphaeroderus canadensis*, Treapi = *Trechus apicalis*, Tregra = *T. crassiscapus*.

tributed across distances from the ski trail (G -test, all $G > 12.6$, all $df = 6$, $P < 0.05$, Figure 4). Pooling sampling locations into ski trail, edge, and forest revealed three relatively distinct patterns: open habitat species, edge species, and forest species (Figure 5). *Agonum cupripenne* and *Poecilus lucublandus*, and all four species in the genus *Amara* (pooled) were found nearly exclusively in the ski trail. Four species (*Agonum retractorum*, *Calathus ingratus*, and *Sphaeroderus canadensis*, *Pterostichus coracinus*) showed greater than expected use of edge habitats, and less than expected use of the ski trail and/or forested sites. *A. retractorum* and *S. canadensis* both tended to group closer to the forest sites (Figure 2),

as both species tended to be somewhat generalized in their distribution. Finally, over 95% of all individuals of *Pterostichus brevicornis*, *P. punctatissimus*, *Trechus apicalis*, and *T. crassiscapus* were found in forested sites. All four of these species used edge sites less than expected, two significantly less so. Additionally, two species (*P. adstrictus* and *Platynus decentis*) were best classified as forest species but did not show strong habitat affinities.

Although species richness was lower in Elateridae, the patterns were similar. All *Hypnoidus bicolor* and 94% of *H. abbreviatus* were found in the ski trail and 100% of *Eanus maculipennis* were in edge and forested sites (Figure 5). Sample sizes were less than 8

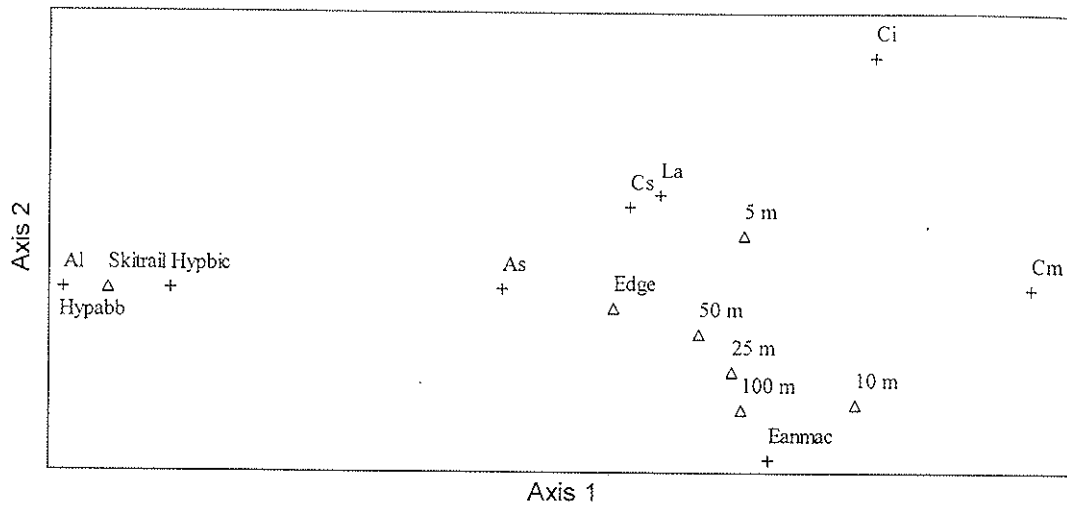


Figure 3. Detrended correspondence analysis of elaterid species collected using pitfall traps across transects from a ski trail to 100 m into unfragmented forest on Mt. Mansfield, VT, June–August, 2000. Open triangles represent sample locations (ski trail opening, edge, and 5, 10, 25, 50, and 100 m into the unfragmented forest). "+" represent species distributions. Species with six letters represent those with adequate sample sizes to use in more detailed analyses; those with two or three letters are represented by 2–7 individuals. Al = *Agriotes limosus*, As = *Ampedus* sp., Ci = *Ctenicera insidiosa*, Cm = *C. mendax*, Cs = *C. spinosa*, Eanmac = *Eanus maculipennis*, La = *Limonium aeger*, Hypabb = *Hypnoidus abbreviauis*, Hypbic = *H. bicolor*.

for all other species. However, all *Ampedus* spp. ($n = 5$) were found in the ski trail, and *Ctenicera spinosa* ($n = 7$) was found exclusively in edge and forested sites.

Discussion

Although carabid diversity and species richness showed little variation from the ski trail to 100 m into the forest, species composition changed dramatically, such that we found nearly complete turnover from the ski trail, to the edge, to 5 meters into the unfragmented forest. Our results agree with those of Margules et al. (1994) who concluded that investigations of the distributions of individual species would provide a better understanding of edge dynamics than more general studies of species richness and diversity.

The nearly complete absence of forest species in the ski trail suggests that these trails act as barriers to dispersal for many ground beetles. The forest carabids are poor dispersers and many are flightless (*Pterostichus punctatissimus*, *P. brevicornis*), dimorphic with most of the population (> 99%) having short wings (*T. apicalis*, *T. crassiscapus*), or have such reduced wings that flight, if possible, is inefficient (*Platynus decentis*, Lindroth (1961, 1966), R. T. Bell, unpubl. data). Thus, if these species dispersed across ski trails, they would presumably do so by walking and we

would expect to find them in pitfall traps occasionally. This is in contrast to highly mobile species (e.g. *Amara* spp.) for which pitfall traps may provide misleading assessments of habitat use patterns (Riecken and Raths 1996).

Of the species found in the ski trail for which we have adequate sample sizes, none were captured > 5 m into the forest. Additionally, forest species showed no consistent directional change in abundance between 5 m and 100 m from the edge. Thus, the edge effect appears to be ≤ 5 m for forest beetles and the creation of a ski trail destroys little habitat for these forest species beyond the actual area cleared. Consequently, the greater concern is not for the populations of beetles that occupy the large forest patches on the margins of the ski area, but those populations that are within the boundaries of the ski area. The network of ski trails across the mountain creates numerous forest "islands", which isolate populations of forest beetles with limited gap-crossing abilities. On the Stowe ski area, there are approximately 94 forest islands created by ski trails, lifts, and access roads, of which 39 are in the spruce-fir zone where our study was conducted. The populations of epigeic beetles in these smaller fragments will be at risk of local extirpation through stochastic processes as there will be little or no rescue effect from larger populations. Further, ski trails that run perpendicular to the climatic gradient may limit opportunities for the movement of species in the

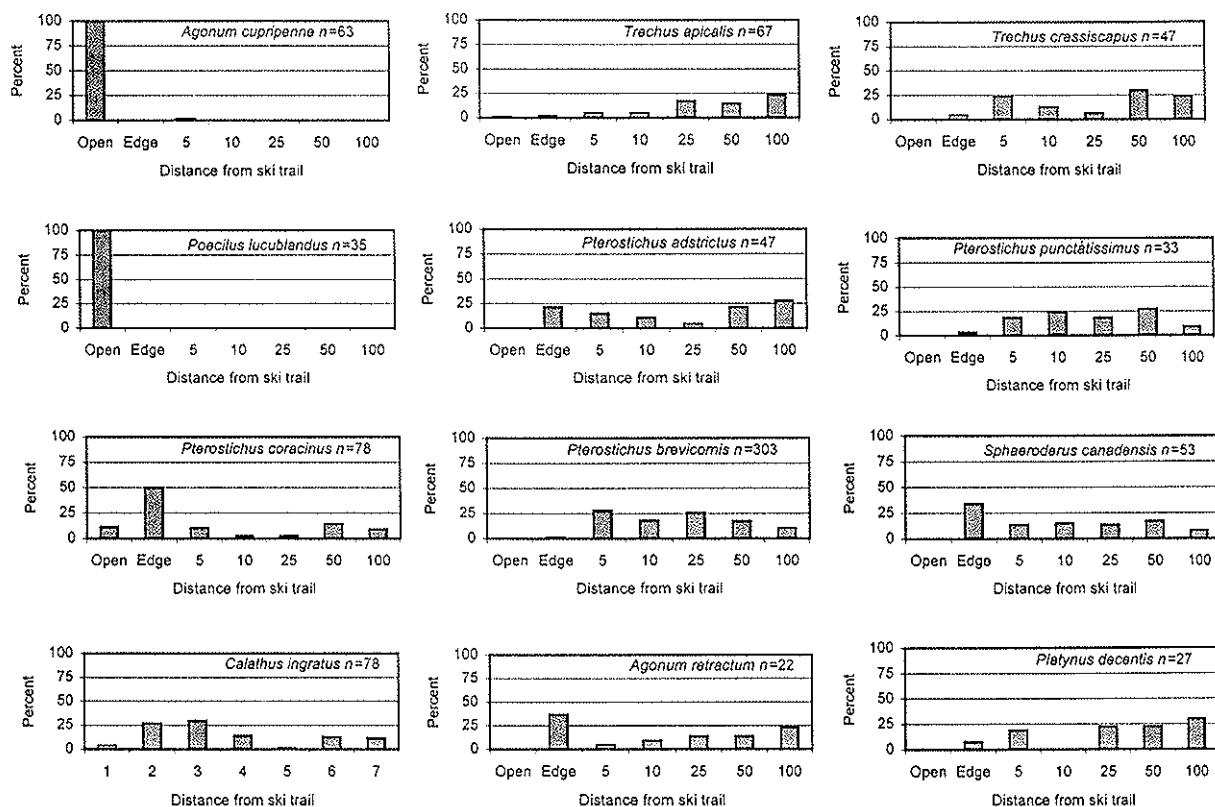


Figure 4. Percent of total capture for 12 species of carabids across transects from a ski trail to 100 m into unfragmented forest on Mt. Mansfield, VT, June–August, 2000. Distributions were significantly different from random for all species with $n > 35$ (G-test, all $G > 12.6$, all $df = 6$, all $P < 0.05$).

face of global changes in temperature and subsequent shifts in tree species distributions (Iverson and Prasad 1998; Noss 2001). Because these ski trails will prevent movement to higher elevations, populations in many of these isolated fragments will probably become extirpated over longer time scales (Ashworth 1996). Even without climatic variation, long-term studies of carabid populations in fragmented landscapes in the Netherlands have shown extirpation of isolated populations (Turin and den Boer 1988) and extinction of flightless species (De Vries and Den Boer 1990) and poor dispersers (Niemiälä et al. 1998) in habitat fragments. Further, Hopkins and Webb (1984) showed that spiders with poor powers of dispersal were restricted to the largest remaining heathland fragments.

We expected that the ski trail-forest edge would be permeable to open habitat species, with many colonizing the edge of the forest. However, only 2 of 173 individuals of these five open habitat species were collected in the forest (1 on the edge and 1 at 5 m). Thus, the forest edge acted as nearly an impermeable

reflective boundary. Despite being long-winged and good dispersers (e.g., *Agonum cupripenne* and *Poecilus lucublandus*), they are apparently highly stenotypic. Interestingly, all the open habitat species appeared to have colonized the mountain slope from open habitats at lower elevations with the exception of *H. bicolor*, a high elevation elaterid that colonized the ski trail from above the tree line. Thus, the ski trails may create suitable habitats for some high elevation species with limited distributions (sensu Everham et al. (1996)).

We also expected the ski trail edge would have a much greater spatial effect on forest beetle distributions, perhaps as great as 50–100 m into the forest interior (Spence et al. 1996; Didham 1997b). We did find a strong edge effect, such that all four species that showed greater than expected use of forest habitat used the edge significantly (*Pterostichus brevicornis*, *Trechus crassiscapus*) or somewhat (*T. apicalis*, *P. punctatissimus*) less than expected. However, although this effect was pronounced, it was limited in spatial extent to approximately 5 m from the ski trail

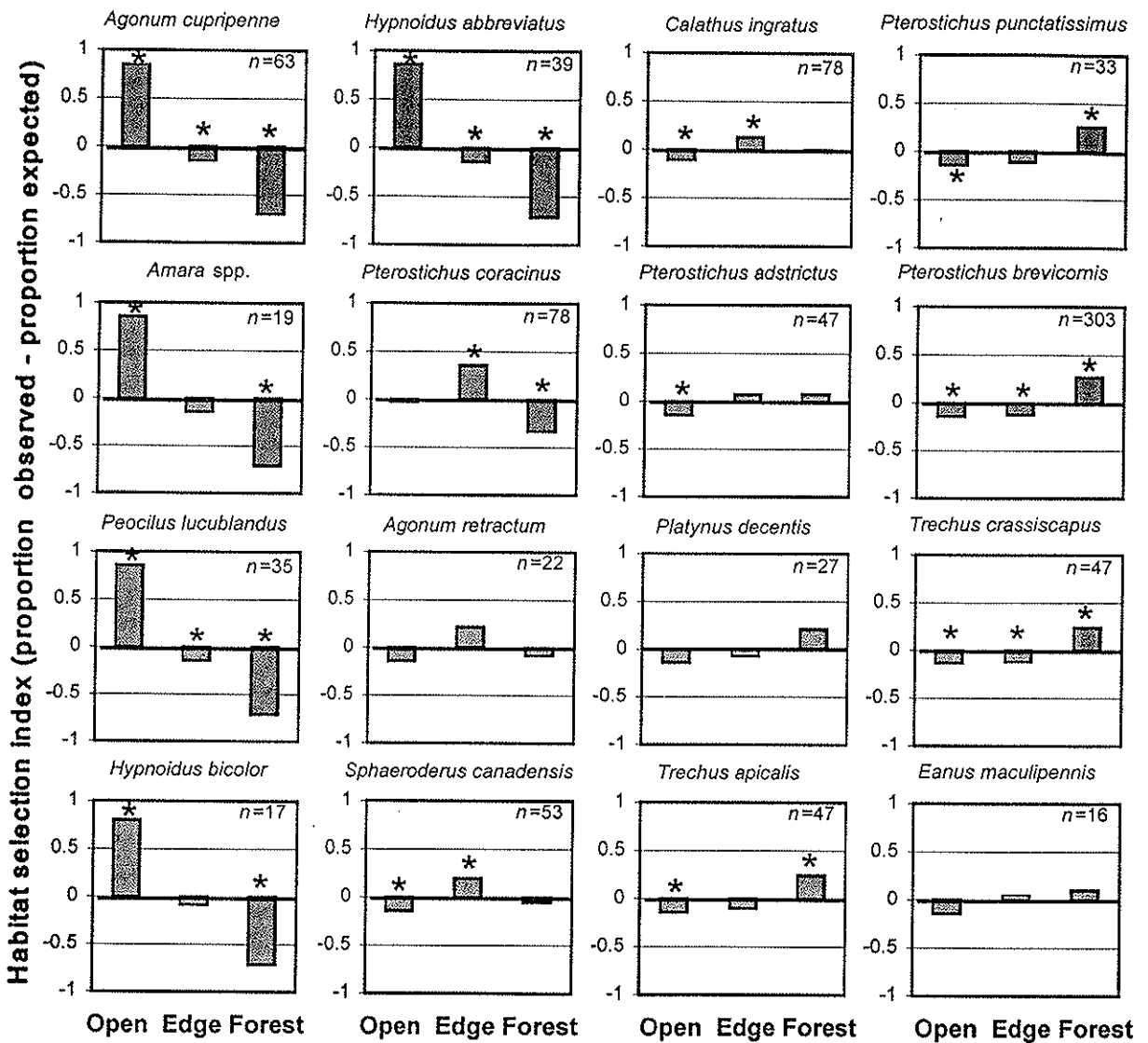


Figure 5. Observed versus expected abundances for 16 species of beetles within ski trail openings, edges and forested habitat (5 to 100 m from the edge) on Mt. Mansfield, VT, June–August, 2000. Bars above or below the 0 line indicate that species were more or less abundant than expected, respectively; asterisks indicate use was significantly greater or less than expected.

edge, with the possible exception of *T. apicalis* (Figure 4). We suggest two possible hypotheses for the limited spatial effect of the edge. First, in comparison to roads, land use practices on ski trails that have a direct impact on ground beetle populations are relatively benign. Human activity is dispersed, except during the ski season, at which time the vegetation is covered in snow. The use of motorized vehicles is relatively minor: mowing at most once per year, occasional snowmobile (winter) and ATV (summer) use for transportation of ski area employees up and down the slope, irregular transportation of heavy machinery

for construction and repair of facilities, and use of ski trail grooming equipment during the winter. Second, the actual edge type that we studied may have reached an equilibrium of community dynamics not found in studies of forest-clearcut edges or forest-agricultural edges. The ski trail that we studied was created in 1968, thus the edge was over 30 years old. Consequently, species have had a relatively long time to shift their distributions in response to changes in vegetation composition and structure, microclimatic conditions, and predator and competitor distributions. Further, the human-maintained canopy dripline edge

is a "hard" edge, with practically no grasses or forbes colonizing the forest and no canopy trees extending into the ski trail. The limited spatial extent of the edge effects may be due to the spruce-fir vegetation along the ski trail "sealing" itself over time (Williams-Linera 1990) as stem density increases along edges in response to light availability (Ranney et al. 1981), insulating the forest from conditions in the ski trail opening. Consequently, habitat conditions on either side of the edge are highly divergent, as are the beetle communities.

The strongest edge effect was the characterization of four carabids as "edge species". Previous research has suggested that there is no characteristic ground beetle community in forest-agriculture, -clearcut, or -savannah edges (Spence et al. 1996; Didham 1997b; Heliölä et al. 2001; Kotze and Samways 2001). However, in our study, the carabid edge community appeared to be somewhat distinct and not simply a composite of forest and ski trail species, as we found four species that showed greater than expected use of edges (three significant, one non-significant). Although these species were not restricted to edge sites, 25–50% of the total catch for each species was in edge sites. Generalizations about the ecology of these species may be impossible, but all appear to be forest species that have taken advantage of some attribute of the edge habitat. We can provide a research hypothesis for the distribution of *S. canadensis*, a snail predator. Over 85% of the snails captured ($n = 91$ from the same pitfall traps) were either in the edge or the ski trail, suggesting that this species has colonized edge habitats in response to prey availability. The remaining species are either typically found in deciduous habitats (*Agonum retractum*, *P. coracinus*) or are edge species at lower elevations (*Calathus ingratus*) and therefore may tend to use edges more than expected at higher elevations where deciduous trees may reach slightly higher densities than in the interior of the montane forest.

The results of this study allow us to put ski trail edges into a continuum of edge types that have varying effects on ground beetle communities. The degree to which particular edge types act as barriers to dispersal appears to be related primarily to the contrast in vegetation structure across the ecotone, time since disturbance, and the degree to which the edge acts as a barrier to dispersal. Roads create extreme habitat discontinuities, with edge effects extending up to 100 m into contiguous forest (Haskell 2000). The causal mechanism behind this strong edge effect has been

hypothesized to be related to penetration of wind and sun into the forest edge, decreasing the accumulation of organic matter. For non-volant, neophobic species, the extreme change in habitat structure from vegetation to the road surface may act as a complete barrier to dispersal (Plat et al. 1995). Similar effects have been cited for forest-agriculture edges in South America (Didham 1997b) and Australia (Davies and Margules 1998).

In contrast, the edge effects generated by clearcuts appear to be less extreme, as some species of forest carabids will remain in clearcuts after cutting (Jennings et al. 1986; Niemälä et al. (1993, 1996); Jennings et al. 1986). Clearcuts may not immediately become "hostile" environments for carabids, particularly if the site is left undisturbed for regeneration to proceed, slash is left on site, and some portion of the herbaceous and shrub layer remains. Similar results have been shown for carabids across edges with little contrast in structure between habitats (Bauer 1989; Duelli 1990). The edge effects of ski trails appear to be most similar to those of buffer strips along riparian zones, or hedgerows or grassy buffer strips in agricultural habitats. In these situations, most species appear to stay in one habitat type or another, but there does not appear to be a significant edge effect in either habitat (Luff 1990; Frampton et al. 1995; Petit and Burel 1998). As with ski trails, the moderate edge effect appears to result from the strong divergence in habitat structure, limited human activity, and longer times since disturbance.

In summary, our results suggest that ski trail edges along large patches of contiguous forest result in limited edge effects. However, further study of forest fragments created by ski trails is warranted, as these patches may come to harbor reduced populations as a result of stochastic events. Because of the nearly complete turnover in ground beetle species composition between ski trails and forests, we suggest that species richness and diversity are inappropriate measures of the effects of edges, and that documenting the effects on individual species will lead to a better understanding how edges affect invertebrate communities. Even our results (presence-absence data) are limited in their utility in population modeling as they fail to incorporate habitat-specific demographics across different habitat types. Finally, we suggest that researchers make a concerted effort to better describe edges, as much of the inconsistency in quantifying edge effects may result from variation in edge types and ages.

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