

Habitat loss decreases predator–prey ratios in a pine-bark beetle system

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Increasing intensity of land use by humans has led to loss of natural habitats, resulting in isolation of remaining habitat fragments. Using a pine-bark beetle ecosystem as a model, we tested the hypothesis that the ratio of abundance of predators to prey should decrease with increasing habitat loss at the landscape scale. We selected ten red pine (*Pinus resinosa*) sites, representing extremes of available habitat within a 2 km radius surrounding each stand. The bark beetle, *Ips pini*, and its coleopteran predators were sampled using baited multiple funnel traps. Effects of stand isolation were considerable; ratios of predators to prey (mean number of predators/number of prey \pm SE) were significantly reduced in isolated stands (0.38 ± 0.09) as compared to those with large amounts of surrounding conifer habitat (1.63 ± 0.41). The decline in ratio occurred both because there was: a) a lower abundance of predators (ca $0.5\text{--}0.8 \times$) captured in isolated stands; and b) a significantly higher number of prey (ca $2.2 \times$) captured in isolated stands. Isolation or loss of habitat, therefore, differentially affected the two trophic levels, supporting theoretical predictions. Reductions in predator abundance and, presumably, enemy-caused mortality may lead to changes in the population dynamics of their prey species, possibly leading to increased outbreaks as habitat becomes increasingly isolated.

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Increasing intensity of land use by humans has led to the loss of natural habitats, resulting in the isolation of remaining habitat fragments. The impact of such isolation on single species abundance and persistence, and also species diversity has received considerable attention (Saunders et al. 1991, Fahrig and Merriam 1994, With and King 1999). Isolation of habitat can also influence interactions among species, such as among interspecific competitors, predators and their prey, or parasitoids and their hosts (Didham et al. 1996). Theoretical studies examining the effects of habitat loss typically predict that specialist predators (i.e. species at higher trophic levels that are restricted to a particular prey species or habitat) require more habitat for persistence than do their prey. Both occupancy of patches and extinction thresholds

were predicted to be lower for specialist predators than for their prey with increasing destruction of habitat (Bascompte and Solé 1998, Nakagiri et al. 2001, Swihart et al. 2001). The disproportionate vulnerability of higher trophic levels to habitat loss may thus facilitate escape from predation pressure by prey populations.

Empirical studies explicitly addressing this theoretical prediction are rare. Reductions in predation or parasitism with increasing habitat loss and isolation have been reported in four previous studies (Roland 1993, Kruess and Tscharntke 1994, 2000, Zabel and Tscharntke 1998). Most of these studies (all except Roland 1993) were conducted at spatial scales that were small relative to the dispersal distances assumed in theoretical models, i.e. small relative to the between-generation movement

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distance. While Roland's 1993 study on the forest tent caterpillar (*Malacosoma disstria* Hbn.) was conducted at a sufficiently large scale, predator or parasitoid activity was not measured and was only assumed to be responsible for changes in prey population dynamics as related to habitat loss and fragmentation. Hence, no empirical studies have measured predator-prey ratios at a scale appropriate to the models.

We tested the prediction that predator-prey ratios decrease with decreasing habitat amount, in a pine-bark beetle system. Bark beetles (Coleoptera: Scolytidae) are forest insect pests, typically breeding in stressed trees but in some cases capable of colonizing healthy trees (Rudinsky 1962). Scolytids are an interesting model system because their biology may fit the metapopulation models used in theoretical research more appropriately than do other taxa. For example, many species use patchily-distributed food resources (Wood 1982, Nilssen 1984, Forsse and Solbreck 1985, Weslien and Lindelow 1989). In addition, natural enemies, particularly predators, have been implicated as important regulatory agents in scolytid population dynamics (Turchin et al. 1991, 1999, Schroeder 1996, Reeve 1997, Ryall 2003). No studies have examined how the amount of habitat at the landscape scale affects scolytid predator-prey interactions.

To select an appropriate spatial scale, we must identify the dispersal capabilities and tendencies of the focal species, information that is typically lacking in previous studies. Most reports of scolytid dispersal have found that dispersal distances are usually less than two kilometres (Zumr 1992, Turchin and Thoeny 1993, Cronin et al. 1999, Barak et al. 2000, Dodds and Ross 2002). Limited data on one species of predator suggested that they may also disperse up to two or three kilometres (Cronin et al. 2000), although a small proportion of predators dispersed farther than their scolytid prey. The spatial scale in our study (two km radius) was selected based on this information.

We quantified the abundance of a scolytid relative to its associated coleopteran predators in highly isolated vs less isolated conifer stands, where isolation was measured as the amount of conifer forest within two km of each of the stands. We predicted that: 1) the ratio of predators to prey would be lower in more isolated stands and 2) the decrease in ratios would be due to both lower abundance of predators and increased abundance of prey in more isolated stands located in landscapes with less habitat.

Methods

The focal species in this study was the native pine engraver beetle (*Ips pini* (Say), Coleoptera, Scolytidae), the most common scolytid species in our study

region (Ryall 2003). It uses a variety of conifers, primarily pines (*Pinus* spp.), for reproduction, reproducing only in stressed or dying trees in our study area (Thomas 1961, Ryall 2003). Across eastern Ontario, the most common and abundant host is red pine (*Pinus resinosa* Ait.), which is typically found in monoculture plantations.

The predators examined in this study (*Thanasimus dubius* F. (Col., Cleridae); *Enoclerus nigripes* Say (Col., Cleridae); *Platysoma* spp. (Col., Histeridae)) are the most abundant predators of *I. pini* in the Great Lakes region (Raffa 1991, Aukema et al. 2000, Erbilgin and Raffa 2001, Ryall 2003). *Thanasimus dubius* (Coleoptera, Cleridae), in particular, has been shown to be a significant source of mortality of various scolytid species (Thatcher and Pickard 1966, Turnbow et al. 1978, Reeve 1997, Aukema and Raffa 2002, Ryall 2003). While predators such as *T. dubius* feed on a variety of prey species in the sub-cortical habitat, they are restricted to the same coniferous habitat as their prey. This habitat restriction is a key feature of specialist predators in the theoretical models (Bascompte and Solé 1998, Nakagiri et al. 2001, Swihart et al. 2001). In addition, previous work has demonstrated *I. pini* to be the key prey species for these predators in this region (Ryall 2003).

We sampled ten 35–50-year old red pine stands across eastern Ontario, Canada, distributed over an area of approximately 250 × 150 km. Stands were selected to represent the extremes of habitat availability across the region, while standardizing variables such as stand age, density, species composition and presence of coarse woody debris. Half of the stands (n = 5) were isolated, with little other conifer forests within a two km radius (mean 14.9%, range 6–22%). The other half (n = 5) were selected based on a high proportion of conifer forest within two km of the sites (mean 55.0%, range 37–72%). Stands were separated by a minimum of five km, so the 2-km radius landscapes were non-overlapping. Sites were selected based on forest inventory maps from the Ministry of Natural Resources and through discussions with local forest managers. The proportion of conifer habitat within a radius of two km surrounding a given site was calculated using data provided by the Canada Centre for Remote Sensing.

Stand-level information was collected for each site using a 300-m transect, 2 m in width, randomly located but not following a row within the plantation. For each tree in the transect, diameter at breast height (1.2 m, DBH) and "health" (green crown recorded as healthy, red crown as dying or recently dead) were recorded. Stand density (no. trees ha⁻¹) was calculated by converting the number of stems within the 600 m² transect into a per-hectare value.

We sampled *I. pini* and its associated natural enemies using baited funnel traps, from June to September 2003. Three eight-unit funnel traps were placed in each site,

typically in a straight line through the middle of the stand with a minimum of 50 m between each trap. No trap was located less than 30 m from an edge. Traps were suspended between two trees, using twine, at a height of approximately 2 m at the top in locations with a minimum of understory vegetation in the immediate vicinity. The traps were each baited with two bubblecap lures; racemic ipsdienol (50%+/50%−) and lanierone (PheroTech®). Lures were attached on the opposite sides of the trap to the fourth, or middle, funnel. Collecting cups were half-filled with ethylene glycol (Plumbing antifreeze) to collect the beetles. Funnel traps were checked every other week; all captured beetles were collected and brought to the laboratory for identification and counting, and collecting cups were refilled as necessary.

Results

As expected (by design), isolated stands had significantly lower percentage of conifer forest cover in the surrounding 2-km landscape than did non-isolated stands (Mann–Whitney $U=25.0$, $p=0.009$, Table 1). There was no significant difference in mean stand size (Mann–Whitney $U=9.00$, $p=0.806$, Table 1), mean stand density (Mann–Whitney $U=5.5$, $p=0.142$, Table 1), or mean DBH (Mann–Whitney $U=18.5$, $p=0.207$, Table 1) between isolated and non-isolated stands. The number of recently dead or dying trees was extremely low in all sites (Table 1).

A total of 8706 insects were captured and identified during the sampling periods; 61.7% were the bark beetle, *I. pini*. The remainder included the predators: *T. dubius* (19.1%), *E. nigripes* (1.5%), *Platysoma* spp. (6.7%) (including *P. cylindrica* (Paykull) and *P. parallellum* (Say)) and *Zenodosus sanguineus* (Say) (0.1%). Also common in the samples was *Glischrochilus fasciatus* (Oliv.) (Col., Nitidulidae) (10.8%); however this species is likely not a predator and was not included in the analyses. Small numbers of scolytids and other coleopterans were also collected, but not included in the analyses.

The ratio of predators to *I. pini* prey was significantly lower in isolated conifer stands than in less-isolated stands ($F=51.1$, $p<0.0001$; Fig. 1a). Significantly more *I. pini* (the prey species) were captured in isolated as compared to non-isolated stands ($F=14.78$, $p=0.001$;

Fig. 1b). The abundance of all predators combined was slightly, but not significantly, lower in the isolated stands ($F=0.588$, $p=0.465$; Fig. 1c). A slight (non-significant) reduction in mean abundance between isolated and non-isolated stands was observed for *T. dubius* ($F=2.65$, $p=0.119$; Fig. 1c) and *E. nigripes* ($F=2.0$, $p=0.173$; Fig. 1c). Significantly fewer *Platysoma* spp. ($F=4.73$, $p=0.042$; Fig. 1c) were captured in isolated as compared to non-isolated stands.

Discussion

Our results supported both of our predictions. Predator–prey ratios were lower in the isolated stands than in the non-isolated stands. This was due to much larger prey numbers and slightly lower predator numbers in the isolated stands. Most previous research on scolytids has been conducted at the smaller patch or stand scale, with no consideration of the landscape context of the patch. For example, the abundance of scolytids and their associated predators has been shown to be influenced by stand-level variables such as thinning (Schroeder 1999, Hindmarch and Reid 2001) and stand condition (Erbilgin and Raffa 2002, Erbilgin et al. 2002). Decreases in predator to prey ratios in isolated stands in our study are likely not due to such factors because stand conditions (size, age, tree density, tree species, number of recently dead or dying trees) were similar for the two landscape types. Our results are the first to demonstrate the differential impact of habitat loss on scolytid predators and their prey at the landscape scale.

Our results are consistent with the few empirical studies on other insect species and their specialist predators and parasitoids. Previous research has found that with increasing isolation of habitat patches, there is a considerable reduction in levels of parasitism and predation (Kruess and Tscharntke 1994, 2000, Tscharntke et al. 1998) and significantly lower rates of patch colonization by parasitoids (Corbett and Rosenheim 1996, Lei and Hanski 1997, Cronin and Strong 1999). Increased prey populations as a result of habitat loss and, presumably, reduction in predator populations have also occasionally been reported (Karieva 1987, Roland 1993, Braschler et al. 2003), although in some studies, the abundance of herbivores declined with increasing habitat isolation (Kruess and Tscharntke

Table 1. Comparison of percentage conifer forest cover, patch size, stem density, DBH, and number of dying trees between non-isolated and isolated stands. Means (\pm SE) followed by same letter are not significantly different within each column.

Stand type	% conifer in 2-km radius	Patch size (ha)	Stem density (no. ha $^{-1}$)	DBH (cm)	No. dying trees (ha $^{-1}$)
Non-isolated	14.88 (4.28)a	11.32 (2.57)a	1050 (138)a	22.84 (1.45)a	0.4 (0.24)
Isolated	55.02 (7.56)b	10.42 (2.82)a	1390 (154)a	20.18 (3.39)a	0.2 (0.21)

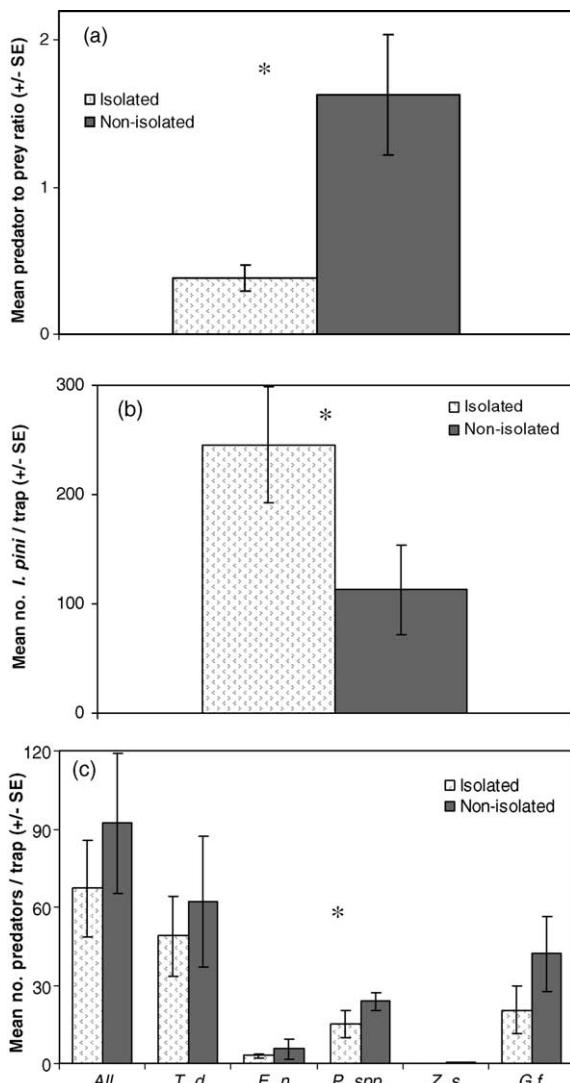


Fig. 1. (a) Mean predator-prey ratios and (b) mean abundance of *I. pini* and (c) its associated coleopteran predators combined (All, except *G. f*) and by species in isolated and non-isolated areas of pine habitat across eastern Ontario during 2003. N = 5 non-isolated and 5 isolated stands. Standard errors indicated by vertical lines. Asterisk indicates significant differences ($p < 0.05$) in mean ratio or mean abundance between isolated and non-isolated habitats using ANOVA. (All = all predators combined; *T. d* = *Thanasimus dubius*; *E. n* = *Enoclerus nigripes*; *P. spp.* = *Platysoma* spp.; *Z. s* = *Zenodosus sanguineus*; *G. f* = *Glischrochilus fasciatus*).

1994, 2000). Hence, the limited number of previous studies mostly supports the prediction of a greater negative effect of habitat loss on specialist predator and parasitoid species than on their prey or host species.

Is the increase in prey abundance in isolated sites actually due to decreased predation? Predators can reduce adult bark beetle establishment by 30–60% (Thatcher and Pickard 1966, Reeve 1997, Aukema and Raffa 2002) and can reduce bark beetle offspring production by 20–80% within infested trees (Riley and Goyer 1986, Weslien 1992, Weslien and Regnander 1992, Schroeder and Weslien 1994, Aukema and Raffa 2002). In addition, predators have been implicated in the

regulation of bark beetle populations (Weslien 1992, Reeve 1997, Turchin et al. 1999, Ryall 2003), reducing the rate of increase of scolytid populations by up to 70% (Turchin et al. 1999). In our study the prey population more than doubled, while the predator population density decreased by 20–40%. If predation accounts for 20–80% of the typical annual mortality of scolytids, the resulting annual decrease of 4–32% mortality due to the lower predator densities could result in a doubling of the prey population within 4–20 generations. In our study, the habitats had been isolated for a minimum of 30–40 years, corresponding to at least 50–70 generations of *I. pini* and 30–40 generations of predators.

Based on these arguments, we can conclude that it is at least possible that the increase in prey populations in isolated stands was due to decreased predation.

However, there is at least one possible alternative explanation: the lower predator abundance and higher prey abundance in more isolated stands could be a result of differential immigration of predators and prey, rather than a result of local predator–prey dynamics. Scolytids are widespread and have the capacity to colonize highly-dispersed, patchy, ephemeral resources (Wood 1982, Nilssen 1984, Forsse and Solbreck 1985, Weslien and Lindelow 1989). If bark beetles are easily able to move through non-habitat areas and find host stands, we would expect larger numbers to accumulate in isolated stands due to a lack of alternate habitat within the landscape. If, at the same time, the predators are less able to find the bark beetles in isolated stands than non-isolated stands, their numbers would be lower there than in non-isolated stands. This could result in persistently higher abundances of adult bark beetles and lower abundances of their predators in isolated stands.

There is in fact little information on movement ranges and host-finding abilities of the bark beetle predators. However, for one predator species (*T. dubius*), the dispersal range has been demonstrated to be up to several kilometres (Cronin et al. 2000). In addition, predators are known to use aggregation pheromones and plant volatiles to locate bark beetle infestations (Herms et al. 1991, Aukema et al. 2000). Since the bark beetles themselves represent a patchy, ephemeral resource, we would expect their predators to have evolved to be highly dispersive. If true, it is actually somewhat surprising that we found an effect of habitat loss at the landscape scale. Studies of more sedentary species feeding on consistently-available resources would likely result in an even stronger effect of habitat isolation on predator–prey ratios.

Reductions in natural-enemy mortality of forest insects with habitat loss has important management implications. Many scolytid species are serious forest pests (Rudinsky 1962) and natural-enemy mortality is increasingly recognized as an important factor in their regulation (Reeve 1997, Turchin et al. 1999). Hence, reductions in predator populations associated with habitat loss could lead to worsened pest outbreaks of these and possibly other forest insect pests. Finally, to further our understanding of the effects of habitat loss on predator–prey interactions, future research should incorporate predators with different feeding strategies (i.e. ranging from feeding on only one to many prey species, as well as the ability to persist in multiple habitat types). Based on the predictions of the theoretical models (Swihart et al. 2001, Cantrell et al. 2002), generalist predators should be less affected by habitat loss as compared to specialists.

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