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Distribution of a bark beetle, *Trypodendron lineatum*, in a harvested landscape

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Abstract

The response of the striped ambrosia beetle, *Trypodendron lineatum* (Olivier) (Coleoptera: Curculionidae, Scolytinae), to direct and indirect measures of habitat availability was examined across a heterogeneous forest subjected to various intensities of harvest. The study area was classified into four stand types (conifer-dominated, mixed, deciduous-dominated, and deciduous-dominated with conifer understory) each of which was treated with four harvest intensities (unharvested, and 50%, 80%, and 90% harvested) and replicated three times each. The abundance of *T. lineatum* was measured using baited funnel traps. In the year prior to harvest, *T. lineatum* was most abundant in conifer-dominated stands, although the measured abundance of freshly dead conifers (their breeding habitat) did not differ from mixed stands. In the first and second summers after harvest, *T. lineatum* abundance varied with both stand type (least in deciduous-dominated stands) and harvest level (least in unharvested stands). In particular, abundance increased exponentially with the percent of spruce, *Picea* spp., in the canopy and the number of spruce stumps in the stand. These results suggest that *T. lineatum* search more in areas with more actual (stumps) or potential (live spruce) habitat, consistent with the resource concentration hypothesis. Because of the disproportionate response of *T. lineatum* to habitat cues, managers should minimize the concentration of freshly dead boles, particular in conifer stands.

Keywords: Habitat; Ideal free distribution; Resource concentration hypothesis; Bark beetle; Thinning; Host; Abundance; Coarse woody debris

1. Introduction

The relationship between the distribution of organisms across the landscape and the abundance of its habitat depends on the processes by which individuals seek resources. These processes include cues that animals use to find habitat and the scale of their movement relative to that of the variation in resource abundance. Anthropogenic changes in resource abundance can provide both an opportunity to examine these processes experimentally as well as providing direct and needed observations of the consequences of particular human activities on species distributions and abundances. Here we examine the response of the striped ambrosia beetle, *Trypodendron lineatum* (Olivier) (Coleoptera: Scolytinae) to variation in forest stand composition and intensity of harvesting, to elucidate the processes by which forestry practices alter its distribution and abundance. *T. lineatum* is an economically important pest to the forest industry (McLean, 1985), as it can cause damage to stored wood in millyards (Lindelow et al., 1992). By understanding the effects of forest harvesting on populations of *T. lineatum*, forest managers may develop practices that minimize the risk of infestations of this species and possibly of other ecologically similar species.

In general, we expect to find more individuals where their resources are more abundant. The ideal free distribution (IFD, Fretwell and Lucas, 1970) provides a basic expectation that numbers of individuals should be directly proportional to resource abundance. However, it assumes that individuals are knowledgeable about the distribution of resources and competitors and that there are no search costs. If these assumptions are lifted, then we might expect animal abundance would be disproportionately larger in areas with more resources. The resource concentration hypothesis

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(Root, 1973) was an early recognition that search costs may influence the distribution of individuals. This hypothesis suggests that herbivorous insects focus their habitat search to areas with high densities of host plants. As predicted, many studies have shown that insects concentrate their search for habitat in areas of high habitat concentration, leading to higher insect abundance in these areas (e.g. Batch, 1984; Turchin, 1988; Andow, 1990).

The habitat of *T. lineatum* is dead and dying coniferous wood (*Picea*, *Pinus*, *Abies*), particularly 1 or 2 years following tree death (Dyer and Chapman, 1965). As with other bark beetles, *T. lineatum* is attracted by host volatiles (Moeck, 1970; Lindelow et al., 1992) and deterred by non-host volatiles (Borden et al., 1997). In forests unaltered by humans, the natural habitat of *T. lineatum* includes windthrow, snags and coarse woody debris. Due to the rare and ephemeral nature of this habitat, we might expect individuals searching for habitat to respond to indirect cues from live host trees at the stand level that would correlate with the abundance of habitat. However, stumps left behind by harvesting provide a large increase in actual breeding habitat for the first 1 or 2 years following harvesting. The release of host volatiles increases greatly in damaged or wounded trees (Byers, 1995; Schade and Goldstein, 2003), potentially allowing individuals to respond to differences in actual habitat abundance using the same cues as used at the stand level.

T. lineatum are capable of flying up to 40 km (Salom and McLean, 1991), so they may be able to track resource abundance across a large area. However, during dispersal, they lose approximately one quarter of their stored lipids (Nijholt, 1967), which may have implications for subsequent reproduction (Elkin and Reid, 2005). Such costs could limit the response to habitat availability. Previous studies on *T. lineatum* suggest that their abundance, as measured in kairomone-baited traps, corresponds with habitat abundance. In the first 3 years following commercial thinning, *T. lineatum* was more abundant in thinned stands than unthinned stands (Hindmarch and Reid, 2001), but 4 years later they were more abundant in unthinned stands in the same study area (Simpson and Reid, 2004). This pattern is consistent with the idea that habitat availability increases immediately following thinning due to stumps and fresh logging debris, but that these cease to be suitable in successive years making stands with more abundant live host trees (unthinned stands) more attractive. However, these studies had limited data on actual habitat. Moreover, they considered only pure conifer stands making it difficult to distinguish between the effects of live host abundance and environmental differences in stand density that may influence distribution (Salom and McLean, 1991).

Using an experimental design that varied both stand composition and harvesting intensities, we describe the effects of forest management practices on the abundance of *T. lineatum*. In particular, we investigate the relative importance of indirect cues of habitat abundance (from live host trees) and actual habitat abundance (conifer stumps) in determining their responses. In addition, we contrast these patterns with more limited observations from the year prior to harvest.

2. Methods

2.1. Site

The study site was located at the EMEND (Ecosystem Management by Emulating Natural Disturbance) project site located in the boreal mixedwood forest northwest of Peace River, Alberta (Work et al., 2004) and with a spatial extent of over 1000 ha. In 1997, four forest stand types were identified within this area: deciduous-dominated (DDOM; 70–95% deciduous: *Populus balsamifera* (L.), *P. tremuloides* (Michx)), deciduous-dominated with conifer understory (DDOMU), mixed (MX; 35–65% deciduous and conifer), and conifer-dominated (CDOM; 70–95% conifer: *Picea glauca* (Moench), *P. mariana* (Miller), *Abies balsamea* (L.)). Each stand type had three replicates. The replicates were divided into compartments of 10 ha that were subjected to the harvesting treatments. Harvest treatments used in this study consisted of four harvest levels, 90% harvested, 80%, 50%, and control (no harvest). To apply the treatments, trees were harvested from 5 m machine corridors, where all vegetation was removed. Stem removal from the machine corridors contributed 25% net removal, with the remaining selected felling in the 15 m retention strips contributing the additional removal of stems. Within the retention strips, the 50% treatment had 1/3 trees removed, while 3/4 and 7/8 trees were removed for the 80% and 90% harvest treatments, respectively (Sidders and Luchkow, 1998). Entire trees, except the stump, were removed to a landing within each compartment where cutting and delimbing occurred. Stand compositions following harvest were consistent with classification pre-harvest (unpublished data, EMEND). Harvesting occurred in the winter of 1998–1999, and all harvested material was removed from the site before the following spring.

3. Bark beetle distribution and abundance

We measured *T. lineatum* abundance in stands using a standard stimulus that consisted of a 12-funnel multiple-funnel trap (Lindgren, 1983) baited with host kairomones (Phero Tech Inc., Delta, BC). A 1 cm^3 of solid insecticide (Vapona™) was placed in each collection cup. To examine the effect of conifer abundance alone on the distribution of *T. lineatum*, beetles were sampled during the summer of 1998, prior to harvesting. Thirty-two baited traps were erected in 6 deciduous-dominated stands, 6 deciduous-dominated with conifer understory, 12 mixed-wood, and 8 conifer-dominated stands. These 32 stands were candidate stands from which three replicates of each stand type were chosen for application of the harvest treatments in 1999. Traps were centrally located within a stand; at least 100 m from the stand edge, at a height of approximately 1.5 m from the ground. Traps were baited with tree kairomones ethanol and α-pinene (release rates for both ethanol and α-pinene were 1 g/day). Previous studies have shown that *T. lineatum* are attracted to α-pinene (Bauer and Vité, 1975; Salom and McLean, 1988, Lindelow et al., 1992) and ethanol (Moeck, 1970) during dispersal. Traps were emptied every 2 weeks between 31 May 1998 and 3 August 1998, which corresponds with the peak flight activity period of *T. lineatum*.