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Edge effects resulting from forest fragmentation are likely to alter the distributions and interactions of resident species. I evaluated changes in species composition, species turnover, and relative abundance of ground arthropods across replicated transects extending from regenerating clearcuts into old-growth Douglas-fir forests. Arthropods were collected from 3-August to 14-September in 1997 and 23-May 1998 to 31-July 1998 using pitfall traps. Pitfall traps were positioned at –75 m (in the clearcut), -25, 0 (forest edge), 50, 100 and 200 m into the forest in 1997. In 1998, traps were repositioned at –25, 0, 25, 50 ,100, and 200 m into the forest. Changes in species composition and relative abundance were compared using non-metric multidimensional scaling ordination. Two-hundred, five species representing 24,178 individuals were collected. Edge effects on species composition and relative abundance were apparent up to 100 m into old-growth forests. Species were characterized as edge-phobic (interior forest associates), edge-philic, edge-insensitive or as edge-input (clearcut associates). The majority of species were characterized as either edge-phobic or edge-input species. Seasonal patterns in activity are also reported. To further address the impacts of edges on community structure, changes in species abundance of predator taxa across the edge-forest gradient were compared to four models of resource partitioning. Observed patterns of species abundance did not differ across the edge-forest gradients and were consistent with a model of random assortment (or non-equilibrium) where an individual predator species utilizes resources independently of other predators. This pattern was consistent whether species abundance was expressed as numerical abundance or biomass. This study suggests that edge effects resulting from forest fragmentation alter species composition and may negatively affect interior forest species. Furthermore, although species composition changes across forest edges, this study suggests that resource partitioning by a trophic group such as predators remains unaffected by forest edges.

Edge Effects of Clearcut Harvesting on Ground Arthropod Species Composition and Predator Community Structure in Old-Growth Douglas-fir Forests

by

Timothy T. Work

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Timothy T. Work, Author

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Edge Effects of Clearcut Harvesting on Ground Arthropod Species Composition and Predator Community Structure in Old-Growth Douglas-fir Forests

Chapter 1

INTRODUCTION

Land transformation (including land conversion, habitat loss and fragmentation) is the primary agent for loss of global biodiversity (Vitousek *et al.* 1997). Widespread deforestation in both tropical (Lovejoy *et al.* 1986) and temperate regions (Wilcove *et al.* 1986) has resulted in the conversion of large, contiguous forest into smaller sized remnants that are dispersed throughout the landscape. Thus far, ecologists have concentrated on understanding the spatial nature of species interactions between forest fragments in terms of metapopulation dynamics (Hanski and Thomas 1994; Tilman *et al.* 1994), critical thresholds in landscape connectivity (With and King 1999) and source-sink models (Pulliam and Danielson 1991; Pulliam 1998).

However in addition to the decrease in connectivity of forest fragments, fragmentation also increases the amount of peripheral 'edge' around individual fragments (Wilcove *et al.* 1986). Edges can alter abiotic factors such as light distribution and temperature (Saunders *et al.* 1991; Chen *et al.* 1995; Cadenasso *et al.* 1997; Chen and Franklin 1997) as well as ecosystem processes such as seed predation (Burkey 1993), nest parasitism (Donovan *et al.* 1997), dispersal (Murcia 1995), pollination (Aizen and Feinsinger 1994) and decomposition rates (Klein and Perkins 1988). Without clear understanding of the extent of edge effects into remaining forest fragments, predictions about habitat quality (and thus the potential for patch occupancy in landscape models) are impossible.

Within forests, arthropods function as important regulators of ecosystem processes that may be affected by edge conditions. Arthropods comprise a major part of the biodiversity of forests (Wilson 1985; Probst and Crow 1991) and are important food sources for many vertebrate taxa such as birds, amphibians and small mammals. Arthropod herbivores and decomposers can regulate nutrient cycling and productivity within a forest (Mattson and Addy 1975; Seastedt and Crossley 1981). Likewise, arthropods predators and parasitoids play an important role as ecosystem regulators through top-down effects on primary consumers (Price 1987). Because of the variety of ecological roles they play and their short generation times, arthropods are often used as indicators of environmental change (Kremen *et al.* 1993; Niemela *et al.* 1993; Kremen 1994; Andersen 1997; Rykken *et al.* 1997).

Arthropod predators and parasitoids have been shown to be particularly sensitive to habitat fragmentation. For example, fragmentation of red clover patches reduced natural enemy diversity and effectiveness, resulting in an increase in herbivore populations (Kruess and Tscharntke 1994). Likewise, fragmentation of goldenrod patches decreased foraging efficiency of predatory beetles, resulting in outbreaks of aphids (Kareiva 1987). Abundance of arthropod predators was lower, while abundance of sap-feeding insects was greater, in regenerating Douglas-fir stands than in old-growth stands (Schowalter 1989). Increased fragmentation promoted outbreaks of defoliating forest tent caterpillar (*Malacosoma americanum*) by reducing the dispersal ability of the parasitic fly, *Pateolla pachypyga* (Roland and Taylor 1995; Roland and Taylor 1997).

Consequently, the impact of fragmentation on arthropod taxa in higher trophic levels may be influential on the population dynamics of other taxa and ecosystem processes overall (Chapin *et al.* 1997).

In the Pacific Northwest region of the United States and Canada, the impact of forestry management, including edge effects, has been an area of considerable interest because of its economic and ecological consequences. Fragmentation resulting from timber production has been a matter of public concern because of the interactions of edge effects with endangered species such as the spotted owl (*Strix occidental*). Within this region, clearcutting of forests has replaced natural wildfire as the major disturbance factor (Hansen *et al.* 1991). In the Cascades of Oregon, the area of natural interior forest decreased 18% between 1972 and 1987 due to timber harvest (Hansen *et al.* 1991). Likewise, by 1988, the amount of forest edge increased from 1.9 to 2.5 km/km^2 of forest and mean size of interior forest patches fell from 160 to 62 ha (Spies *et al.* 1994). Within old-growth Douglas-fir remnants, microclimatic effects of edges have been detected as far as 240 m into the forest (Chen *et al.* 1995; Chen and Franklin 1997). Likewise, seedling density and growth rate of dominant trees such as Douglas-fir and western hemlock increased along a forest-edge gradient (Chen *et al.* 1992). These differences have the potential to alter arthropod distribution, activity, and community structure.

In this dissertation, I present results of a large-scale field study that examined changes in arthropod abundance, species composition, and community structure across the transition zone between regenerating clearcuts and old-growth Douglas-fir forests. In Chapter 2, I provide a comprehensive analysis of the change in species composition of epigaeic arthropods across edge-forest gradients. Also within this chapter, I have identified species that are sensitive to edge-effects and I have developed an empirical classification of characteristic response patterns across forest edges. In Chapter 3, I have described seasonal differences in abundant taxa and correlate seasonal activity to differences in air temperature, soil temperature and precipitation. Quantifying seasonal patterns in activity is a necessary precursor to the development of hypotheses regarding community structure and resource partitioning later in this dissertation. In Chapter 4, I examined compositional changes within a single trophic group, epigaeic predators, and compare changes in species abundance to four models of resource partitioning. Finally, in Chapter 5, I have concluded by summarizing the results of this study and discussing my findings within the broader scope of conservation and land management.

Chapter 2

RESPONSES OF GROUND ARTHROPODS TO FOREST EDGE-EFFECTS IN OLD-GROWTH DOUGLAS FIR FORESTS

Introduction

Edges caused by forest fragmentation do not affect all species equally (Margules *et al.* 1994; Murcia 1995; Didham *et al.* 1996; Didham *et al.* 1998a). Individual species' responses collectively reflect life-history (Bellinger *et al.* 1989), physiological preferences (Matlack 1994), scale-dependency (Wiens 1989) and interactions with other species (Kareiva 1987). Given that diverse communities of organisms may elicit a diverse array of responses, the impacts of edge-effects on biodiversity are at best complex and at worst seemingly intractable.

Ecological theory has been inconsistent in its predictions as to which species may be affected by fragmentation and habitat edges. Food web theory suggests that species within higher trophic levels should be negatively affected by fragmentation (Pimm and Lawton 1977). However in many systems, species loss is consistent across all trophic levels (Mikkelson 1993). Spatial models of fragmentation suggest species with poor dispersal abilities are prone to extinction in fluctuating habitat patches (Levins 1970). If dispersal ability (attribute of r-strategy) is assumed to be a trade-off with competitive ability (attribute of K strategy), then species that are superior competitors may be most threatened by fragmentation (Tilman *et al.* 1994). Likewise, habitat loss may bring result species with limited dispersal abilities close to their extinction thresholds (Lande 1987).

However in spatial models where a species' dispersal pattern is non-random, extinction thresholds were approached by poor dispersers only when a species' reproductive rate was near replacement (With and King 1999). Diffusion models suggest species are affected by edges through 1) alteration of movement 2) differential mortality 3) cross-boundary subsidies or allochthonous input and 4) the introduction of novel interactions (Fagan *et al.* 1999). Clearly our understanding of edge effects is limited not by the amount of ecological theory but rather by the paucity of empirical evidence.

The response of arthropods to edge-effects may be particularly critical to our understanding of how edges affect species diversity. Arthropods have been successfully used as indicators of land-use (Niemela *et al.* 1993; Kremen 1994; Michaels and McQuillan 1995; Andersen 1997) because of their high diversity (Wilson 1985), and their ability to reflect fine-grain spatial and temporal patterns (Kremen *et al.* 1993). Arthropods have been shown to be sensitive to the effects of habitat fragmentation and edges at a variety of spatial scales. Likewise, these responses are strongly species dependant. For example, small-scale field experiments have demonstrated that increased fragmentation inhibited aggregation and searching behavior of specialist predators and thus allowed lower trophic levels to flourish (Kareiva 1987; Kruess and Tscharntke 1994). In temperate forests, rates of parasitism by medium-sized tachinid flies were negatively affected by edges where as parasitism rates of smaller species were higher at the forest edge (Roland and Taylor 1997). In contrast, within tropical forests, species richness of predator taxa was positively affected by edges while species richness of xylophages decreased with distance from the edge (Didham *et al.* 1998b). However despite these trends, edges were demonstrated to affect species within all trophic levels

(Didham *et al.* 1998b). In a similar study, diversity of dung beetles and dung decomposition rate were lower in smaller forest remnants than in larger fragments and continuous forest (Klein 1989).

However, the lack of large-scale studies limits generalizations regarding which species will be affected and what characteristics make them resistant or susceptible to edge-effects. Identifying species that are affected by forest edges and identifying characteristic edge-response patterns is a first step to understanding the mechanics of edge-effects. In this paper I analyzed changes in the abundance and community composition of ground-dwelling arthropods across a gradient extending from regenerating clearcuts into old-growth Douglas-fir forests. I hypothesized that distributions of species across transects would reflect four general response patterns (Figure 2.1).

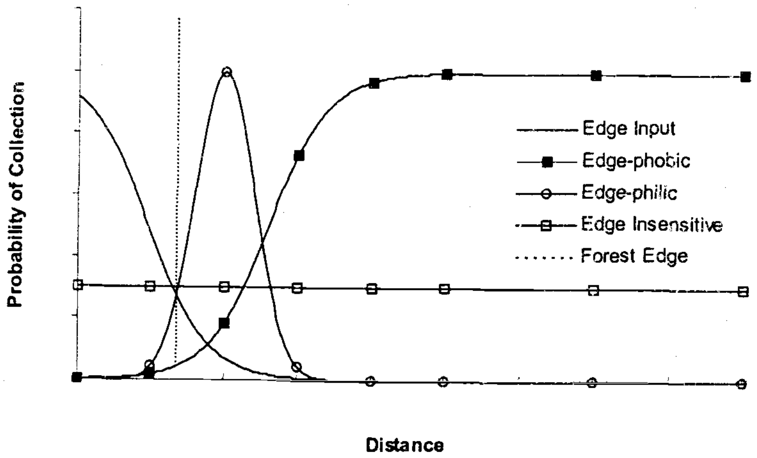

Figure 2.1. Four hypothesized distributions across an edge-forest gradient. Probability of collecting edge-phobic species increases with distance from the forest edge. Probability of collecting edge-philic species is maximized at some intermdiate point along the gradient. Edge-insensitive species do not change across the gradient. Edge-input species decrease with increasing distance from the forest edge.

Species that were edge-phobic would have low abundance near the forest edge, but would increase in abundance as distance from the forest edge increased. Edge-philic species would be characterized by a unimodal pattern, where peak abundance was located at near the edge and no overall trend with distance was observed. Species that are edge-insensitive should show little or no change in abundance across the gradient. Edge-input species are those species associated with the forest edge but are in greatest abundance in the adjacent clearcut. These response patterns were meant to capture the spectrum of individual species responses to edge-effects, and were expected to vary in their representation among species.

Methods

Study Sites

This study took place at the H. J. Andrews Long-Term Ecological Research Site (LTER) near Blue River, Oregon, in the Western Cascade Mountains of the United States. This forest is dominated by large Douglas-fir (*Pseudotsuga menziesii* (Mirib.) Franco), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), and Pacific silver fir (*Abies amabilis* Dougl. Ex Forbes) and is among the most productive forests in the world. Old-growth forest with dominant trees greater than 400 years of age comprised 40% of the LTER site. Individual stands are broadly characterized by understories of vine maple (*Acer circinatum* Pursh) and western hemlock with large amounts of coarse woody debris on the forest floor.

Litter arthropods were sampled from 7 replicated transects that began in regenerating clearcuts and extended across the forest edge and into old-growth Douglas-fir forests (Table 2.1). In this study, the transition between clearcuts and old-growth forest represented a steep biological gradient in terms of forest biomass, structure and composition.

Table 2.1. Location, elevation, aspect, slope, clearcut harvest date, and soil class for 7 study site located in the H.J. Andrews Experimental Forest.

Site Number	Harvest Unit	Elevation (m)	Aspect	Slope	Harvest Date	Soil Type
1	L241	850	Northwest	>60%	1960	Cobbly,heavy loam,bedrock talus
2	L109C	850	East	30-60%	1986	Gravelly,sandy loam
3	L503A	800	Southeast	<30%	1980	Gravelly, loam
4	L352	1100	West	>60%	1974	Gravelly,sandy loam
5	L704A	1250	West	>60%	1981	Gravelly,loam
6	FR13	1250	Southwest	>60%	1988	Gravelly,loam
7	FR10	1300	Southwest	>60%	1973	Gravelly,sandy loam

Along each transect, litter arthropods were sampled at 6 intervals. In 1997, samples were taken at two locations within clearcuts at 75 and 25 m from the edge (hereafter noted as –75 and –25 m), directly at the forest edge (0 m) and at 50, 100 and 200 m into old-growth. At each interval, 3 pitfall traps, 12.5 cm in diameter, containing propylene glycol as a preservative were spaced approximately 1 m apart. In 1998, arthropod sampling was modified to concentrate sampling effort near the forest edge. An additional sampling site at 25 m was added, while pitfall trapping at –75 m was discontinued, resulting in a finer scaled transect extending from 25 meters within clearcuts (hereafter noted as -25 m), directly at the edge between clearcuts and forest (0 m), and at 25, 50, 100, and 200 m into the old-growth forest. Sampling effort was also increased in 1998 to 5 pitfall traps spaced approximately 1 m apart and arranged pentagonally at each sampling point.

Pitfall traps were used to compare relative abundances between species, rather than absolute densities, because they reflect activity of ground-dwelling organisms (Niemela *et al.* 1990). Arthropods collected in pitfall traps were pooled at each transect interval for analysis. All traps were operated continuously between 3-Aug and 15-Sept 1997 and 22-May and 31-July 1998 and were emptied at two week intervals. All specimens larger than 5 mm in length were identified using keys provided by Hatch (1953, 1957, 1961, 1968, 1971) (Coleoptera: excluding Carabidae), Lindroth (1969) (Coleoptera:Carabidae), and Dondale and Redner (spiders) (1987, 1990). In addition, all material was verified against the H. J. Andrews Long-Term Ecological Research Collection and the Oregon State University Arthropod Collection at Corvallis OR. Voucher material was deposited at the Oregon State Arthropod Collection in Corvallis, OR.

Community Pattern and Non-Metric Multidimensional Scaling

Non-metric multidimensional scaling (NMS) was used to qualitatively summarize the overall distribution of species assemblages across the edge-forest gradient. NMS was used in lieu of other ordination methods because it avoids the 'zero-truncation' problem of Beals (1984). Other methods, such as principal components analysis and detrended correspondence analysis, can make very dissimilar points along a gradient appear similar because they share null values. NMS, however, relies on ranked distances and tends to linearize the relationship between environmental gradients and differences in species composition (Beals 1984). For this reason, NMS has performed better than other methods at recovering simulated gradients (Minchin 1987) and has been widely used in ecological gradient studies (Clarke 1993).

Collection data from 1997 and 1998 were analyzed separately because of differences in sampling dates and sampling effort. In each year, NMS was applied to a subset of the original data; species present in less than 5% of the sampling plots were excluded from the analysis. These species were removed from the total matrix to minimize effects of sporadic collections of species on the interpretation of community pattern. In 1997, 35 abundant species from a total of 75 species were included in the analysis. In 1998, 93 abundant species from a total of 186 were analyzed. To maximize the chance that NMS would converge on a stable solution for the ordination, starting coordinates for the NMS were generated using Bray-Curtis polar ordination.

Species assemblages were characterized as groups of species that had similar distributions across transects. The response of a species along a transect was determined by the correlation between abundance and axis scores from the NMS ordination. Specificity of a species distribution along transects was empirically based on the magnitude of axis correlation scores. A high correlation would indicate that a species is abundant at one end of the edge-forest gradient. However, correlations between a species' abundance and axis scores will misrepresent species with edge-philic responses across transects. Such species could be concentrated at an intermediate distance along transects, ubiquitously distributed across the transect, or be so few in number that meaningful interpretation is impossible. For these species having low correlations with axis scores, abundance was simply plotted against sampling position along the gradient and visually inspected for spatial pattern. Species with correlation coefficients greater than 0.13 typically exhibited narrow distributions (<50 m) along transects. Species with correlation coefficients between 0.08 and 0.13 had broader distributions (>50 m) across transects.

Abundant Species Response and Logistic Regression

Logistic regression was used to quantitatively describe the changes of abundant species across edge-forest gradients and to assess differences between edge-phobic, edge-input and edge insensitive species. In this analysis, changes in relative abundance of individual species were evaluated as a function of distance from the forest edge. In logistic regression a binary response variable, such as presence or absence in a sample, is expressed linearly as the logit of the probability of the response variable (equation 1) (Sokal and Rohlf 1995).

$$\text{logit}(\pi) = \log(\pi/1-\pi) = \alpha + \beta'(x) \qquad (1)$$

In this equation, changes in the logit of the probability of a species being present (π) are expressed as changes in the distance across the transect (x), where α is the intercept and β' is the slope. The logit of the response probability can easily be converted to probability of a species being present using equation 2 (Sokal and Rohlf 1995):

$$p = \exp^{\text{logit}(\pi)}/1 + \exp^{\text{logit}(\pi)} \qquad (2)$$

Relative abundance of a species within a sample was weighted, with weights equal to sample size. To avoid spurious errors resulting from small sample size, only species with total abundance greater than 50 individuals were analyzed with logistic regression. Because sampling effort was increased in 1998, the number of species collected with abundance greater than 50 individuals was larger than in 1997. Consequently, a modified significance level reflecting the number of comparisons (or species) was used in each year's analysis. The null hypothesis of no overall change with increasing distance from the forest edge was rejected at a modified alpha of 0.0033 in 1997 and 0.0016 in 1998 according to the Bonferonni correction for multiple tests.

Results

Non-metric Multidimensional Scaling

Patterns in overall community composition across forest edges were remarkably consistent between 1997 and 1998. In each year, a two dimensional solution minimized stress within each ordination (21.7% and 17.8% respectively). Samples collected within clearcuts and directly at the forest edge differed in species composition from interior forest sites. In both years, species composition was similar in sites beyond 100 m suggesting an upper limit of edge effects on community compositional changes.

In 1997, changes in species composition across edge-forest gradients were reflected along axis 1 of the ordination (Figure 2.2). In this ordination axis 1 and axis 2 explained 36.9% and 23.1% of the variance between sampling points ($p<0.05$) (Table 2. 2). Sampling points located within clearcuts and directly at the forest edge

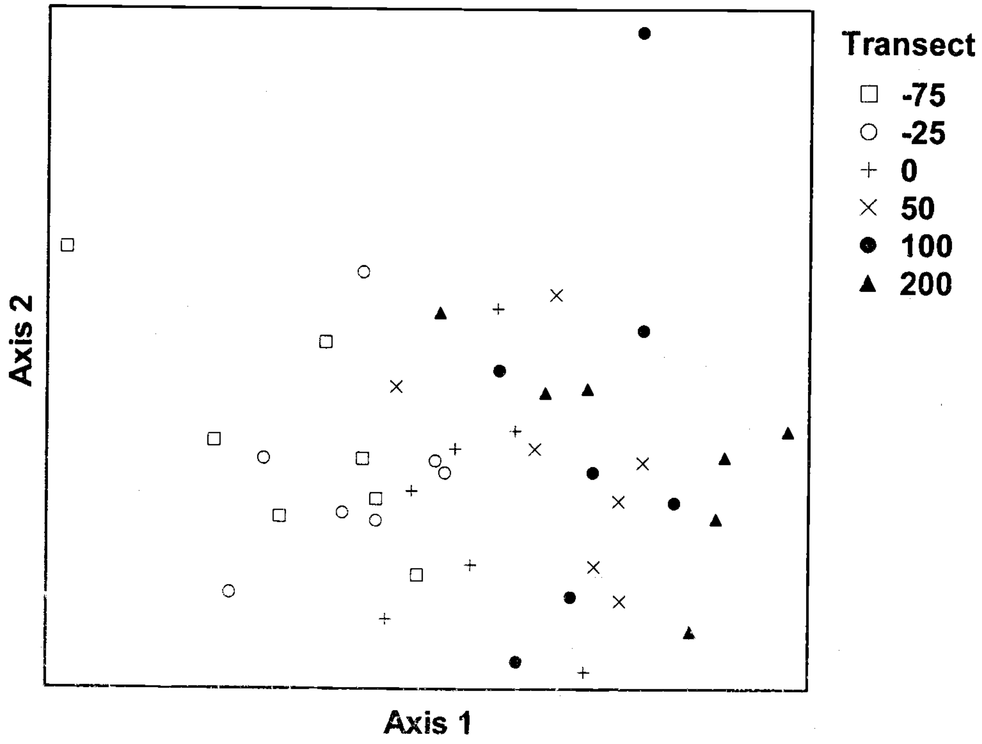

Figure 2.2. NMS ordination of 42 sampling points based on similarity of 35 species collected in 1997 with sampling position across edge forest gradient overlayed.

Table 2.2. Variance explained in a 2-dimensional NMS ordination of 35 species along edge-forest gradients in 1997.

Axis	% Variance Explained	Cumulative %Variance Explained	Monte Carlo Ranomization Test p-value[1]
1	36.9	36.9	0.0196
2	23.1	60.0	0.0196

[1] p-values are the proportion of randomized runs with stress less than or equal to the observed stress in the 2 dimensional NMS. Monte Carlo tests were based on 50 randomizations.

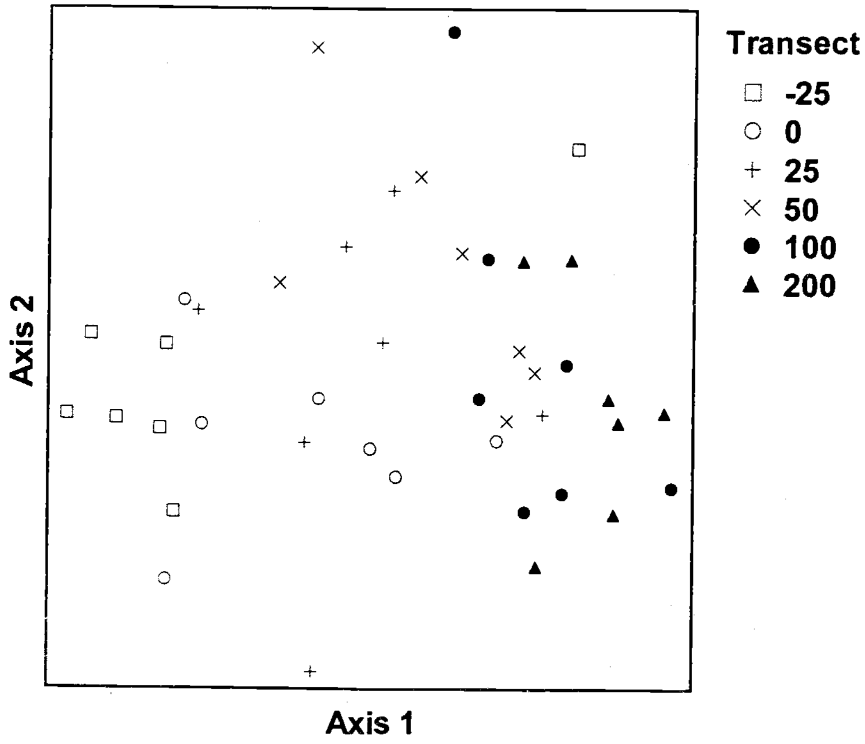

Figure 2.3. NMS ordination of 42 sampling points based on similarity of 93 species collected in 1998 with sampling position across edge forest gradient overlayed.

Table 2.3. Variance explained in a 2-dimensional NMS ordination of 93 species along edge-forest gradients in 1998.

Axis	% Variance Explained	Cumulative %Variance Explained	Monte Carlo Ranomization Test p-value[1]
1	48.6	48.6	0.0392
2	29.9	78.5	0.0196

[1] p-values are the proportion of randomized runs with stress less than or equal to the observed stress in the 2 dimensional NMS. Monte Carlo tests were based on 50 randomizations.

predominantly clustered separately from interior old-growth sampling points. However changes in species composition were apparent within 50 m from the edge.

Likewise in 1998, changes in species composition across edge gradients were recovered along axis 1 of the ordination (Figure 2.3). In this ordination, the variance explained by axis 1 and axis 2 increased to 48.6% and 29.9% respectively ($p<0.05$) (Table 2.3). With increased sampling effort in 1998 changes in species composition were detectable in as little as 25m. With the exception of a single clearcut site, three distinct clustering patterns were observed. Sampling points located within the clearcuts and sampling points beyond 100 m into interior forest formed separate clusters along axis 1. However in contrast to 1997, sampling points located between the forest edge and 50 m from the forest edge were more variable along axis 1 than sites located at each end of the gradient.

Species that characteristized different segments of the edge gradient found during 1997 and 1998 are listed in Table 2.4 and 2.5 respectively. Species characterizing interior forest had relatively high positive correlations with axis 1 but varied in their specificity of response across the gradient. In 1997, four species, all carabid beetles, most positively associated with axis 1 ($r^2>0.13$) (Table 2.4) were predominately found beyond 50 m from the forest edge. Another carabid, *Scaphinotus marginatus* (Fischer von Waldheim) which was moderately correlated with axis 1 ($r^2>0.12$) (Table 2.4) was also predominately found beyond 50 m but was found in greatest abundance at 50 m from the forest edge. In 1998, six species had strong positive associations with axis 1 ($r^2>0.13$) (Table 2.5). With the exception of *Pterostichus* sp., these were species that had strong positive associations with axis 1 in 1997 as well as two abundant beetles, *Tachinus*

Table 2.4. Summary of arthropod assemblages associated with 4 distributional patterns across edge-forest gradients in 1997.

Taxa		Total Abundance	Pearson's Correlation Coefficient (r^2) with Axis 1[1]
A) Edge-phobic species			
Carabidae	*Pterostichus herculaneus* Mannerheim	756	0.312
Carabidae	*Scaphinotus angusticollis* (Mannerheim)	596	0.367
Carabidae	*Pterostichus spp.*	246	0.149
Carabidae	*Zacotus matthewsii* LeConte	225	0.176
Carabidae	*Scaphinotus marginatus* (Fischer von Waldheim)	196	0.122
B) Edge Insensitive species			
Carabidae	*Pterostichus lama* (Menetries)	116	0.035
Curculionidae	*Steremnius carinatus* (Boheman)	57	0.076
Carabidae	*Scaphinotus rugiceps* (Horn)	110	0.043
Scarabeidae	*Aphodius opacus* LeConte	55	0.005
C) Edge-philic species			
Formicidae	*Camponotus modoc* Wheeler	1235	0.003
D) Edge Input species			
Formicidae	*Formica subnuda* Emery	592	0.221
Formicidae	*Camponotus laevigatus* (F. Smith)	285	0.454
Lycosidae	*Pardosa dorsuncata* Lowrie & Dondale	160	0.118
Formicidae	*Camponotus vicinus* Mayr	136	0.141
Carabidae	*Carabus taedetus* Fabricus	106	0.081

[1] Pearson's correlation coefficient (r^2) with axis 1 from NMS ordiantion in Figure 2.2.

Table 2.5. Summary of arthropod assemblages associated with 4 distributional patterns across edge-forest gradients in 1998.

Taxa		Total Abundance	Pearson's Correlation Coefficient (r^2) with Axis 1[1]
A) Edge-phobic species			
Staphylinidae	*Tachinus semirufus* Horn	6397	0.496
Carabidae	*Zacotus matthewsii* LeConte	201	0.254
Carabidae	*Pterostichus herculaneus* Mannerheim	1910	0.238
Leptodiridae	*Catops basilaris* Say	1132	0.187
Carabidae	*Scaphinotus angusticollis* (Mannerheim)	420	0.167
Carabidae	*Scaphinotus marginatus* (Fischer von Waldheim)	244	0.164
Carabidae	*Promecognathus crassus* LeConte	65	0.096
Cryptophagidae	*Heniticoides lorna* Hatch	51	0.089
Thomisidae	*Xysticus pretiosus* Gertsch	456	0.087
B) Edge Insensitive species			
Curculionidae	*Lepesoma lecontei* (Casey)	78	0.000
Silphidae	*Nicrophorus defodiens* (Mannerheim)	100	0.005
Carabidae	*Pterostichus lama* (Menetries)	125	0.002
Curculionidae	*Steremnius carinatus* (Boheman)	598	0.016
Carabidae	*Scaphinotus rugiceps* (Horn)	178	0.013
Staphylinidae	*Staphylinus saphyrinus* LeConte	76	0.067
C) Edge-philic species			
Formicidae	*Camponotus modoc* Wheeler	2237	0.036
Staphylinidae	*Staphylinus pleuralis* LeConte	336	0.017
D) Edge Input species			
Scarabeidae	*Aphodius opacus* LeConte	124	0.237
Formicidae	*Camponotus spp.*	50	0.240
Formicidae	*Formica spp.*	56	0.286
Formicidae	*Camponotus laevigatus* (F. Smith)	79	0.305
Buprestidae	*Anthaxia expansa* LeConte	133	0.339
Thomisidae	*Xysticus montanensis* Keyserling	57	0.360
Lycosidae	*Alopecosa kochi* (Keyserling)	268	0.387
Lycosidae	*Pardosa dorsuncata* Lowrie & Dondale	1791	0.461

[1] Pearson's correlation coefficient (r^2) with axis 1 from NMS ordiantion in Figure 2.3.

semirufus Horn and *Catops basilaris* Say. Also in 1998, three additional species, *Promecognathos crassus* LeConte, *Heniticoides lorna* Hatch, and a spider, *Xysticus pretiosus* Gertsch, were positively correlated with axis 1 (r^2 between 0.08 and 0.13) but were collected over a broader range of transect positions in interior forests (Table 2.5). These species were predominantly found beyond 25 m from the forest edge.

In 1997, twenty-one species were weakly correlated with axis 1 ($r^2<0.08$), sixteen of which were represented by fewer than 50 individuals. Of the five abundant species (Table 2.4), one weevil, *Sterminius carinatus* (Boheman), was disproportionately abundant at a single sampling point located 50 m from the edge. Large collections of the formicid, *Camponotus modoc* (Wheeler) were highly variable across sampling transects. Two carabids, *Pterostichus lama* (Menetries) and *Scaphinotus rugiceps* (Horn) and a dung beetle *Aphodius opacus* (LeConte) were broadly distributed across the transects.

In 1998, sixty species were weakly correlated with axis 1 ($r^2<0.08$), forty-seven of which were represented by fewer than 50 total individuals. Of the thirteen most abundant species, five species were disproportionately abundant at a single sampling point along the transects. *Formica* ants tended to be concentrated in individual sampling points. For example, over 250 individuals of *Fomica subnuda* (Emery) were collected within a single clearcut sampling point. This species was largely responsible for the variability seen in clearcut sites across axis 1 (Figure 2.3). A second formicid species was represented by 53 individuals in a single edge site. Likewise, a lycosid spider, *Pardosa californica* Keyserling and a carabid beetle, *Pterosthicus inanis* Horn were collected in high abundance at two separate sampling points within the clearcut and at the forest edge respectively. Only one staphylinid, *Hapalarea stouti* (Hatch), was isolated within a single sampling point 200 m into interior forest. Because of high variability in abundance, the response of these species to edge-effects could not be determined.

Species that were insensitive to edge effects in 1998 and that were weakly correlated with axis 1 ($r^2<0.08$) are listed in Table 2.5. As in 1997, *P. lama* was broadly distributed across sampling transects during 1998. In addition a weevil, *Leposoma lecontei* (Casey), and the carrion beetle *Nicrophorus defodians* (Mannerheim), were also broadly distributed across sampling transects. In contrast to the previous year, *S. carinatus*, *S. rugiceps* and the staphylinid, *Staphylinus saphyrinus* LeConte were isolated within a single transect, but were broadly distributed across all sampling points within that transect. However in 1998, the abundance of two species, *C. modoc* and the staphylinid *Staphylinus pleuralis* LeConte was consistent with an edge-philic response. *C. modoc* showed peak abundance at the forest edge and 25 m into the forest and decreased in abundance as distance into the forest increased. *S. pleuralis* was more broadly distributed across interior forest and most abundant between 25 and 100 m.

In 1997, only six species were consistently collected within clearcut sites and at the forest edge. Of these species that had strong negative correlations with axis 1 ($r^2>0.08$) only five were collected in abundances greater than 50 individuals (Table 2.4). Among these species, *Carabus taedetus* Fabricus was collected only within a single transect. The remaining species were represented by three species of *Camponotus* ants and a single lycosid spider species, *Pardosa dorsuncata* Lowrie & Dondale. These species were found almost exclusively within clearcuts and directly at the forest edge. In 1998, twenty-two species had strong negative correlations with axis 1 ($r^2>0.08$) (Table 2.5). Of these species only nine were collected in abundance greater than 50 total individuals. Again, *C. taedetus* was isolated within the same transect as in 1997. The abundance of this species decreased between -25 and 100 m into the forest and was absent beyond 100 m. Six species were most abundant in clearcut sites and quickly decreased in abundance at the forest edge. These species were represented again by *Camponotus* and *Formica* species, lycosid spiders *Alopecosa kochi* (Keyserling) and *P. dorsuncata*, and a single wood borer, *Anthaxia expansa* LeConte. These species were rarely collected beyond 25 m in interior forest (Table 2.5). In contrast to 1997, *A. opacus* was predominately associated with clearcuts and the forest edge and *P. dorsunctata* was found across a larger range of sampling points in 1998. Both of these species decreased across the forest edge but extended beyond 50 m into interior forest (Table 2.5).

In each year, axis 2 of the non-metric scaling ordination explained less variation between sampling points than axis 1 (Table 2.2 and Table 2.3). Variability between sampling points along axis 2 was largely influenced by isolated collections of four species in 1997 and four different species in 1998. In 1997, sporadic collections of *Pterostichus inopinus* (Casey) and *Usechus nucleatus* Casey yielded fewer than 5 individuals at any sampling point but were important in defining sampling points at each end of axis 2 (Figure 2.2). Larger collections of *C. basilaris* and *N. defodiens* were also important in defining axis 2. In 1998, sporadic collections of *Phausis skelleyi* Fender, *Pterostichus spp.*, *Phellopsis porcata* LeConte, and *Agathidium jasperinum* Fall yielded fewer than 2 individuals at any sampling point but were important in defining axis 2 (Figure 2.3). When environmental variables associated with each transect such as elevation, slope and aspect were overlaid on both NMS ordinations no obvious patterns corresponding to axis 2 were observed.

Table 2.6. Tests of significance for logistic regression models, estimates of slopes and standard errors for taxa positively associated with distance from the forest edge in 1997.

Taxa	G-statistic	Significance of model	Slope	SE	Wald χ^2	Significance of Slope
Scaphinotus angusticollis	551.421	0.0001	0.01130	0.000525	462.51	0.0001
Pterostichus herculaneus	214.622	0.0001	0.00607	0.000421	208.34	0.0001
Zacotus matthewsii	109.765	0.0001	0.00804	0.000797	101.61	0.0001
Pterostichus spp.	94.799	0.0001	0.00664	0.000695	91.28	0.0001
Scaphinotus marginatus	15.798	0.0001	0.00282	0.000705	16.02	0.0001
Steremnius carinatus	11.237	0.0008	0.00462	0.001380	11.25	0.0008

Table 2.7. Tests of significance for logistic regression models, estimates of slopes and standard errors for taxa negatively associated with distance from the forest edge in 1997.

Taxa	G-statistic	Significance of Model	Slope	SE	Wald χ^2	Significance of Slope
Formica subnuda	1683.965	0.0001	-0.04900	0.002130	531.94	0.0001
Camponotus laevigatus	538.692	0.0001	-0.02830	0.001840	236.32	0.0001
Camponotus vicinus	128.914	0.0001	-0.01470	0.001630	81.41	0.0001
Pardosa dorsuncata	78.464	0.0001	-0.00919	0.001180	60.27	0.0001
Carabus taedatus	55.997	0.0001	-0.00961	0.001480	42.28	0.0001

Logistic Regressions

In 1997, of the fifteen species analyzed using logistic regression, eleven were significantly associated with edge-forest gradients. Six species, all beetles, were positively associated with increasing distance from the forest edge (Table 2.6). The remaining five species were negatively associated with increasing distance from the forest edge (Table 2.7). In 1998, thirty-one species were analyzed using logistic regression. Logistic models were significant for twenty-four species. However, only twenty-two species had significant slopes. Seven species, again all beetles, were positively associated with increasing distance from the forest edge (Table 2.8). The remaining fifteen species were negatively associated with distance from the forest edge (Table 2.9).

Table 2.8. Tests of significance for logistic regression models, estimates of slopes and standard errors for taxa positively associated with distance from the forest edge in 1998.

Taxa	G-statistic	Significance of Model	Slope	SE	Wald χ^2	Significance of Slope
Tachinus semirufus	1495.251	0.0001	0.00749	0.000199	1418.82	0.0002
Scaphinotus angusticollis	541.624	0.0001	0.01540	0.000787	380.67	0.0008
Catops basilaris	388.948	0.0001	0.00731	0.000377	376.37	0.0004
Scaphinotus marginatus	171.974	0.0001	0.01050	0.000853	150.37	0.0009
Pterostichus herculaneus	79.759	0.0001	0.00262	0.000292	80.87	0.0003
Steremnius carinatus	71.403	0.0001	0.00422	0.000497	72.20	0.0001
Zacotus mathewsii	18.937	0.0001	0.00371	0.000845	19.25	0.0001

Table 2.9. Tests of significance for logistic regression models, estimates of slopes and standard errors for taxa negatively associated with distance from the forest edge in 1998.

Taxa	G-statistic	Significance of Model	Slope	SE	Wald χ^2	Significance of Slope
Pardosa dorsuncata	2651.794	0.0001	-0.03000	0.000898	1115.01	0.0001
Formica subnuda	1000.568	0.0001	-0.10840	0.007500	209.03	0.0001
Camponotus modoc	631.844	0.0001	-0.00803	0.000351	522.52	0.0001
Alopecosa kochi	454.335	0.0001	-0.03500	0.002650	174.43	0.0001
Anthaxia expansa	237.774	0.0001	-0.03750	0.003990	88.21	0.0001
Camponotus laevigatus	226.148	0.0001	-0.07890	0.010200	59.40	0.0001
Pardosa californicus	188.780	0.0001	-0.02570	0.002780	85.36	0.0001
Camponotus herculaneus	126.899	0.0001	-0.06360	0.010400	37.38	0.0001
Xysticus montanensis	108.976	0.0001	-0.04110	0.006610	38.75	0.0001
Formica sp 1	96.479	0.0001	-0.03570	0.005900	36.61	0.0001
Formica sp 2	65.239	0.0001	-0.02390	0.004320	30.68	0.0001
Aphodius opacus	57.605	0.0001	-0.01060	0.001640	42.02	0.0001
Carabus taedatus	45.219	0.0001	-0.01040	0.001790	33.31	0.0001
Pterostichus inanis	22.523	0.0001	-0.00941	0.002270	17.22	0.0001
Pterostichus lama	20.157	0.0001	-0.00553	0.001320	17.68	0.0001

Edge-Phobic Responses

Logistic models captured the overall trends of four species associated with interior forest in 1997. Although, statistically significant, relative abundance of *S. angusticollis*, *P. herculaneus*, *Pterostichus sp.* and *Z. mathewsii* tended to be overestimated at both ends of sampling transects and underestimated at intermediate distances along sampling transects (Figure 2.4). *Scaphinotus marginatus* also increased with distance from the forest edge. However large collections of this species (more than 100 individuals) 50 m from the forest edge obscured this trend. Likewise, *S. carinatus* was collected in relatively high abundance 50 m from the forest edge, thus limiting inference from logistic models although peak abundance differed by less than 20 individuals between adjacent sampling points.

Of the species positively associated with interior forest in 1998, two carabid beetles, *S. angusticollis* and *S. marginatus* increased most quickly with distance from the forest edge (Figure 2.5). Initially, relative abundance increased slowly from the forest edge. However, beyond 100 meters, relative abundance increased by 80% for *S. angusticollis* and 71% for *S. marginatus*. Logistic models described the relative abundance of both these species reasonably well. Predicted abundances were within a single standard error for all sampling distances in *S. angusticollis* ($p<0.0008$), and for 5 of the 6 sampling distances in *S. marginatus* ($p<0.0009$). *Catops basilarius* showed similar patterns in abundance and increased by 61% beyond 100 m (Figure 2.5). However, differences between observed abundances and model predictions were greater than a single standard error of model predictions for 4 of the 6 sampling distances, suggesting this pattern was less pronounced than in *S. angusticollis* and *S. marginatus*.

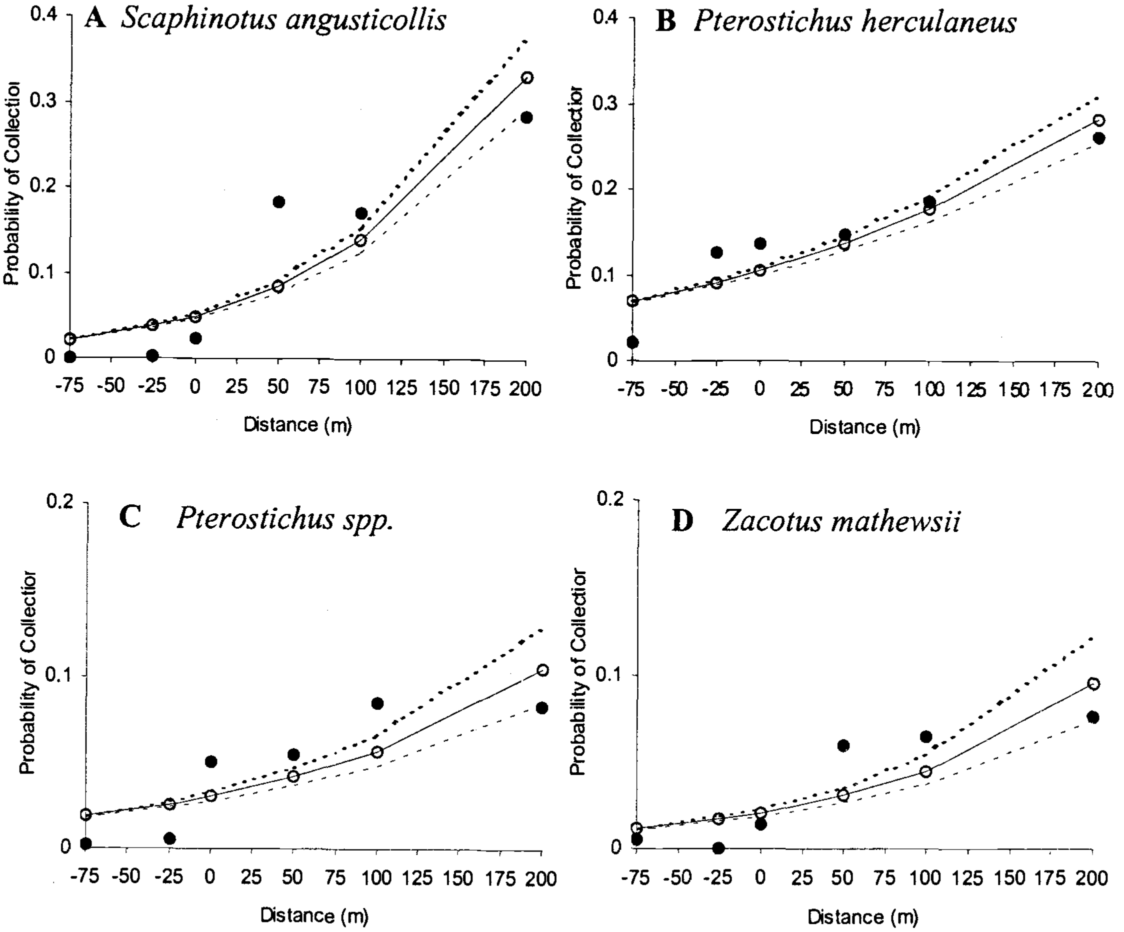

Figure 2.4. Fitted logistic regressions of four species positively associated with interior forest in 1997. Closed circles represent observed mean weighted by sample size, open circles represent relative abundance predicted by logistic model, dotted lines represent a single standard error from predicted means.

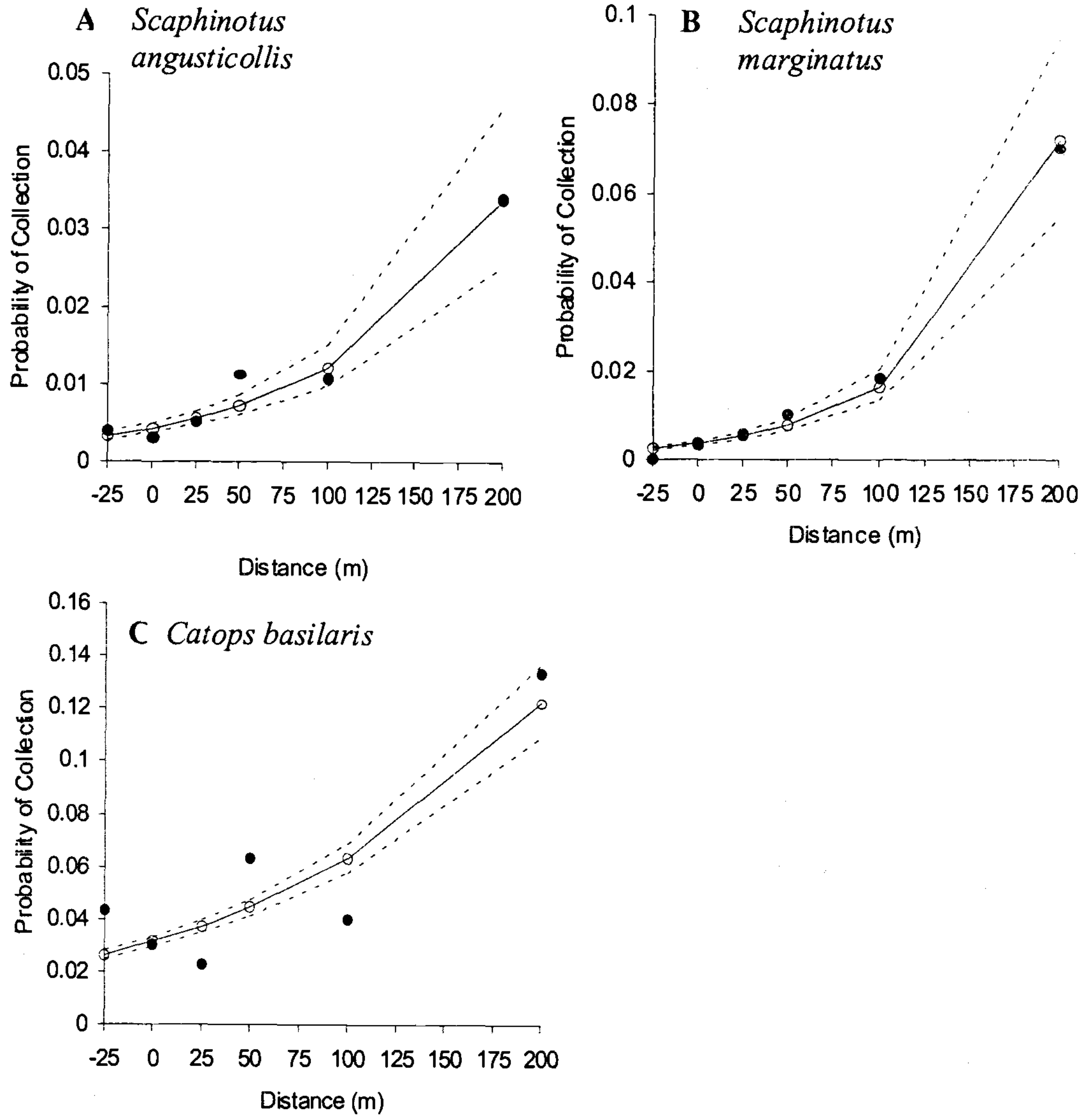

Figure 2.5. Fitted logistic regressions of three species positively associated with interior forest in 1998. Closed circles represent observed mean weighted by sample size, open circles represent relative abundance predicted by logistic model, dotted lines represent a single standard error from predicted means.

Tachinus semirufus and *Pterostichus herculaneus* had greatest relative abundance at an intermediate point along the sampling transect, although an overall increasing trend in relative abundance was apparent as distance from the edge increased (Figure 2.6). Likewise *Zacotus mathewsii* and *S. carinatus* had highest relative abundance at some intermediate distance along the transect, but showed considerable variability across the sampling transect. In each case, species that have greatest relative abundance at an intermediate level, are not accurately described by logistic models. Rather, logistic models only capture overall trends in relative abundance across the gradient.

Edge Input Responses

In both 1997 and 1998, spider and ant species were a major component of those species collected in clearcuts and near the forest edge (Table 2.7 and 2.9). In 1997,

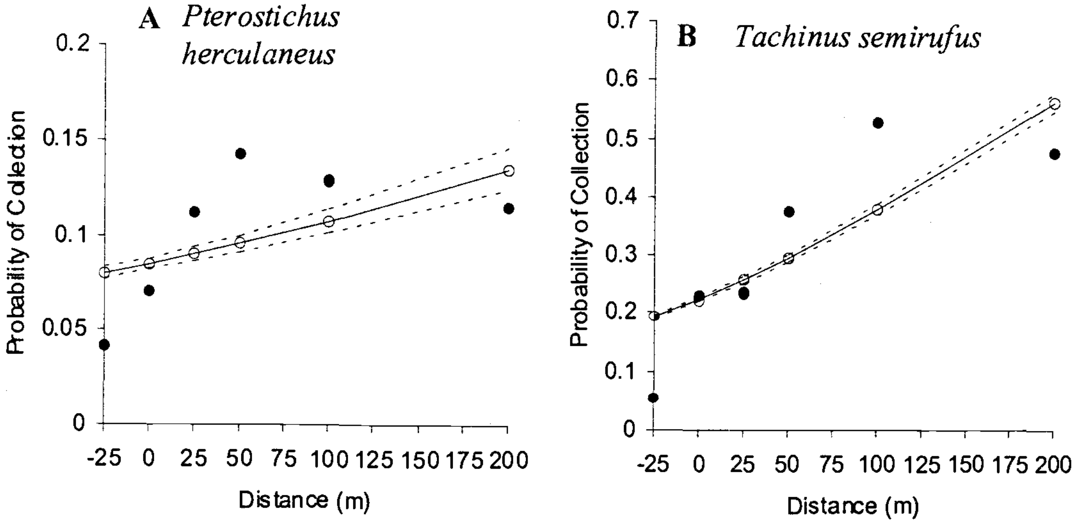

Figure 2.6. Fitted logistic regressions of two species positively associated with interior forest in 1998. Closed circles represent observed mean weighted by sample size, open circles represent relative abundance predicted by logistic model, dotted lines represent a single standard error from predicted means.

F.subnuda and *C. laevigatus* were the most abundant species collected at –75 m from the forest edge (Figure 2.7). These species rapidly decreased in abundance across the forest edge and were nearly absent 50 m into old-growth stands. While the logistic model captured the response of these species, the large abundance of *F. subnuda* and *C. laevigatus* decreased the relative proportion of other species collected at this sampling point. As a consequence, less abundant species such as *C. vicinus* and *P. dorsuncata* were under-represented at –75 m from the forest edge and logistic models tended to under-estimate the specificity of response across the forest edge (Figure 2.7).

In 1998, *F. subnuda,C. laevigatus,* and *P. dorsuncata* had similar responses along sampling gradients as in 1997 (Figure 2.8). However in 1998, an additional ten species were negatively associated with interior forest (Table 2.9). Again spider and ant species were a major component of the diversity of edge-input species. *Camponotus modoc* was the most common ant species collected and was collected in highest abundance at the forest edge and 25 m into the forest. *C. modoc* also decreased into interior forest but the probability of collection never decreased below 3%. Differences between the relative abundance of *C. modoc* and predicted abundance was greater than 1 standard error for the first four sampling points along the transect. The probability of finding ant species other than *C. modoc* greater than 50 m into interior forest was near zero. *Formica* species, *C. laevigatus* and *Camponotus* sp.1 were most abundant within the clearcut and at the forest edge, but decreased quickly as distance into the forest increased. With the exception of two Formicid morpho-species, observed abundances were within a single standard error of logistic predictions.

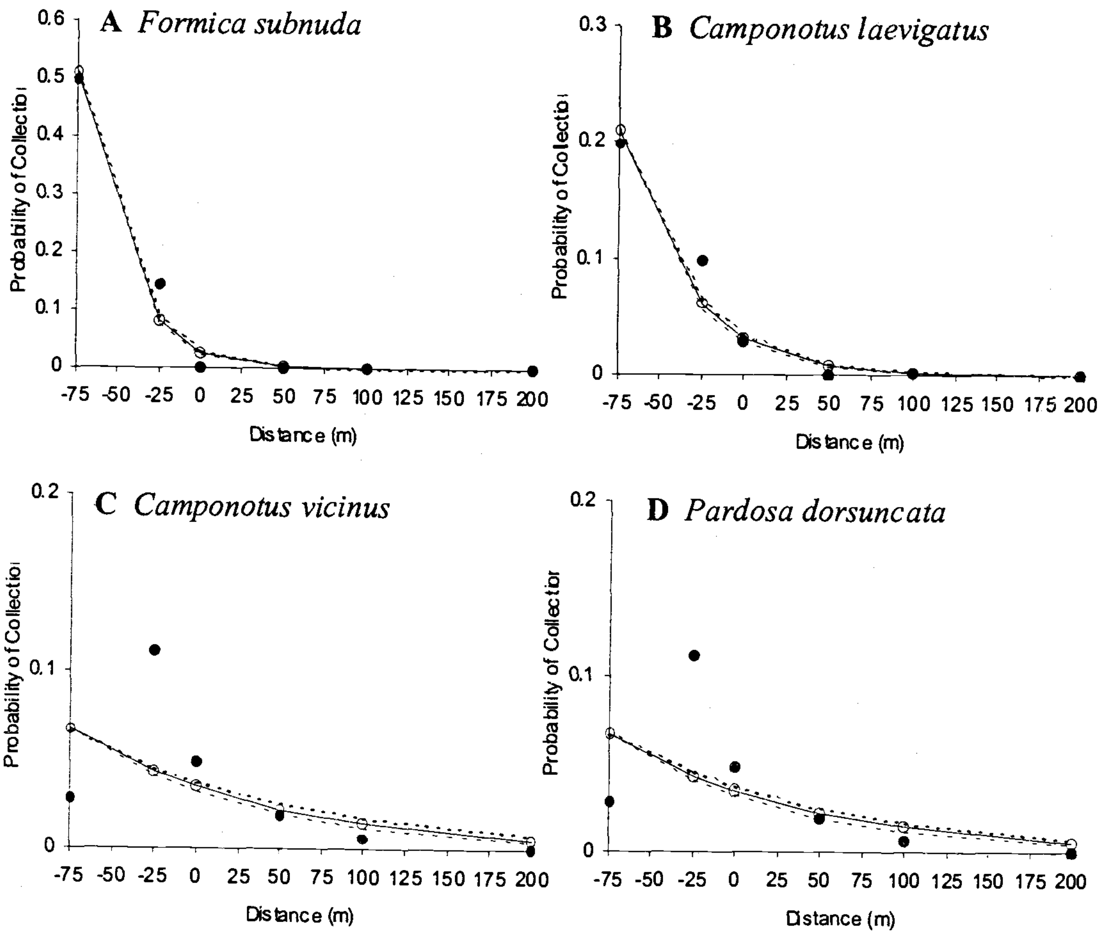

Figure 2.7. Fitted logistic regressions of four species negatively associated with interior forest in 1997. Closed circles represent observed mean weighted by sample size, open circles represent relative abundance predicted by logistic model, dotted lines represent a single standard error from predicted means.

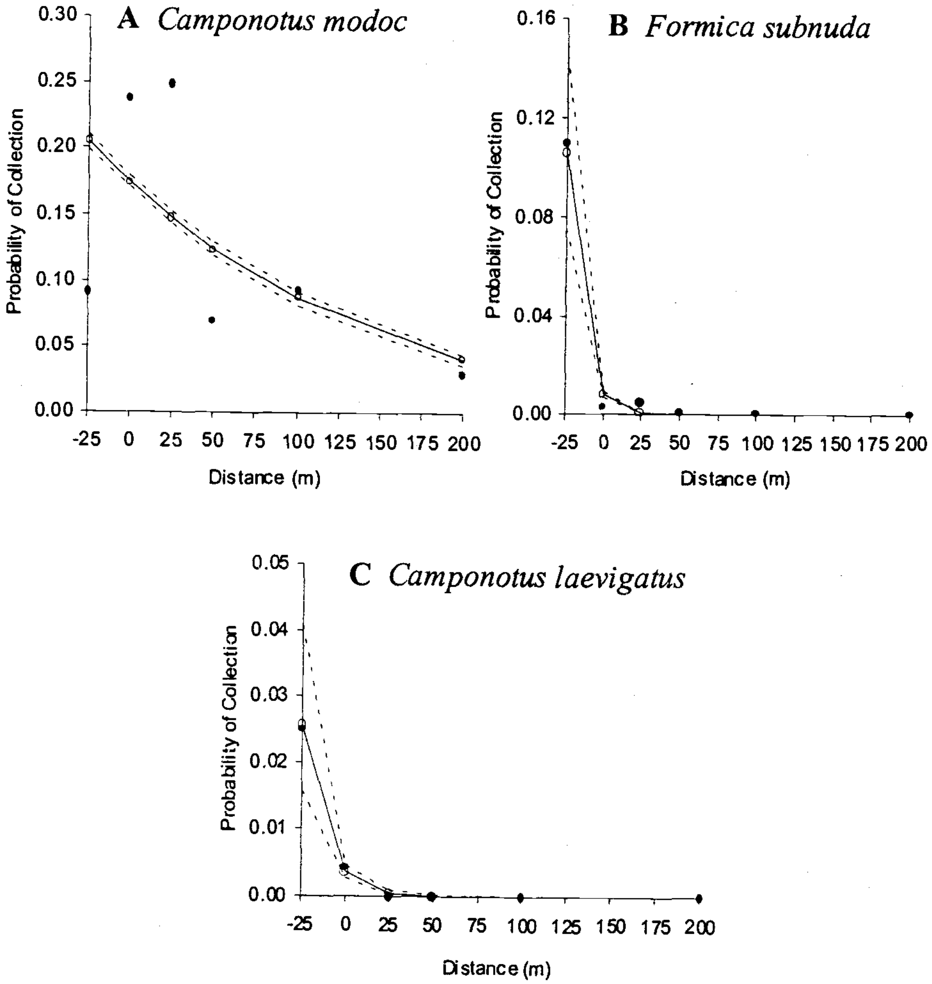

Figure 2.8. Fitted logistic regressions of three species of ants negatively associated with interior forest in 1998. Closed circles represent observed mean weighted by sample size, open circles represent relative abundance predicted by logistic model, dotted lines represent a single standard error from predicted means.

Also in 1998, *A. kochi* and *P. dorsuncata*, and one species of crab spider (Thomisidae), *Xysticus montanensis* were negatively associated with interior forest (Table 2.9). The probability of collecting each of these species decreased quickly until 50 m, where the probability of collection was near zero (Figure 2.9). *Anthaxia expansa*, was also negatively associated with interior forest, with a probability of collection quickly decreasing to near zero at 50 m (Figure 2.10). The probability of collecting *A. opacus* gradually declined as distance into the forest increased, but differences in relative abundance differed from model predictions for the first four sampling points along the transect (Figure 2.10).

Discussion

Edge Effects on Species Composition

My results suggest that edge-effects from clearcutting alter species composition of arthropod communities as far as 100 m into interior forest. Changes in species composition were also largely defined by either edge-phobic or edge-input response patterns. While compositional changes likely reflect numerous abiotic and biotic interactions, it is surprising how well these results parallel gradients in abiotic conditions reported in other studies (Chen *et al.* 1995; Chen and Franklin 1997). Within old-growth Douglas-fir forests, the extent of abiotic edge effects was much greater during the day than at night (Chen and Franklin 1997). For example, increased air temperature was detected as far as 180 m into interior forest during the day but less than 60 m at night

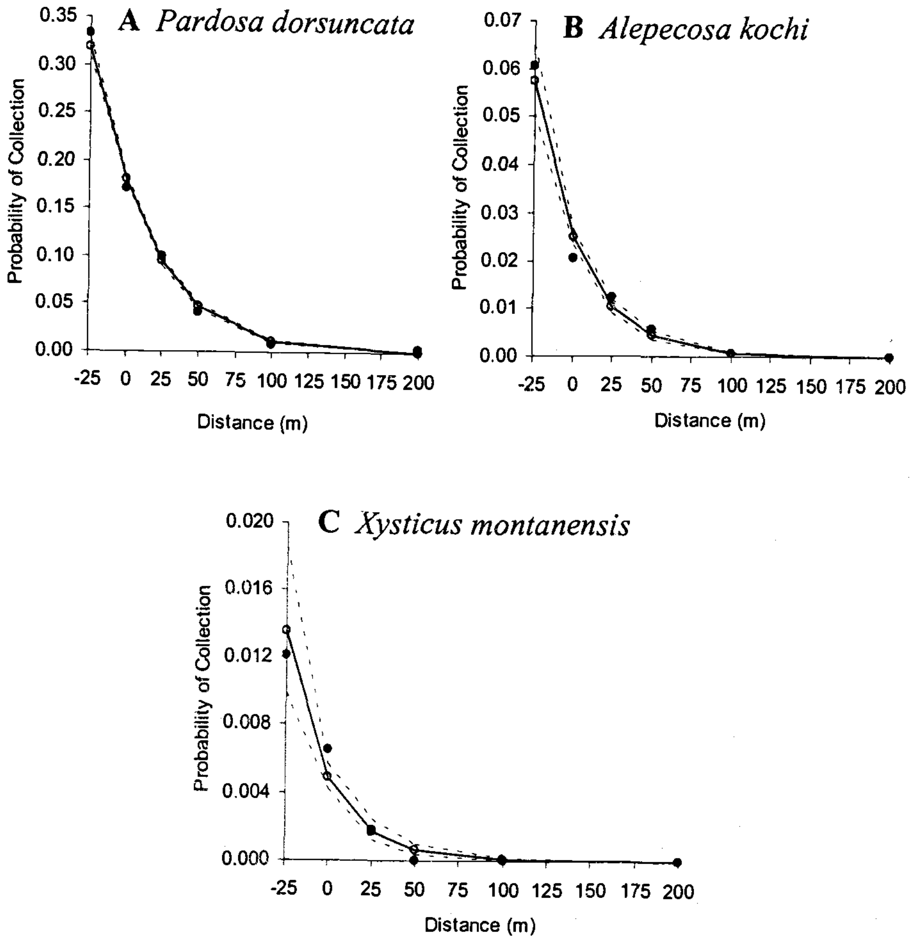

Figure 2.9. Fitted logistic regressions of three species of spiders negatively associated with interior forest in 1998. Closed circles represent observed mean weighted by sample size, open circles represent relative abundance predicted by logistic model, dotted lines represent a single standard error from predicted means.

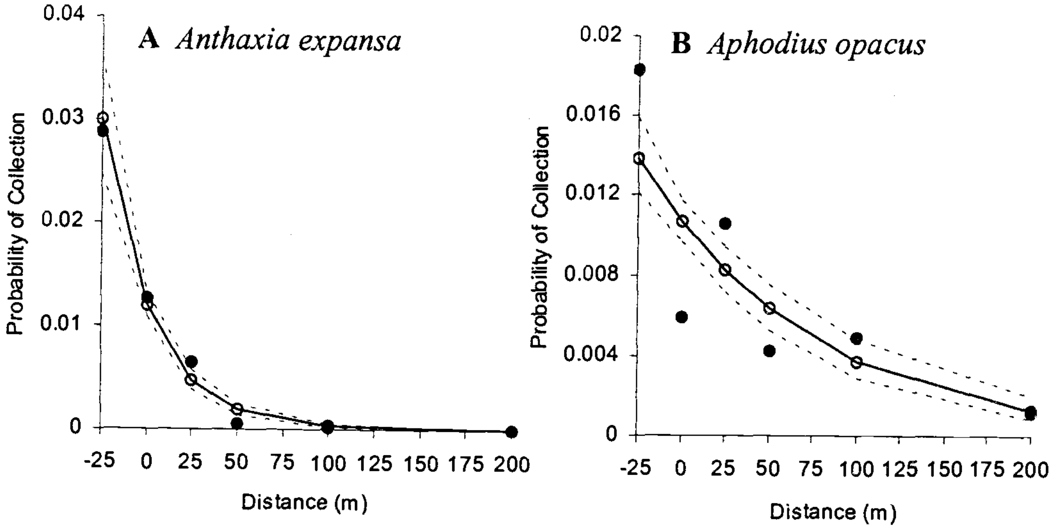

Figure 2.10. Fitted logistic regressions of two beetle species negatively associated with interior forest in 1998. Closed circles represent observed mean weighted by sample size, open circles represent relative abundance predicted by logistic model, dotted lines represent a single standard error from predicted means.

(Chen *et al.* 1995). Likewise, increased soil temperature was detected up to 120 m during the day but ranged from 15 to 120 m at night. Furthermore, diurnal variations in relative humidity were observed up to 240 m into interior forest but were not observed at night as relative humidity reached 100% across edge-forest transects. The high variability in arthropod species composition I observed between 0 and 50 m was consistent with the night-time extent of abiotic changes as a result of the forest edge.

In my study, edge-phobic species were represented largely by nocturnal predators and scavengers with strong affinities for cool, humid habitats (Lindroth 1969). While distribution of these species may be in part due to microclimatic changes resulting from edge effects, they may also reflect prey availability across the gradient. Species such as *S. angusticollis* (Lindroth 1969) and *S. marginatus* (Lindroth 1969; Niemela *et al.* 1992; Digweed 1993) are thought to specialize on terrestrial gastropods which are often closely associated with moist interior forest conditions. Likewise, another carabid, *P. crassus,* is thought to specialize on a millipede, *Harpaphe haydeniana*, which is associated with forest litter (Parsons *et al.* 1991).

In contrast, edge-input species were represented largely by taxa with strong affinities for warmer, drier habitats. A major component of the this fauna was *Formica* and *Camponotus* ant species. *Formica* and *Camponotus* (Akre *et al.* 1994) species show differential preferences across temperature and moisture gradients. However, in addition to microclimatic sensitivity, ants have the potential to alter species composition across forest edges through interspecific competition. For example, increased abundance of an early successional species of *Formica* along forest edges in managed boreal forests in Finland was attributed to faster rates of colony division and subsequent displacement of interior ant species (Punttila *et al.* 1994). Interestingly, *Formica* species have been reported to have a negative effect on carabid beetles (Niemela *et al.* 1992) but little impact on spider densities (Bruning 1991). A similar pattern was observed within this study.

Ambush predators such as lycosid spiders were most abundant in clearcuts but extended further into interior forests than did ant species. Abundance of species such as *A. kochi* have been shown to be correlated with temperature and litter depth (Hagstrum 1970). In Pacific Northwest old-growth forests, the depth of forest litter increases up to 60 m, beyond which litter depth stays relatively constant (T. Haynes *pers comm*). Consequently, lycosids may be responding to microclimatic changes caused by structural differences in the forest floor across forest edges.

Species within other trophic groups, such as flower-feeding herbivores and detritivorous dung-beetles, were also associated with clearcuts presumably because of their direct and indirect linkage to flowering shrubs and herbaceous vegetation. Large collections of *A. expansa*, a common buprestid that feeds on flower parts and pollen as an adult, were likely associated with more flowering plants in clearcuts and near the forest edge (Hatch 1971). Large mammals such as deer are often associated with forest edges because of the availability of plant material for browsing (Alverson *et al.* 1988). Subsequently, dung-beetles associated with deer pellets, such as *A. opacus,* may also be more common within clearcuts and near the forest edge (Hatch 1971).

Surprisingly, only one species, *C. modoc,* exhibited an edge-philic response in multiple sampling transects. *C. modoc* is a nocturnal foraging species that is closely associated with damp or rotting wood (Hansen and Akre 1985). Previous studies have shown that within old-growth Douglas-fir forests, the number of dead trees (snags) and fallen boles was greatest at the forest edge and decreased with increasing distance into interior forest (Chen *et al.* 1992). The unimodal response of *C. modoc* may represent the availability of suitable nesting sites, and indirectly, the mortality gradient of overstory trees across forest edges.

Clearly, the role of microclimatic edge-effects may be confounded with predator-prey and competitive interactions, host-plant associations, host-plant phenology, and structural changes. Other studies have also concluded that distance from the forest edge is a better predictor of changes in arthropod abundance than simple environmental measurements (Didham *et al.* 1998a). Unfortunately, I cannot separate the direct role of microclimatic edge-effects from these interactions in this study. Rather, my results stress the numerous possibilities by which edge-effect may alter species composition.

Variability in species composition was greatest between the forest edge and 50 m into interior forest. Didham *et al.* (1998a) suggested that high variability of species composition at the forest edge implies an extremely large species pool that may impart a stochastic component to species composition at forest edges. The variability in species composition I observed at the forest edge was primarily due to mixing of species with edge-phobic and edge-input response patterns. Given that overall species richness (and consequently the local species pool) was much lower in my study sites than in the tropical forest edges examined by Didham *et al.* (1998a), species composition may be less stochastic along forest edges in the Pacific Northwest.

Consequences of Forest Harvest

The generalized response patterns of individual species that I observed were consistent with other studies of fragmentation from a range of forest types including boreal forests in Western Canada (Niemela *et al.* 1993), oak forest in Eastern United States (Lenski 1982) and tropical rainforest in Amazonia (Didham *et al.* 1998a). As with my data, these studies suggest that fragmentation consistently has a negative effect on the abundance of forest specialist species.

In the Western Cascade range of the United States , clearcut harvesting of forests has replaced natural wildfire as the dominant disturbance (Spies *et al.* 1994). Consequently by 1988, the amount of edge increased from 1.9 to 2.5 km/km^2 of forest and the mean size of interior forest patches fell from 160 to 62 ha by 1998 (Spies *et al.*

1994). Spatial models of dispersed clearcutting predict that 50% cutover of forest with a 100 m edge-effect would result in the loss of 75% of interior forest (Franklin and Forman 1987). Edge-phobic species such as *S. angusticollis* and *S. marginatus* which are found in relatively low abundances up to 100 m from the edge will likely be negatively affected at the landscape level under such conditions. However, interpretations of arthropod edge responses at the landscape level should be viewed with caution, given the confounded nature of edge and area effects of fragmentation. Clearly, fragment size and distance between fragments will affect the probability of extinction (Tilman *et al.* 1994) as well as depth of influence of edge effects (Didham *et al.* 1998).

Incursion of the Edge Fauna and Invasion Potential

Whether or not edge-effects promote the spread of invasive species is still being debated (Robinson *et al.* 1995; Donovan *et al.* 1997). The incursion of edge fauna into the forest interior that I observed does not necessarily suggest that edges pose risks for invasion by exotic species. Fifty-five exotic arthropod species have been reported to occur in the H. J. Andrews Experimental Forest, thirteen of which are litter arthropods associated with clearcut or open habitats (Parsons *et al.* 1991). Interestingly, none of these species were collected in my study. Only one exotic species, *Adrius nodifer* Westwood, a lathridiid beetle commonly associated with closed canopy forest was collected in low abundance during this study. If exotic species have arrived, the question remains 'why have they not thrived?' An answer to this question is clearly beyond the scope of this study. However, given that the impacts of forest harvesting may superficially emulate natural disturbances such as wildfire, native edge-input species may be better adapted to utilizing forest edges than are invasive species that are associated with different disturbance regimes.

Utility of Arthropods as Indicator Taxa

Obviously, changes in species composition across a spatial gradient reflect the variety of scales of activity of the individual taxa, as well as sampling effort (Wiens 1989), and ecological indicators should reflect the scale of interest (Weaver 1995). Other studies of litter arthropods in eastern hardwood forests (Rykken *et al.* 1997) and coniferous forests in Finland (Niemela 1990), have shown certain species of ground arthropods to be sensitive at scales of 10's of meters but to have high variability at larger spatial scales. Likewise, I was able to detect variations in species composition across forest edges in as little as 25 m. However, overall patterns in species composition across forest edges were apparent up to 100 m. These results suggest that ground-dwelling arthropods may be particularly well-suited as an indicator of fragmentation impacts within forest remnants.

Conclusions

The generality that edges alter the distribution of some species is of limited use in our understanding of fragmentation. Given the complexity of possible interactions, the identification of species that are affected by edges and a quantified description of their response in large-scale studies are imperative (Harrison and Burns 1999). In this study I found species composition of ground arthropods to be affected up to 100 m from the forest edge. Likewise, I also identified individual species that are likely to be affected by large-scale fragmentation and provide plausible explanations for their responses across forest edges. Taken as a whole, this study provides a starting point from which the impacts of fragmentation on arthropod communities can be evaluated.

Chapter 3

SEASONAL PATTERNS IN ACTIVITY AND SPECIES RICHNESS OF GROUND-DWELLING ARTHROPODS IN OLD-GROWTH DOUGLAS-FIR FORESTS IN WESTERN OREGON

Introduction

Nature is spatially and temporally heterogeneous. Therefore the relevance of spatial patterns of ecological systems must be considered within an appropriate timeframe (Wiens 1989). Whereas spatial patterns of the microcosm may change in the order of seconds, landscape patterns may persist for centuries. As a consequence landscape changes such as forest fragmentation and associated edge-effects present an interesting juxtaposition of scale with short-lived animals such as arthropods. Edge effects caused by forest harvesting have been shown to alter the spatial distribution of arthropod species (see Chapter 2 and Didham *et al.* 1996; Didham *et al.* 1998). The redistribution of species across forest edges is predicted to alter species interactions by influencing mortality of species and cross-boundary subsidies, and by creating novel interactions between species (Fagan *et al.* 1999). However, novel interactions resulting from edge-effects may be biologically irrelevant, if temporal concordance among species is nonexistent.

Arthropods adapt to long-term, predictable changes in environmental conditions through seasonal cycles in activity. Like other poikilothermic organisms, growth and development of individual organisms, and thus population growth, is dependent on seasonal accumulation of temperature units or degree days. Within populations, seasonal activity also synchronizes mating opportunities (Wiklund 1995) and phenological development with prey-items or host-plants (Varley *et al.* 1973; Barbosa *et al.* 1986).

However, seasonal patterns may also define community interactions for animals with short generation times such as arthropods (Schoener 1974). Temporal differences in activity periods may reduce resource competition among species (Linsley *et al.* 1963) although delayed effects of competition can linger in the form of altered resource quality (Dankert *et al.* 1997). While the clearest examples of seasonal resource partitioning come from herbivorous insect-plant systems (Denno *et al.* 1995), the role of seasonal activity in other trophic levels, particularly predators, is much more elusive. Populations of predators such as carabid beetles are often synchronized with seasonal reproductive cycles (Thiele 1977) although the role of temporal niche partitioning has been argued for (Loreau 1988; Loreau 1989) and against (den Boer and den Boer-Daanje 1990).

In this paper, I present information regarding seasonal changes in activity and species richness of ground arthropod communities in fragmented old-growth forests. In addition, I also report on the correlation between climatic factors and activity of individual species. This analysis is one part of a larger project examining effects of habitat fragmentation and edge-effects on arthropod community composition. In this paper, I assess the potential for seasonal differences in activity to modify species interactions among arthropods. Discrete seasonal preferences among species, especially those within the same trophic level, would likely minimize interspecific interactions and to some extent the impacts of edge-effects. However, broad seasonal overlap in activity would stress the importance of spatial consequences of edge-effects for interspecific interactions.

Methods

This study took place at the H. J. Andrews Long-Term Ecological Research (LTER) site near Blue River, Oregon, in the Western Cascade Mountains of the United States. This forest is dominated by large Douglas-fir (*Pseudotsuga menziesii* (Mirib.) Franco), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), and Pacific silver fir (*Abies amabilis* Dougl. Ex Forbes) and is some of the most productive forest in the world. Old-growth forest with dominant trees greater than 400 years of age comprise 40% of the LTER site. The climate within this region is maritime and is characterized by mild, wet winters and warm, dry summers. Individual stands are broadly characterized by understories of vine maple (*Acer circinatum* Pursh), and western hemlock with large amounts of coarse woody debris on the forest floor.

Litter arthropods were sampled from 7 replicated transects that began in regenerating clearcuts and extended across the forest edge and into old-growth Douglas-fir forests (Table 3.1). Arthropods were collected using pitfall traps, 12.5 cm in diameter, which contained propylene glycol as a preservative. The spatial arrangement of pitfall traps along each sampling transect is described in detail in Chapter 2. For this analysis, sampling points across each transect were pooled to represent total activity for each site. In 1997, a total of 18 pitfall traps were operated at each site. In 1998, the number of pitfall traps was increased to 30 traps per site. Arthropods were collected from 3 August

Table 3.1. Location, elevation, aspect, slope, clearcut harvest date, and soil class for 7 study sites located in the H.J. Andrews Experimental Forest.

Site Number	Harvest Unit	Elevation (m)	Aspect	Slope	Harvest Date	Closest Weather Station	Soil Type
1	L241	850	Northwest	>60%	1960	RS5	Cobbly,heavy loam,bedrock talus
2	L109C	850	East	30-60%	1986	GMACK	Gravelly,sandy loam
3	L503A	800	Southeast	<30%	1980	H15MET	Gravelly, loam
4	L352	1100	West	>60%	1974	CENMET	Gravelly,sandy loam
5	L704A	1250	West	>60%	1981	UPLEMET	Gravelly,loam
6	FR13	1250	Southwest	>60%	1988	RS12	Gravelly,loam
7	FR10	1300	Southwest	>60%	1973	RS12	Gravelly,sandy loam

to 14 September in 1997 and from 22 May to 31 July in 1998.

Pitfall traps were used to compare relative abundances between species rather than absolute densities because they reflect activity of ground-dwelling organisms (Niemela *et al.* 1990). All traps were operated continuously during 1997 and 1998 and were emptied at two week intervals. All specimens larger than 5 mm in length were identified using keys provided by Hatch (1953, 1957, 1961, 1968, 1971) (Coleoptera: excluding Carabidae), Lindroth (1969) (Coleoptera:Carabidae), and Dondale and Redner (spiders) (1987, 1990). In addition, all material was verified against the H. J. Andrews Long-Term Ecological Research Collection and the Oregon State University Arthropod Collection at Corvallis OR. Voucher material was deposited in the Oregon State Arthropod Collection in Corvallis, OR.

Seasonal variation in activity was compared using Spearman's rank correlation (Sokal and Rohlf 1995). Differences in seasonal activity of individual taxa were considered significant if the null hypothesis of no change in activity across sampling dates could be rejected at $p<0.05$. To avoid spurious correlations with rare species, only species represented by more than 50 individuals were analyzed. All statistical analyses were performed using SPSS statistical software (SPSS v. 8.0.2, SPSS Inc).

To determine the extent with which seasonal changes in activity were correlated with abiotic factors, activity of individual species as compared to mean daily air temperature, soil temperature and precipitation for a given sampling period using Spearman's correlation coefficient. All air temperature measurements were taken between 150 and 350 cm above the ground. Soil tempertaure was taken at 10 cm below the soil surface. Climatic data was collected from meteorological monitoring stations located throughout the H. J. Andrews Experimental Forest and obtained from the H. J. Andrews website (www.fsl.orst.edu/lter/datafr.htm). Sampling sites were paired with nearby meteorological stations using GIS software (ArcView v. 3.1, ESRI Redlands, CA) (Table 3.1). However, not all environmental variables were measured at each meteorological station. Air temperature had the highest spatial resolution of all the environmental variables and was measured within 1.5 km of all sampling sites. One monitoring station, RS12, was paired with two sampling sites (Sites 6 and 7). Soil temperature data were only available for five sampling sites. In this case, sites 1 through 3 were paired with station RS5. Likewise, mean precipitation was only available for two sites. Consequently, sites 1 through 3 were paired with one station, CENMET, and sites 4 through 7 were paired with H15MET. However, variations in annual precipitation between study sites has historically been small. Between 1980 and 1989, the range in total precipitation during June was between 9 and 12.5 mm across our study sites. Thus, these pairings are likely to represent realistic estimates of precipitation within each site.

Results

Climatic trends

Overall mean air and soil temperature declined across the three sampling periods in 1997 (Figure 3.1). However, variation between meteorological stations across the three sampling periods was small. Air temperature was more variable than soil temperature on a daily basis, but both variables ranged within approximately 10° C across sampling periods. Rainfall occurred between 19-Aug and 30-Aug and between 9-Sept and 15-Sept. In 1998, mean air and soil temperature gradually increased across the season and reached similar temperatures observed in 1997 (Figure 3.2). Precipitation events were common between 22-May and 1-July but were largely absent during the month of July.

1997

In 1997, average abundance and species richness showed similar temporal patterns between 3-Aug and 15-Sept (Figure 3.3). While temporal differences in abundance were not statistically significant (F=3.301, df=2, p=0.06), species richness was significantly different across sampling periods (F=6.873, df=2, p=0.006). Species richness was significantly lower on 17-Aug than 3-Aug (Least significant difference (LSD) test =10.14, p=0.02). When individual species were analyzed for temporal changes during 1997, no significant differences were observed (Table 3.2).

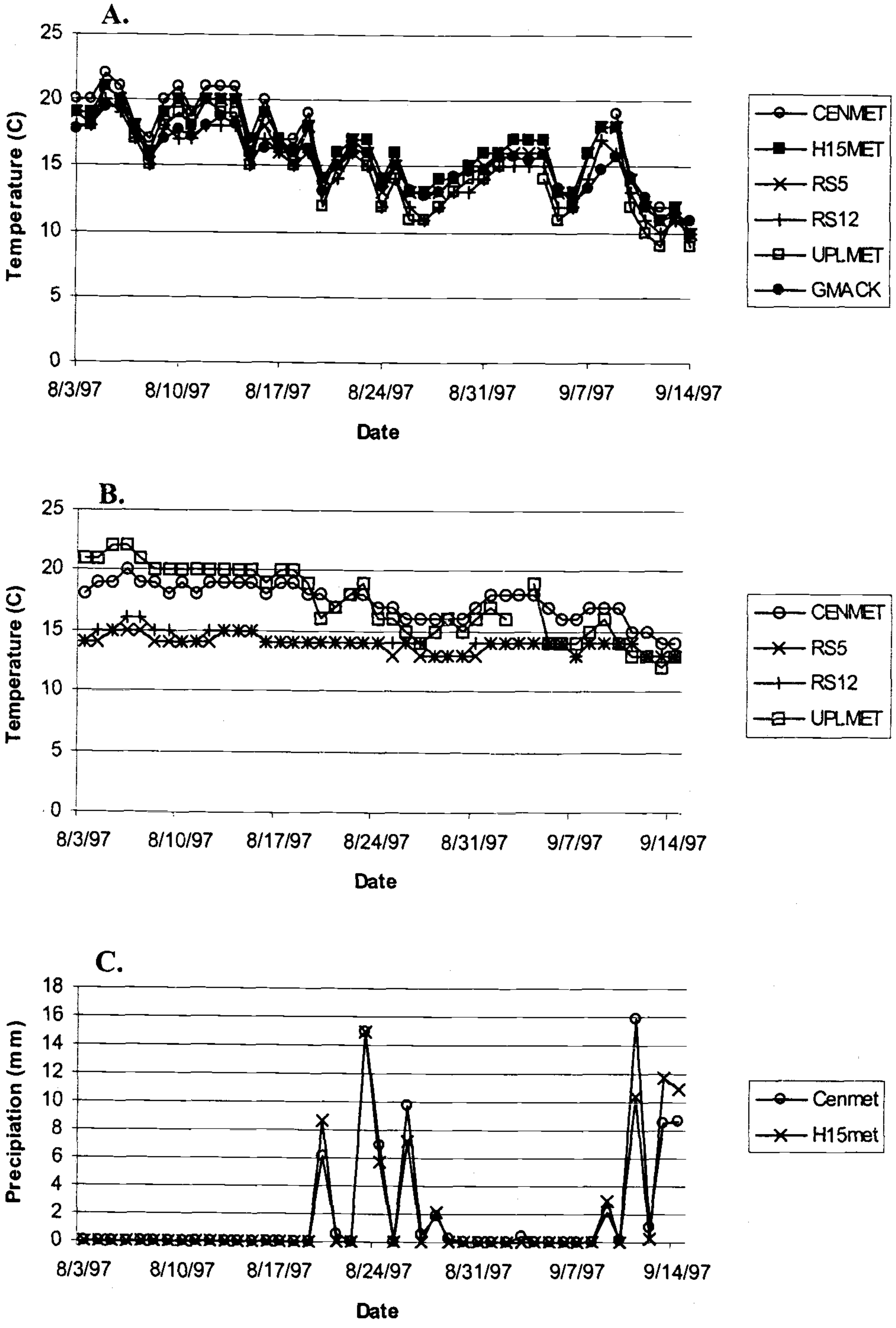

Figure 3.1. Mean daily a) air temperature b) soil temperature and c) precipitation between 3-Aug-1997 and 14-Sept-1997 from meteorological stations near study sites in the H. J. Andrews Experimental Forest. (See Table 3.1 for associations between meteorological stations and study sites)

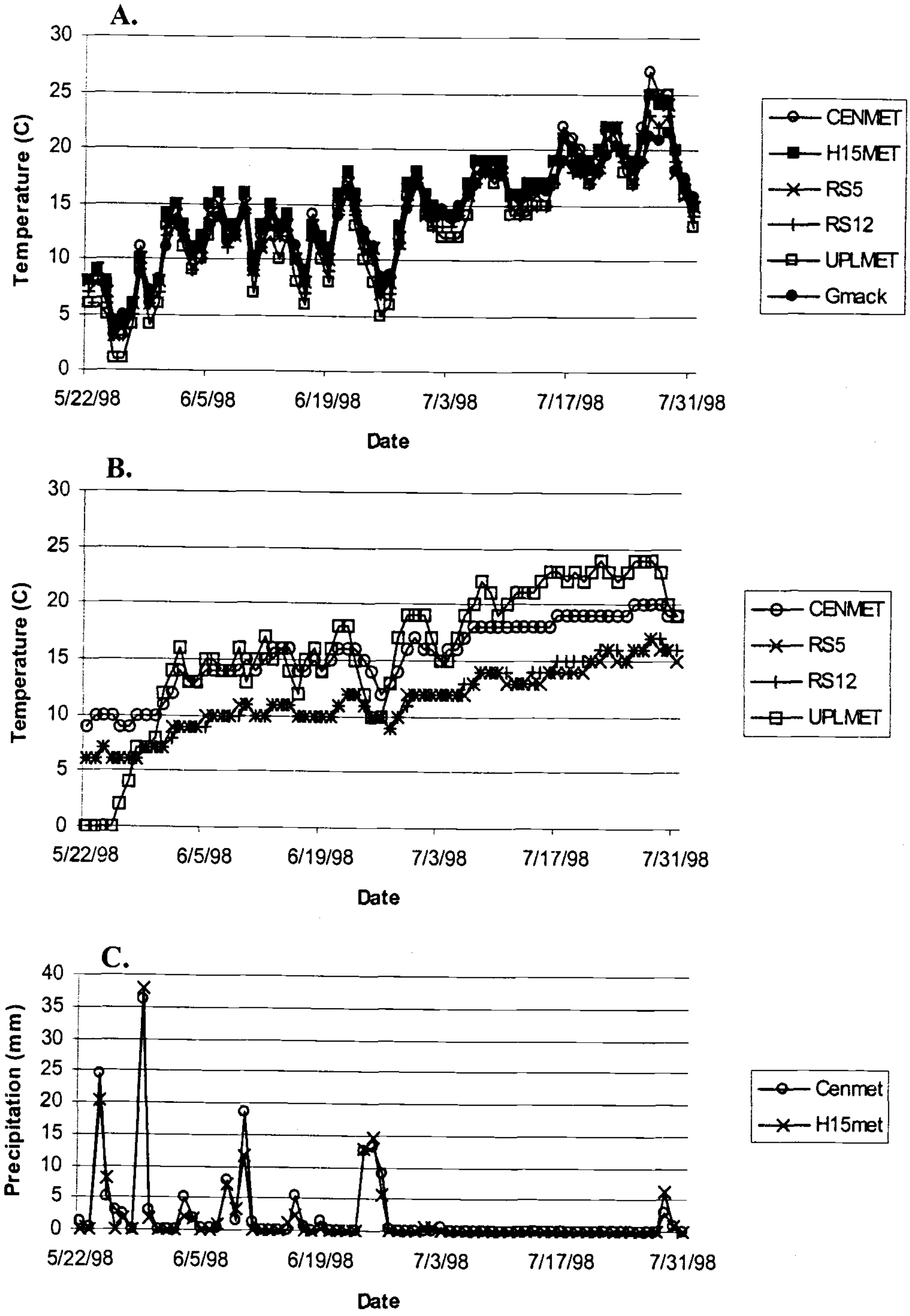

Figure 3.2. Mean daily a) air temperature b) soil temperature and c) precipitation between 22-May-1998 and 31-July-1997 from meteorological stations near study sites in the H. J. Andrews Experimental Forest. (See Table 3.1 for associations between meteorological stations and study sites)

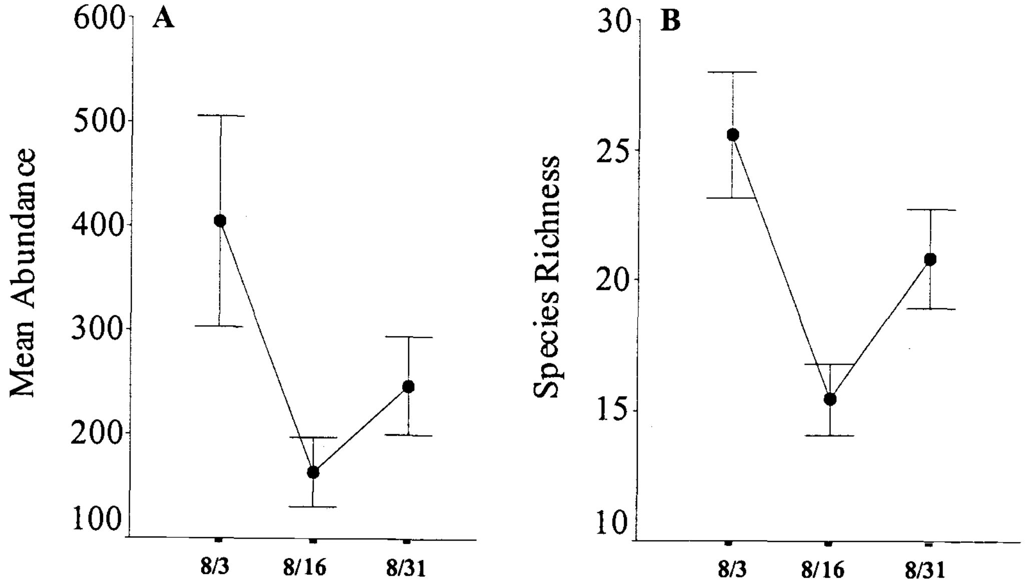

Figure 3.3 a) Mean abundance and b) species richness of ground arthropod taxa over three sampling dates in 1997 (n=7).

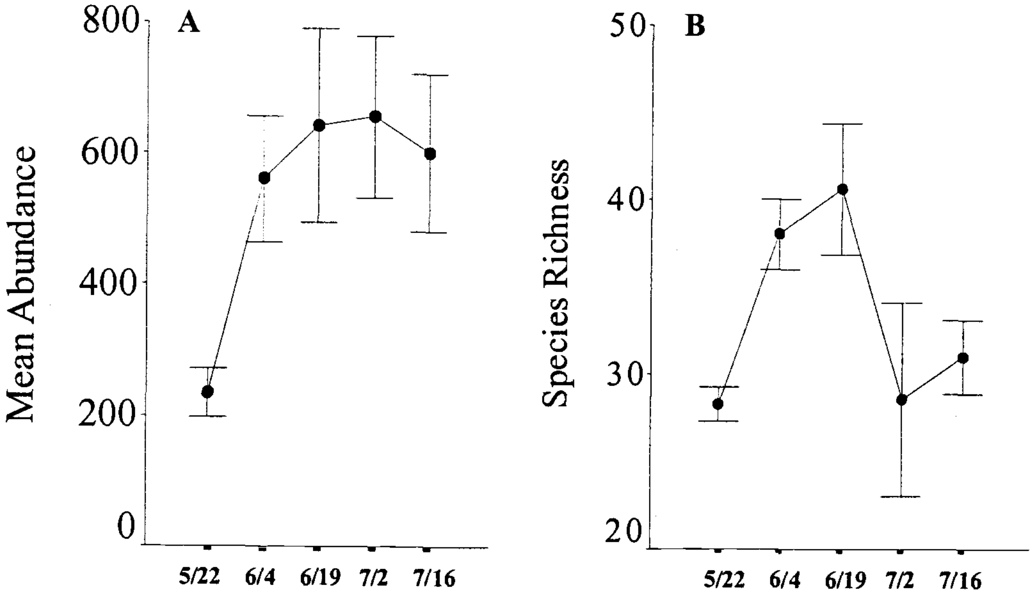

Figure 3.4 a) Mean abundance and b) species richness of ground arthropod taxa over five sampling dates in 1998 (n=7).

Table 3.2. Spearman rank correlation coefficient of seasonal catches for 15 abundant species in 1997.

Taxa	Trophic Level	Spearman's Correlation Coefficient
Aphodius opacus LeConte	D	-0.324 ns
Camponotus laevigatus (F. Smith)	O	-0.106 ns
Camponotus modoc Wheeler	O	0.000 ns
Camponotus vicinus Mayr	O	-0.117 ns
Carabus taedatus Fabricus	Pr	0.066 ns
Formica subnuda Emery	O	-0.309 ns
Pardosa dorsuncata Lowrie & Dondale	Pr	-0.049 ns
Pterostichus herculaneus Mannerheim	Pr	-0.082 ns
Pterostichus lama Menetries	Pr	-0.078 ns
Pterostichus sp.	Pr	-0.095 ns
Scaphinotus angusticollis Mannerheim	Pr	0.171 ns
Scaphinotus marginatus (Fischer von Mannerheim)	Pr	0.218 ns
Scaphinotus rugiceps Horn	Pr	0.096 ns
Steremnius carinatus (Boheman)	H	0.026 ns
Zacotus matthewsii LeConte	Pr	-0.092 ns

Note: Trophic group assignments: Pr= predator, O= omnivore, H= herbivore, and D=dung feeder
Statistical significance: ***p<0.001, **p<0.01, *p<0.05, ns p>0.05

1998

In contrast to 1997, abundance and species richness had different overall temporal patterns in 1998 (Figure 3.4). Seasonal patterns in overall abundance were not statistically significant (F=2.407, df=4, p=0.071) in 1998. However, seasonal patterns in overall species richness were significant (F=2.951, df=4 p=0.036). Species richness was higher between 4-Jun and 16-Jun than other sampling periods. When abundant species were analyzed for differences in activity across 1998, approximately 50% of species showed no difference in activity between sampling periods (Table 3.3). These species were largely represented by predator taxa such as carabid beetles and large staphylinid beetles in the genus *Staphylinus*. Other taxa that showed no seasonal patterns included herbivorous curculionids, a common carrion beetle, *Nicrophorus defodiens*

Table 3.3. Spearman rank correlation coefficient of seasonal catches for 31 abundant species in 1998.

Taxa	Trophic Level	Spearman's Correlation Coefficient
Early Season		
Alopecosa kochi (Keyserling)	Pr	-0.524 **
Anthaxia expansa LeConte	Fl	-0.581 ***
Aphodius opacus LeConte	D	-0.434 **
Hapalaraea stouti (Hatch)	?	-0.706 ***
Pardosa californica Keyserling	Pr	-0.421 *
Pardosa dorsuncata Lowrie & Dondale	Pr	-0.460 **
Promecognathus crassus LeConte	Pr	-0.580 ***
Xysticus montanensis Keyserling	Pr	-0.632 ***
Xysticus pretiosus Gertsch	Pr	-0.486 **
No Seasonal Preference		
Camponotus laevigatus (F. Smith)	O	0.165 ns
Carabus taedatus Fabricus	Pr	0.236 ns
Formica sp 1	O	0.152 ns
Formica subnuda Emery	O	0.158 ns
Henotiderus lorna Hatch	?	0.239 ns
Lepesoma lecontei (Casey)	H	-0.040 ns
Nicrophorus defodiens (Mannerheim)	C	-0.017 ns
Pterostichus herculaneus Mannerheim	Pr	0.086 ns
Pterostichus inanis Horn	Pr	0.069 ns
Pterostichus lama Menetries	Pr	0.322 ns
Scaphinotus angusticollis Mannerheim	Pr	0.194 ns
Scaphinotus rugiceps Horn	Pr	-0.200 ns
Staphylinus pleuralis LeConte	Pr	-0.173 ns
Staphylinus saphyrinus leconte	Pr	-0.303 ns
Steremnius carinatus (Boheman)	H	-0.261 ns
Zacotus matthewsii LeConte	Pr	0.061 ns
Late Season Species		
Camponotus spp.	O	0.530 **
Camponotus modoc Wheeler	O	0.670 ***
Catops basilaris Say	C	0.512 **
Formica sp 2	O	0.487 **
Scaphinotus marginatus (Fischer von Mannerheim)	Pr	0.387 *
Tachinus semirufus Horn	?	0.531 **

Note: Trophic group assignments: Pr= predator, O= omnivore, H= herbivore, C= carrion-feeder, ?=unknown, Fl= flower feeder, and D=dung feeder
Statistical significance: ***p<0.001, **p<0.01, *p<0.05, ns p>0.05

(Mannerheim) and three ant species, *Camponotus laevigatus, Formica subnuda,* and *Formica* spl.

Species that were most active early in 1998 were represented largely by Lycosid spiders and ground dwelling crab spiders (Figure 3.5). Lycosid species such as *Aloplecosa kochi* (Keyserling) and *Pardosa californica* were most active between 22-May and 4-Jun, although *P. californica* was highly variable on those sampling dates. *Pardosa dorsuncata* Lowrie & Dondale was collected in peak abundance on Jun-4. Likewise *Xysticus montanensis* Keyserling and *Xysticus pretiosus* Gretsch were also most active during early June. Four beetle species had peak activity periods between 22-May and 4-Jun (Figure 3.6). *Anthaxia expansa* LeConte, a flower-feeding buprestid, and *Aphodius opacus* LeConte, a dung-feeding scarab, were most active during early June. Interestingly, only one carabid beetle *Promecognathos crassus* LeConte was significantly more active during the early part of the season. Species that were active early in 1998

Table 3.4. Spearman's rank correlation of taxa with peak activity early in 1998 and trends in air temperature, soil temperature, and precipitation.

Taxa	Air Temperature	Soil Temperature	Precipitation
Alopecosa kochi	-0.527 **	-0.360 *	0.506 **
Anthaxia expansa	-0.570 ***	-0.387 *	0.493 **
Aphodius opacus	-0.408 *	-0.301 ns	0.210 ns
Hapalaraea stouti	-0.643 ***	-0.627 ***	0.587 ***
Pardosa californica	-0.351 *	-0.381 *	0.341 *
Pardosa dorsuncata	-0.416 *	-0.323 ns	0.270 ns
Promecognathus crassus	-0.522 **	-0.463 **	0.482 **
Xysticus montanensis	-0.612 ***	-0.402 *	0.376 *
Xysticus pretiosus	-0.504 **	-0.309 ns	0.490 **

Statistical significance: ***p<0.001, **p<0.01, *p<0.05, ns p>0.05

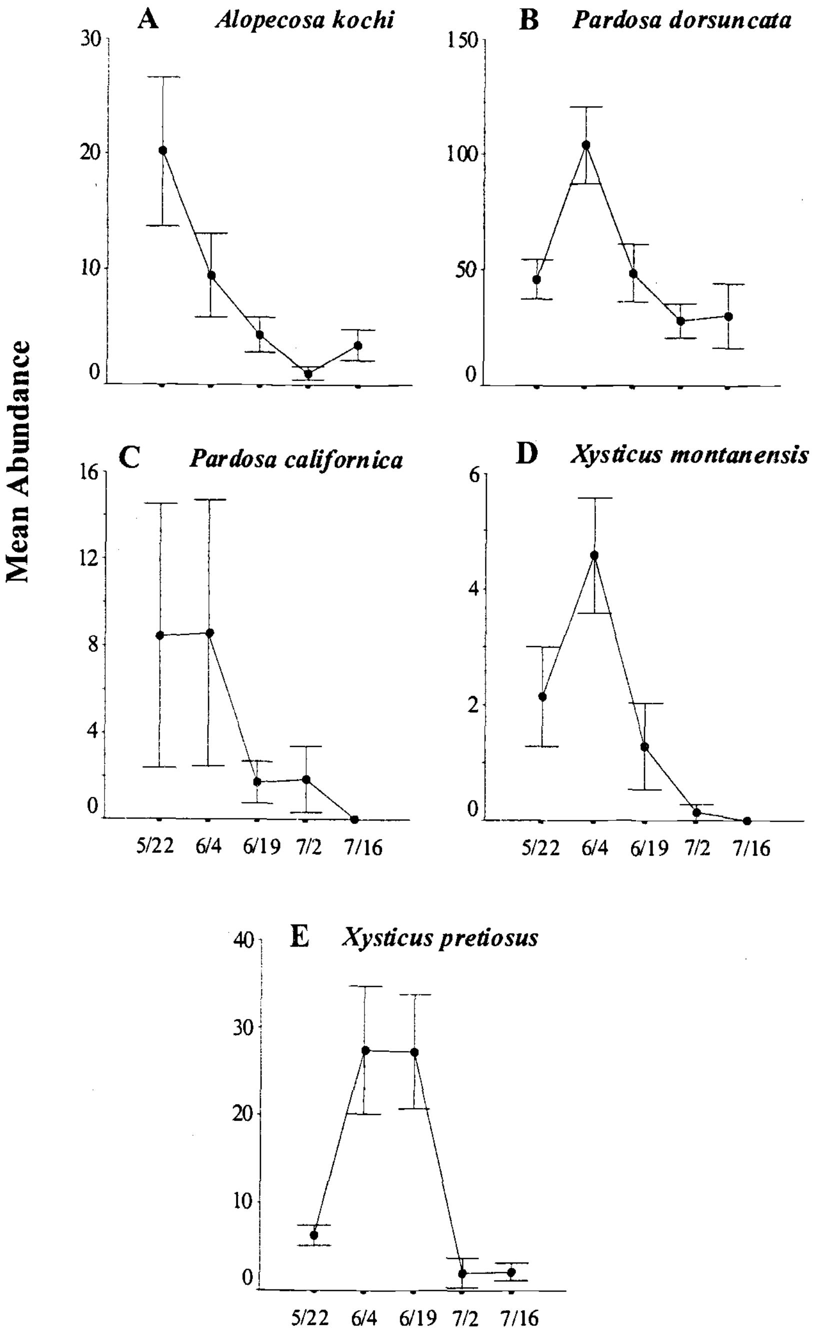

Figure 3.5. A-E. Mean abundance (± 1 standard error) of five spider species with peak activity during May and June of 1998.

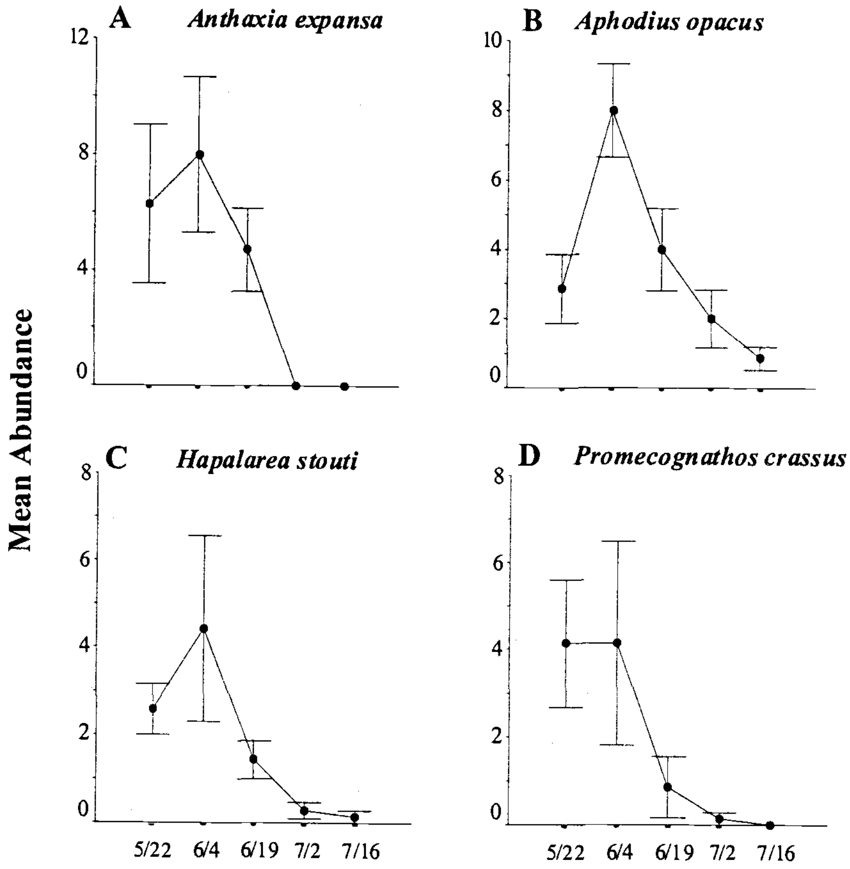

Figure 3.6. A-D. Mean abundance (± 1 standard error) of four beetle species with peak activity during May and June of 1998.

were negatively correlated with increasing air and soil temperatures but were positively associated with increased precipitation (Table 3.4) While most species were significantly correlated with all three environmental factors, three species, *A. opacus, P. dorsuncata,* and *X. pretiosus* showed no significant correlations with increasing soil temperature. Likewise, *A. opacus* and *P. dorsuncata* showed no correlation with increasing precipitation.

Six species had peak activity between 2-July and 16-July 1998 (Table 3.3). Of these species *Camponotus modoc* Wheeler and *Tachinus semirufus* Horn were the most numerous. Two carpenter ants, *C. modoc* and *Camponotus* spp increased in abundance following 2-July and were still increasing on 16-July (Figure 3.7). Likewise a carabid beetle, *Scaphinotus marginatus* (Fischer von Waldheim), also continued to increase through 16-July. However, seasonal increases were more gradual than those seen for either *Camponotus* species (Figure 3.8). Two other species, *Catops basilaris* Say and *T. semirufus* were most abundant during early July, but began to decline by 16-July (Figure 3.8).

Species with activity peaks during July 1998 were positively correlated with air and soil temperature but negatively correlated with increased precipitation (Table 3.5), with three exceptions. *C. basilaris*, a carrion feeding beetle, was not significantly associated with soil temperature. Likewise, activity of *Formica* sp2 was not correlated with precipitation. Interestingly, *S. marginatus* was not significantly correlated with any of the environmental factors measured.

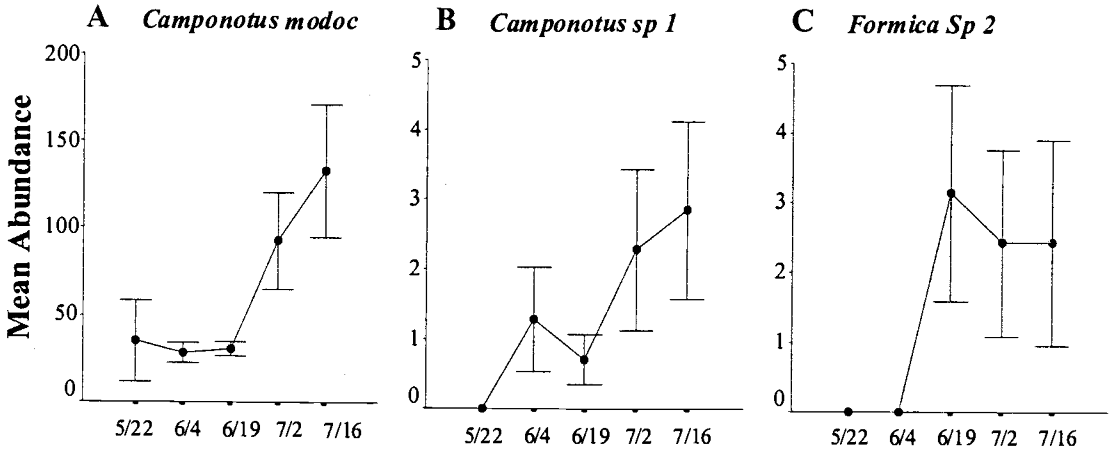

Figure 3.7. A-C. Mean abundance (± 1 standard error) of three ant species with peak activity during July 1998.

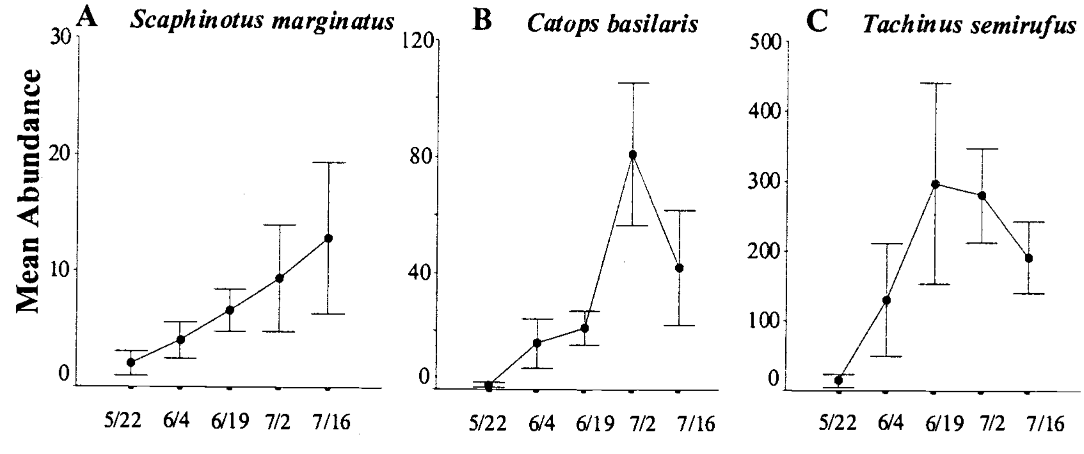

Figure 3.8. A-C. Mean abundance (± 1 standard error) of three beetle species with peak activity during July of 1998.

Table 3.5. Spearman's rank correlation of taxa with peak-activity later in 1998 and trends in air temperature, soil temperature, and precipitation.

Taxa	Air Temperature	Soil Temperature	Precipitation
Camponotus spp.	0.547 ***	0.481 **	-0.457 **
Camponotus modoc	0.573 ***	0.417 *	-0.562 ***
Catops basilaris	0.428 *	0.333 ns	-0.496 **
Formica sp 2	0.439 **	0.525 **	-0.332 ns
Scaphinotus marginatus	0.332 ns	0.331 ns	-0.233 ns
Tachinus semirufus	0.472 **	0.370 *	-0.380 *

Statistical significance: ***$p<0.001$, **$p<0.01$, *$p<0.05$, ns $p>0.05$

Discussion

Overall Patterns in Activity

In 1997, an overall decrease in abundance and species richness of ground-dwelling arthropods was observed over the three sampling periods. This overall decline in arthropod activity parallels seasonal declines in air and soil temperature. However, the relative increase in abundance and richness observed between 17-Aug and 31-Aug corresponded with precipitation events that occurred during this period.

In 1998, abundance and species richness varied in seasonal patterns. The lack of correspondence between abundance and richness was largely due to large collections of *T. semirufus* and *C. modoc* between 19-June and 16-July. For example, *T. semirufus* comprised approximately 50% of the total abundance of arthropods collected between 19-June and 2-July. As a consequence, overall changes in species richness may better describe the overall trends in activity of the arthropod assemblage during 1998.

While increases in species richness initially corresponded with increases in air and soil temperature, species richness declined following 19-June even as temperatures continued to increase. As in 1997, overall species richness corresponded well with precipitation. Increased species richness corresponded with frequent rainfall that occurred between 22-May and 19-June. However, as precipitation decreased beyond 19-June, so did species richness.

Clearly, seasonal changes in both temperature and precipitation are likely to affect activity of ground-dwelling arthropods. At higher elevations, such as where my study sites were located, arthropod activity likely reflects a trade-off between adequate temperature for development and drought stress. However, within the Pacific Northwest, precipitation is important in determining the activity of many soil and litter-dwelling arthropods (Moldenke 1996, McIver 1992). The overall increase in arthropod activity following precipitation events suggests that precipitation may actually synchronize activity among soil and litter arthropods.

Temporal Overlap of Species

In 1997, no significant differences in activity of individual species were observed between sampling periods. However, given the relatively brief sampling period within 1997, the biological significance of these temporal trends should be viewed cautiously. Rather these data give an indication of what species are active during the late summer.

In 1998, when a longer sampling period better reflected seasonal patterns in temperature and precipitation, the majority of species still did not show significant seasonal variation. The majority of these species were represented by predaceous carabid and staphylinid beetles. While patterns of carabid activity have been broadly characterized into spring and autumn breeding periods (Lindroth 1945; Lindroth 1969;

Thiele 1977), this generalization may be unwarranted (den Boer and Boer-Daanje 1990). den Boer (1979) has shown that for many species of European carabids, reproductive cycles of adult beetles can span longer seasonal periods because adults successively reproduce over two and three years. Successive breeding extends the activity period because older beetles typically reproduce earlier than do younger beetles. Such generalizations regarding predacious staphylinids can not be made due to limited information regarding development and seasonal activity (Developmental information pertaining to the Staphylinidae is only available for one-third of one percent of North American species (Moore and Legner 1974)).

However, significant seasonal peaks in activity were apparent for spider taxa in 1998, although the specificity of such responses is questionable. The seasonal peaks in spider activity that I observed were consistent with peak periods reported by McIver *et. al* (1992) and Hagstrum (1970). Although species such as *P. californica, A. kochi,* and both *Xysticus* species occur in May and June, the majority of spider taxa in this area have been reported to be active from April to November (McIver *et al.* 1992). The fact that *P. dorsuncata* was collected through September of 1997 cast doubt as to the early-seasonal specificity of that species. Furthermore at least one species, *A. kochi,* has a two-year life cycle, where juveniles and adults overlap throughout the summer (Hagstrum 1970) which further limits the likelihood of distinct seasonal responses.

Seasonal peaks of other trophic groups, such as carrion beetles, dung beetles and flower-feeding buprestids likely reflect synchrony with ephemeral resources such as dead animals, dung-pats and flowers. Because these trophic groups are notably under-represented in my samples, conclusions regarding the possibility of temporal partitioning are unwarranted.

Species that were most active later in the summer were represented by omnivorous ants, an abundant staphylinid, *T. semiufus,* and a single predatory carabid, *S. marginatus*. The increased activity of omnivorous ants in late July likely reflects the shift in reproductive effort of the colony. Both *Camponotus* and *Formica* species have been known to shift from aphid tending and a carbohydrate-rich diet to extensive foraging and a proteinatious diet in response to larval development within the colony. Again, limited knowledge of the biology of staphylinids precludes meaningful interpretations of the seasonality of *T. semirufus*. The relatively large abundance and broad distribution of *T. semiufus* across 1998 suggest that this species may be fairly ubiquitous throughout the summer. *S. marginatus* was most active in late August, but was not significantly correlated with temperature or precipitation. Similar seasonal patterns in the activity of *S. marginatus* have been reported in other forest ecosystems in Northern Canada (Niemela *et al.* 1992).

Overall, evidence for specific seasonal patterns in activity is limited for the majority of species I collected. Most species showed no significant differences in activity across sampling periods in either 1997 or 1998. Consequently, even species that showed significant seasonal peaks in activity overlapped with those species that are present throughout the season. Likewise, most of the species collected were predators, suggesting a high degree of temporal concordance within that trophic level. Clearly, without experimental evidence, the role of seasonality on temporal resource partitioning cannot be dismissed. However, my assessment of seasonal patterns in activity stresses that species at least have the potential to interact temporally within these forests.

Chapter 4

EDGE-EFFECTS ON PREDATOR SPECIES COMPOSITION AND COMMUNITY STRUCTURE IN OLD-GROWTH DOUGLAS-FIR FORESTS

Introduction

Forest fragmentation has become globally prevalent (Lovejoy *et al.* 1986; Wilcove *et al.* 1986; Groom and Schumaker 1993) resulting in the redistribution of forests into smaller sized patches with more peripheral 'edge'. Edge effects stemming from habitat fragmentation can differentially alter the distributions and interactions of resident species (Didham *et al.* 1998; Fagan *et al.* 1999). Consequently, edges have been shown to reduce rates of decomposition (Klein 1989), seed predation (Burkey 1993), and pollination (Aizen and Feinsinger 1994) while increasing rates of nest parasitism (Andren and Angelstam 1988) and invasion of noxious weeds (Hester and Hobbs 1992). Given the breadth of these effects, specific predictions regarding the impacts of edge-effects are required to avoid over-generalizations and missapplication of ecological theory. Here I present results from a large-scale study examining the impacts of forest edges on resource-partitioning by predatory arthropods.

Theory predicts that organisms in higher trophic levels, i.e., predators and parasitoids will be more sensitive to habitat fragmentation than other trophic levels (Pimm and Lawton 1977; Lawton 1995) although this has been challenged (Mikkelson 1993). Likewise, the body of empirical evidence has failed to produce a concensus as to the effects of fragmentation. Field studies have demonstrated that increased fragmentation inhibited aggregation and searching behavior of higher trophic levels and thus allowed lower trophic levels to flourish (Kareiva 1987; Kruess and Tscharntke 1994). Likewise, parasitoids with smaller body sizes were more inhibited by fragmentation and aggregated at smaller spatial scales than larger species (Roland and Taylor 1995). Consequently, the spatial scale of fragmentation has been shown to determine the outcome of parasitoid-host interactions (Roland and Taylor 1995). In contrast, relative species richness of predator taxa within forest remnants has been shown to decrease with distance from the forest edge (Didham *et al.* 1998; Didham *et al.* 1998). Thus far, empirical evidence has been unambiguous as to the broad question, do edge-effects alter the distribution and interactions of certain higher-trophic level species? More specific questions that remain include which species and which interactions will likely be affected by forest edges?

One approach to understanding the role of edge effects amidst this complexity of conclusions is to compare changes in the distribution of species abundance over the entire community or within a functional group to predictions of niche-partitioning models. Species abundance models can be generally categorized as statistical or biological in their development (Magurran 1988; Tokeshi 1993). Statistical models include such distributions as the general log normal (Preston 1948), canonical log normal (Sugihara 1980), and the log series distributions (Fisher *et al.* 1943). Such models have historically been applied to a variety of taxa including moths (Fisher *et al.* 1943), birds (Preston 1948), and plants (Whittaker 1965). More recently, the log normal model has been used to characterize the impacts of forestry management on patterns of arthropod species abundance with contrasting results (Basset *et al.* 1998; Hill and Hamer 1998; Nummelin

1998; Watt 1998). In a study comparing selectively logged and unlogged tropical forests, butterflies from unlogged forests conformed to the log-normal distribution while species from logged forests were better described by the log-series distribution (Hill *et al.* 1995). In contrast, Nummelin (1998) found the log normal distribution fit arthropod species abundance collected in unlogged and logged sites equally well. However biological interpretations of statistical based models such as the log-normal or canonical log-normal model have been criticized as reflecting mathematical properties of large sample sizes and the central limit therom rather than community organization (May 1975; Ugland and Gray 1982).

In contrast, biologically based models of niche partioning are developed using assumptions consistent with biological mechanisms and are thus readily interpretable. Biological based models of niche partitioning such as the geometric series (Motomura 1932), MacArthur's broken-stick model (MacArthur 1957) and a variety of niche partitioning models developed by Tokeshi (1990, 1993) have been used to identify possible mechanisms by which organisms partition resources within a community. In each case, the underlying model represents a community that is governed by specific rules of resource partitioning to which observed distributions can be compared.

In this paper I compare changes in species composition and abundance of predatory arthropods across transition zones between clearcuts and old-growth Douglas-fir forests in the Pacific Northwest region of the United States. I also compare predator species abundance to four biological based models of resource partitioning to suggest possible mechanisms by which edge effects may influence community structure. Within this region, clearcutting of forests has become a major disturbance factor that has altered the total area and configuration of the forest landscape (Spies *et al.* 1994). I hypothesized that 1) arthropod species composition would change as a function of distance from the forest edge and 2) patterns of species abundance would differ across the transition zone between heavily disturbed clearcuts and undisturbed old-growth forest. I also hypothesized that patterns of species abundance would be conistent with a transition between non-equilibrium communities in disturbed clearcuts and communities at equilibrium within old-growth sites. Surprisingly, such a transition was not evident.

Methods

This study took place at the H. J. Andrews Long-Term Ecological Research Site (LTER) near Blue River, Oregon, in the Western Cascade Mountains of the United States. This forest is dominated by large Douglas-fir (*Pseudotsuga menziesii* (Mirib.) Franco), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), and Pacific silver fir (*Abies amabilis* Dougl. Ex Forbes) and is among the most productive forests in the world. Old-growth forest with dominant trees greater than 400 years of age comprises 40% of the LTER site. Individual stands are broadly characterized by understories of vine maple (*Acer circinatum* Pursh), and western hemlock with large amounts of coarse woody debris on the forest floor. Litter arthropods were sampled from 7 replicated transects that began in regenerating clearcuts and extended across the forest edge and into old-growth Douglas-fir forests (Table 4.1).

In this study, the transition between clearcuts and old-growth forest represented a steep biological gradient in terms of forest biomass and forest composition. Along each transect, litter arthropods were sampled at 6 intervals. Samples were taken within the clearcut at 25 meters from the edge (hereafter noted as -25 m), directly at the edge between clearcuts and forest (0 m), and at 25, 50, 100, and 200 m into the old-growth forest. At each interval, 5 pitfall traps, 12.5 cm in diameter, containing propylene glycol as a preservative were spaced in a pentagonal pattern approximately 1 m apart. Pitfall traps were used to compare relative abundances between species rather than absolute densities because captures reflect activity of ground-dwelling organisms (Niemela *et al.* 1990). Arthropods collected in the 5 pitfall traps were pooled at each transect interval for analysis. All traps were operated continuously between 22 May 1998 and 31 July 1998 and were emptied at two week intervals. All specimens larger than than 5 mm in length were identified using keys provided by Hatch (1953, 1957, 1961, 1968, 1971) (Coleoptera: excluding Carabidae), Lindroth (1969) (Coleoptera:Carabidae), and Dondale and Redner (spiders) (1987, 1990). In addition, all material was verified against

Table 4.1. Location, elevation, aspect, slope, clearcut harvest date, and soil class for 7 study site located in the H.J. Andrews Experimental Forest.

Site Number	Harvest Unit	Elevation (m)	Aspect	Slope	Harvest Date	Soil Type
1	L241	850	Northwest	>60%	1960	Cobbly,heavy loam,bedrock talus
2	L109C	850	East	30-60%	1986	Gravelly,sandy loam
3	L503A	800	Southeast	<30%	1980	Gravelly, loam
4	L352	1100	West	>60%	1974	Gravelly,sandy loam
5	L704A	1250	West	>60%	1981	Gravelly,loam
6	FR13	1250	Southwest	>60%	1988	Gravelly,loam
7	FR10	1300	Southwest	>60%	1973	Gravelly,sandy loam

the H. J. Andrews Long-Term Ecological Research Collection and the Oregon State University Arthropod Collection at Corvallis OR. Voucher material was deposited at the Oregon State Arthropod Collection in Corvallis, OR.

From the total number of arthropods collected, 6,916 individuals from 49 taxa were classified as predators on the basis of previous literature and natural history records (Appendix A). Only arthropods that were unambiguously described as predators were used in this analysis. Trends in predator species richness across sampling transects were analyzed with linear regression (SPSS v8.0.2, SPSS Inc. Ilinois, USA). To estimate how well samples reflect the real abundance of species at each transect point, species area/effort curves were generated using PCOrd software (McCune and Medford 1999). Sampling efficiency across the larger area of the H. J. Andrews LTER was evaluated by pooling samples from all transects. In these analyses, average species richness and standard deviation for a given sample size were estimated using 500 random samples of all possible permutations of the species area/effort curve.

To quantify changes in community composition along edge-forest gradients, sampling points were ordinated on the basis of species composition and abundance using non-metric multidimensional scaling (NMS). NMS was used in lieu of other ordination methods because it avoids the 'zero-truncation' problem of Beals (1984). Other methods such as principal components analysis and detrended correspondence analysis, can make very dissimilar points along a gradient appear similar because they share null values. NMS, however, relies on ranked distances and tends to linearize the relationship between environmental gradients and differences in species composition (Beals 1984). For this reason, NMS has performed better than other methods at recovering simulated gradients

(Minchin 1987) and has been widely used in ecological gradient studies (Clarke 1993). Stress between the original dataset and a reduced dimension ordination was minimized by a two-dimension solution. In addition to the ordination, the spatial effects of distance from the forest edge on changes in species composition were quantified using the Mantel test (Sokal and Rohlf 1995; Koenig 1999). Indicator species analysis was used to identify species that may be closely associated with increasing distance from the forest edge (Dufrene and Legendre 1997). Indicator values represent a combination of the relative abundance and the relative frequency and range between 0 (no indication) and 100 (perfect indication) (Dufrene and Legendre 1997).

Another approach used to estimate change in species composition across edge-forest gradients was to examine changes in species turnover between adjacent points along transects. Species turnover between adjacent sampling points as estimated using the following formula (Tokeshi 1990):

$$S\tau = \sum |P_i(t) - P_i(t+1)|$$

In this formula species turnover, $S\tau$, is the difference in proportional abundance of species i between adjacent sampling points along the edge-forest transects summed over all species i through n. Values range from 0, (no change in species composition), to 1 (complete species turnover).

To test hypotheses regarding resource partitioning by arthropod predators, four conceptual models of niche partitioning were evaluated against data collected from edge-forest transects. These models were 1) Dominance Preemption, 2) Dominance Decay, 3) Random Fraction, and 4) the Random Assortment models (Tokeshi 1990). The Dominance Preemption model is consistent with communities in which dominant species are not subject to invasion by subsequently colonizing species. The Dominance Decay model is the inverse of the Dominance Preemption model and assumes that resources controlled by a dominant species are always utilized by subsequent invading species. These two models represent extremes of equitability in resource partitioning. The Dominance Preemption model represents an inequitable division of resources, while Dominance Decay model represents a much more equitable division of resources. The Random Fraction model assumes no dominance hierarchy in resource partitioning, and thus both dominant and rare species are equally likely to be invaded by subsequent colonizers. This model was consistent with Sugihara's (1980) interpretation of the canonical log-normal model (Tokeshi 1990). Finally the Random Assortment model assumes that individual species utilize resources independently of one another. This is consistent with a community that is not resource limited or a community in which the resource usage of any species changes over a time. One underlying assumption inherent in these models is that dominant species or those represented by a large number of individuals utilize more resources than do species that are represented by small numbers of individuals (Gotelli and Graves 1996). These four models were selected because they represent extreme outcomes of resource partitioning and are meant to be illustrative of possible biological scenarios.

These models were used to generate 10,000 predator communities consisting of 7 species that sequentially partition a resource. Simulations were generated by allowing stochastic parameters to vary within defined limits consistent with each model. Two stochastic parameters were used in all these models and reflect the resource fraction used by subsequent invaders and whether dominant or subdominant species are invaded

(Tokeshi 1990; Tokeshi 1993). Data were considered consistent with a model if the first six ranks were within a single standard deviation of model predictions. All simulations were performed using MATLAB mathematical software (MathWorks 1995). The four models were also evaluated by comparing absolute deviations between predicted and observed values for the mean relative abundance for each of the 7 species.

Because numerical abundance may not directly correspond to biomass as a measure of resource utilization, the four niche models were also compared to relative biomass of each species. Biomass of each species was estimated allometrically using the power function:

$$\text{Mass} = a^*(\text{length})^b$$

Average body lengths were obtained from literature records in Hatch (1953, 1957, 1961, 1968, 1971), Lindroth (1969), and Dondale and Redner (1978, 1990), and Coyle (1971). Parameters a and b were obtained for Coleoptera (Sample *et al.* 1993) and for spiders (Breymeyer 1967). Total biomass of a species was estimated by multiplying abundance by average biomass per individual.

Results

Predator species richness was highly variable across sampling transects ranging from 5 to 18 species/sample. Predator richness declined with distance from the forest edge (F=9.83, df=1, p=0.0032, n=42) although this trend was slight (species richness =

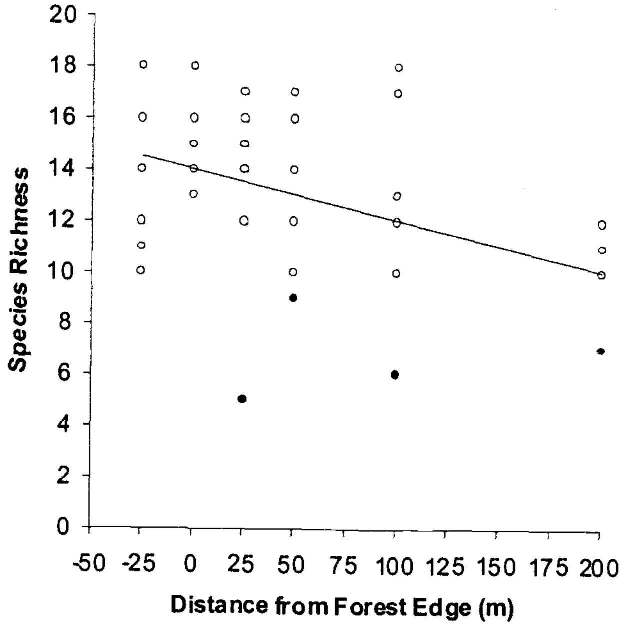

Figure 4.1. Changes in predator species richness at six distances (-25, 0, 25, 50, 100 and 200 m) from replicated edge-forest tansects (n=42). Equation for linear regression line: species richness = 14.05 – 0.02*(Transect), r^2=0.20. Filled circles represent four sites located at low elevation that contained less than 25 individuals.

14.05 – 0.02*(distance from forest edge)) and the fit of the model was relatively low (r^2=0.20) (Figure 4.1). Small numbers of arthropods (fewer than 25 individuals) were collected from four low elevation sampling points resulting in low species richness at these sites (Figure 4.1). Likewise, the decline in species richness across edge-forest gradients were evident as species accumulation curves for each position along sampling transects (Figure 4.2). As sampling intensity increased, species accumulated on average more quickly in clearcut sites than in interior forest sites. The accumulation of new species was relatively small following seven samples and ranged from 2.14 species/sample at –25 m to 0.86 species/sample at 200 m. When all sampling points were pooled and accumulation of species across the larger area of the H. J. Andrews forest was

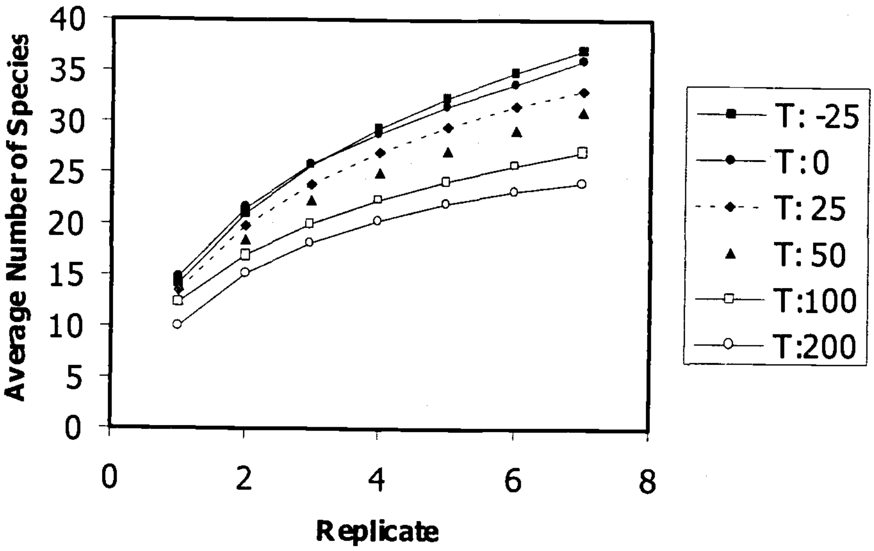

Figure 4.2. Species area/effort curves depicting the average number of species collected with increasing sampling effort (n=7) at 6 locations along edge-forest transects.

evaluated, accumulation of new species was small, suggesting sampling effort was sufficient to represent local species richness (Figure 4.3).

Changes in predator species composition across transects were evident as high rates of species turnover between adjacent sampling points (Figure 4.4). Initially species turnover was small along the forest edge (between –25 and 25 m). However, species turnover increased quickly between 25 and 100 m from the forest edge. Beyond 100 m into interior forest, species turnover remained constant but relatively high. When predator community composition was analyzed with non-metric multidimensional scaling, compositional changes across transects were also evident (Figure 4.5). In this ordination, axis 1 and axis 2 explained 37.0% and 48.4% of the variance observed, respectively. Changes in species composition along axis 1 were consistent with the

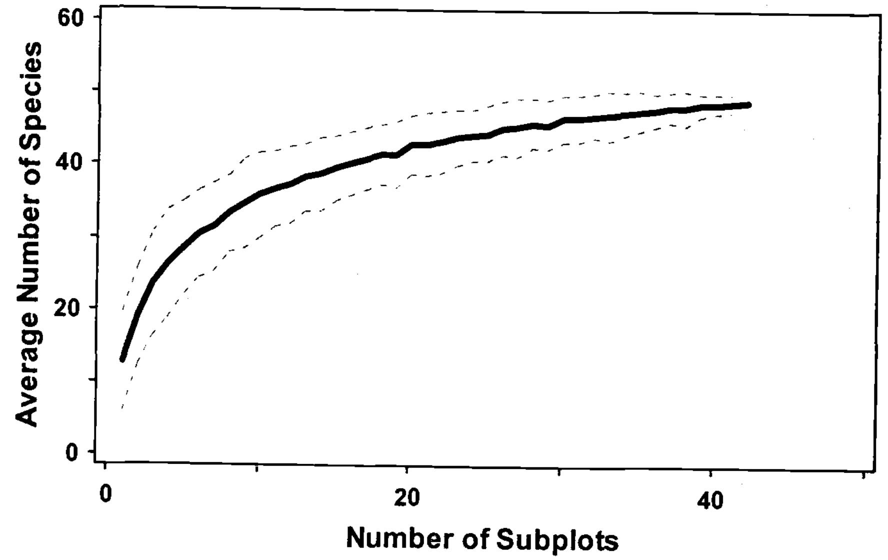

Figure 4.3. Species area/effort curve depicting the average number of species (± 95% confidence intervals) for pooled samples (n=42) collected across the H. J. Andrews Experimental Forest.

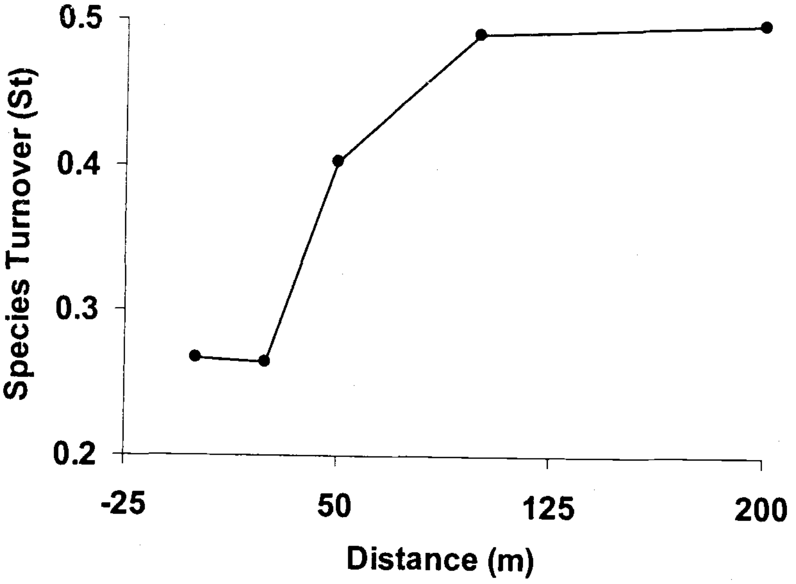

Figure 4.4. Relative species turnover of predator taxa between adjacent sampling points along edge-forest transects.

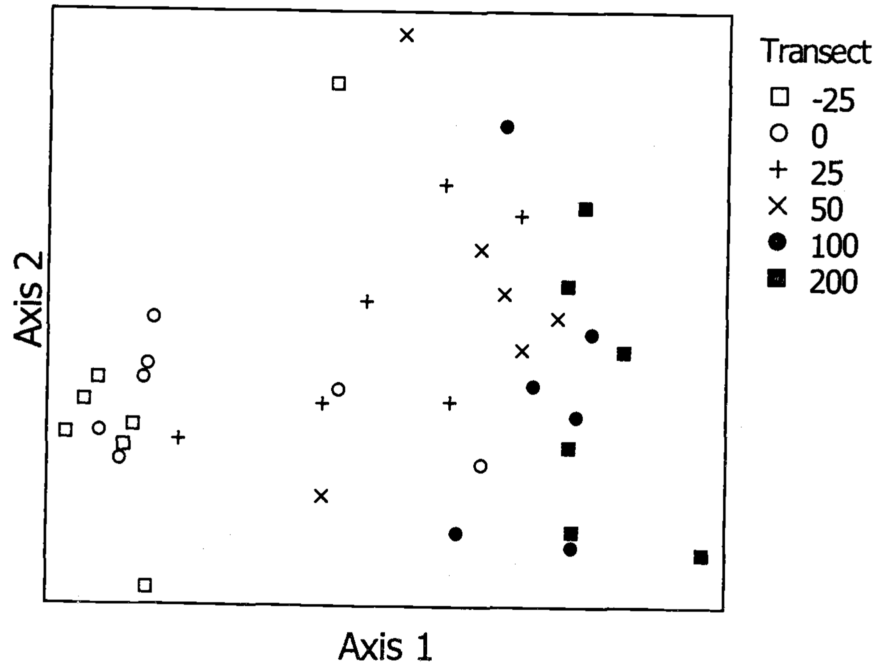

Figure 4.5. Non-metric scaling ordination of 38 sampling locations based on 36 predator taxa collected from replicated edge-forest transects. Axis 1 and 2 explain 63.1% and 25.4% of the total variance respectively. Six distance classes along edge-forest transects are overlayed on sampling points. Rare species (those collected from under 5% of sampling sites) are excluded in this analysis. Four sampling sites (located at 25, 50, 100 and 200 m) were also excluded due to a paucity of species richness.

distance gradient from the forest edge and were characterized by three overall patterns. Sites within clearcuts and at the forest edge clustered to the left of axis 1. Sites at intermediate distances from the forest edge (25 and 50 m) were variable and scattered across axis 1. Sites located at 100 and 200 m clustered to the right of axis 1. Changes in species composition along axis 1 were largely determined by six species (Table 4.2). Each of these species was at least moderately correlated with axis 1 with a correlation coefficient value of greater than 0.4. Three species of spider, *Pardosa dorsuncata* Lowrie and Dondale, *Xysticus montanensis* Keyserling, and *Alopecosa kochi*

Table 4.2. Pearson's correlation coefficients, observed indicator values (IV), and Monte Carlo tests of significance[1] for 3 spiders and 3 carabid beetle species associated with non-metric multidimensional scaling ordination.

Species	Pearson's Correlation r		Observed IV	IV from Monte Carlo test of significance		
	Axis 1	Axis2		Mean	S.Dev	p
Pardosa dorsuncata	0.338	0.762	47.7	26.6	6.72	0.001
Xysticus montanensis	0.225	0.695	46.6	17.5	7.3	0.001
Alopecosa kochi	0.292	0.665	49.9	24.6	8.09	0.009
Pterostichus herculaneus	0.610	-0.469	27.7	24.6	3.32	0.167
Zacotus mathewsii	-0.029	-0.435	33.3	25.3	6.99	0.127
Scaphinotus marginatus	0.289	-0.408	50.9	31.8	9.05	0.028

[1] Monte Carlo tests based on 1000 permutations

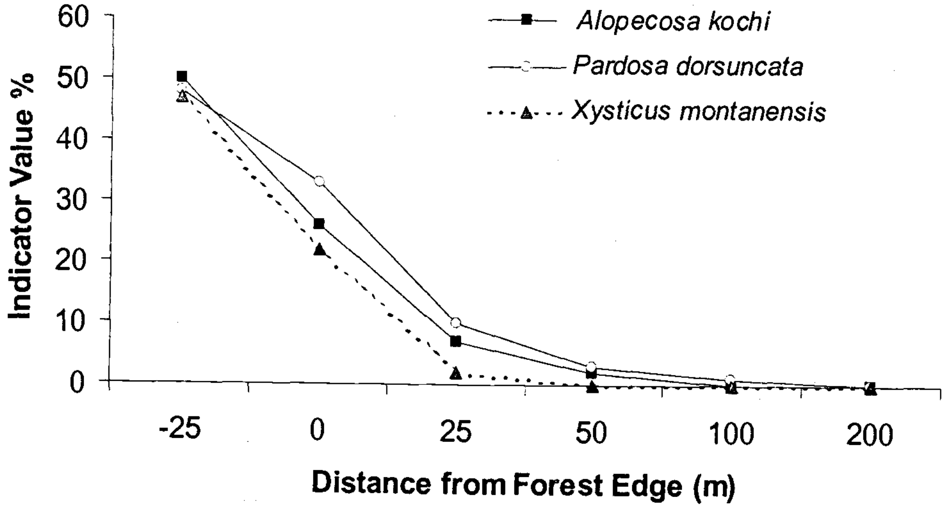

Figure 4.6. Mean indicator values for three spider species at six locations across edge-forest transects

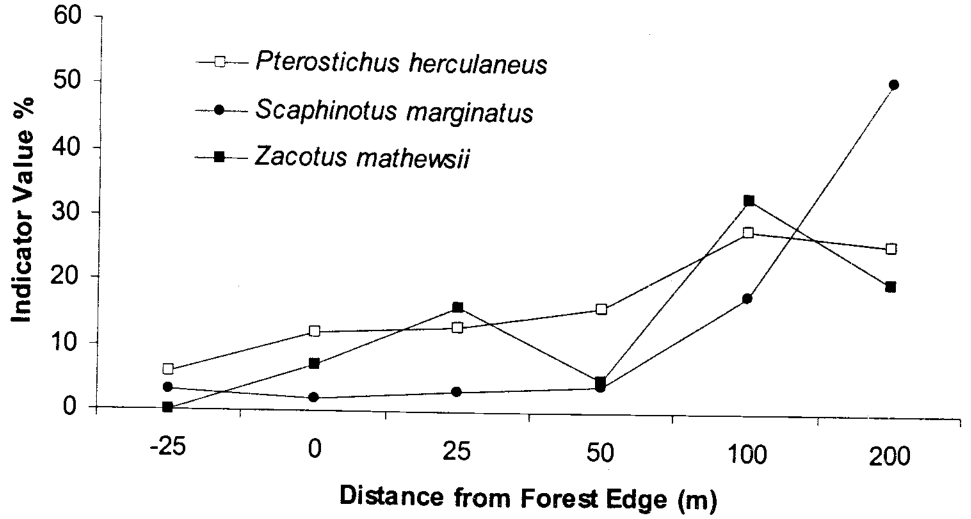

Figure 4.7. Mean indicator values for three carabid beetle spider species at six locations across edge-forest transects.

(Keyserling) were strongly associated with clearcuts and the forest edge but became less abundant as distance increased into the forest (Figure 4.6). Each of these species was a significant indicator of distance along our sampling transects (p<0.01) (Table 4.2). Likewise *Pardosa* spiderlings, and two beetles species, *Amecocerus* sp1 and *Syntomus americanus* (Dejean), were associated with clearcuts and decreased with distance from the edge but were not significant indicators of the distance gradient. In contrast, four species of carabid beetle, *Pterostichus herculaneus* Mannerheim, *Scaphinotus anugusticollis* Mannerheim, *Scaphinotus marginatus* Fischer, and *Zacotus mathewsii* LeConte, were more closely associated with interior forest at distances greater than 50 m from the edge (Figure 4.7). Although each of these species was moderately correlated with axis 1, only *Scaphinotus marginatus* was a significant indicator of distance along the sampling transect (p<0.02) (Table 4.2). Results from Mantel tests showed distance from the edge to be significantly correlated with species composition (r =0.41, p<0.001). Differences in predator species composition observed along axis 2 were largely attributed to 4 sampling points located at low elevations and appeared to be independent of any edge effects along the transect. These four sites clustered together based on small numbers of organisms and the absence of species rather than overall similarity in species composition. When these sites were removed from the original dataset the variance explained by the ordination increased to 63.2% for axis 1 to and decreased to 25.5% for axis 2 further emphasizing the association between axis 1 and distance from the forest edge.

Although predator composition changed with distance from the edge, no differences in patterns of species abundance were observed across the edge-forest gradient (Figure 4.8). When the range of observed species abundances was compared to the four resource partitioning models, observed data were most consistent with the Random Assortment model (Figure 4.9). The range of predator species abundance consistently fell within a single standard deviation of the first 6 ranks predicted by the Random Assortment model. Likewise, the Random Assortment model minimized the absolute deviations between model predictions and observed data (Table 4.3). Observed predator species abundances were more equitable than predicted by the Dominance Preemption hypothesis. Both the Dominance Decay and Random Fraction hypotheses predicted a more equitable division of resources than the observed range of predator species abundances. When resource partitioning models were compared to relative estimates of biomass across species, observed data were again most consistent with the Random Assortment model (Figure 4.10).

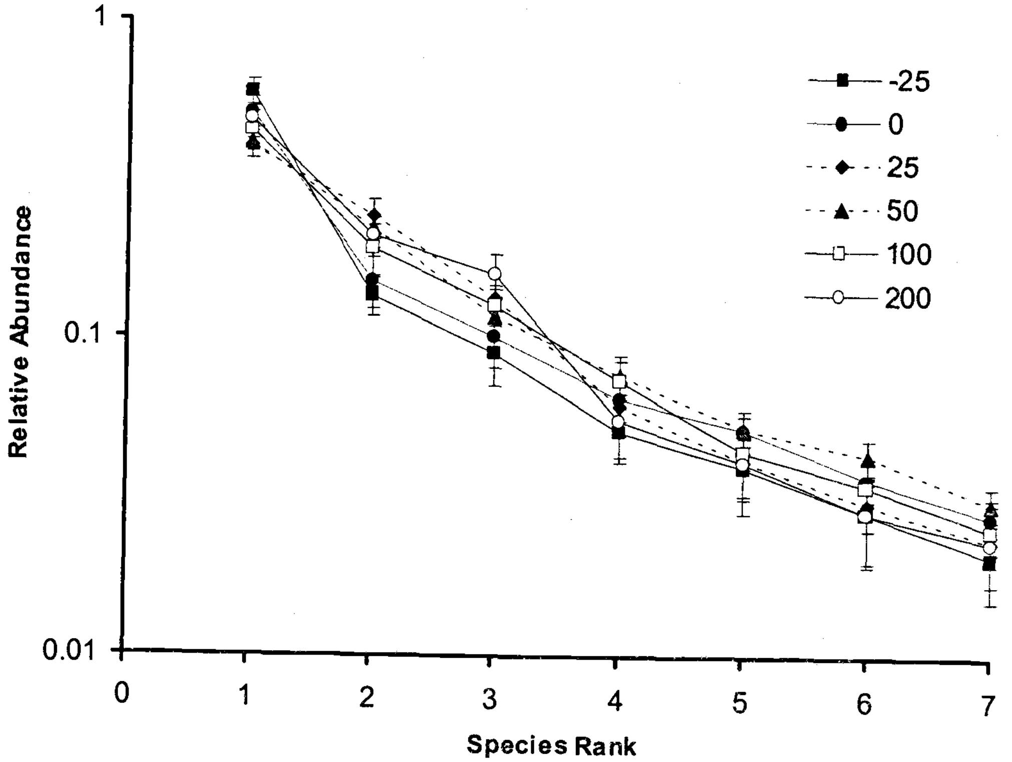

Figure 4.8. Mean species abundance (± 1 standard deviation) for ground predators at six locations across edge-forest transects.

Discussion

Changes in the species composition of ground predators were readily apparent along gradients between clearcuts and old-growth forests. The observed decline in predator species richness as distance from the forest edge increased was consistent with previous work by Didham et al. (1998) in fragmented tropical forests. Didham et al. (1998) concluded that distance from the forest edge, a synthetic variable integrating all microclimatic factors, was a better predictor of species' density than were individual

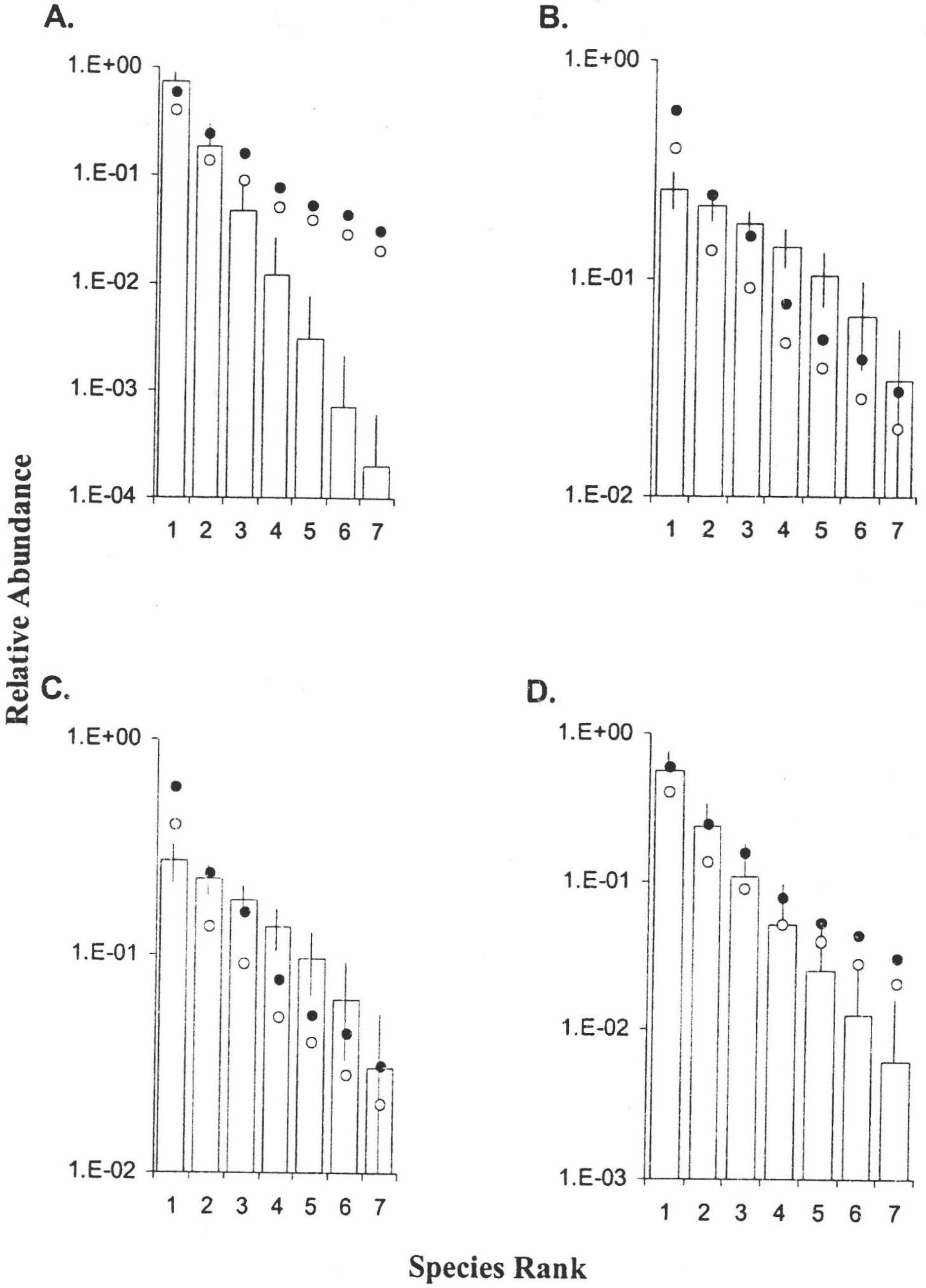

Figure 4.9. Comparisons of the relative numerical abundance of species to predictions of the A) dominance preemption model, B) dominance decay model, C) random fraction model and D) random assortment model. Bars represent mean relative species abundance (± 1 standard deviation) of the seven most dominant species (ranked from most to least abundant). Filled circles represent the upper range of observed data from all transect positions. Open circles represent the lower range of observed data from all transect positions. A model is considered consistent with observed data if model predictions fall within the range of data for the first 6 species ranks.

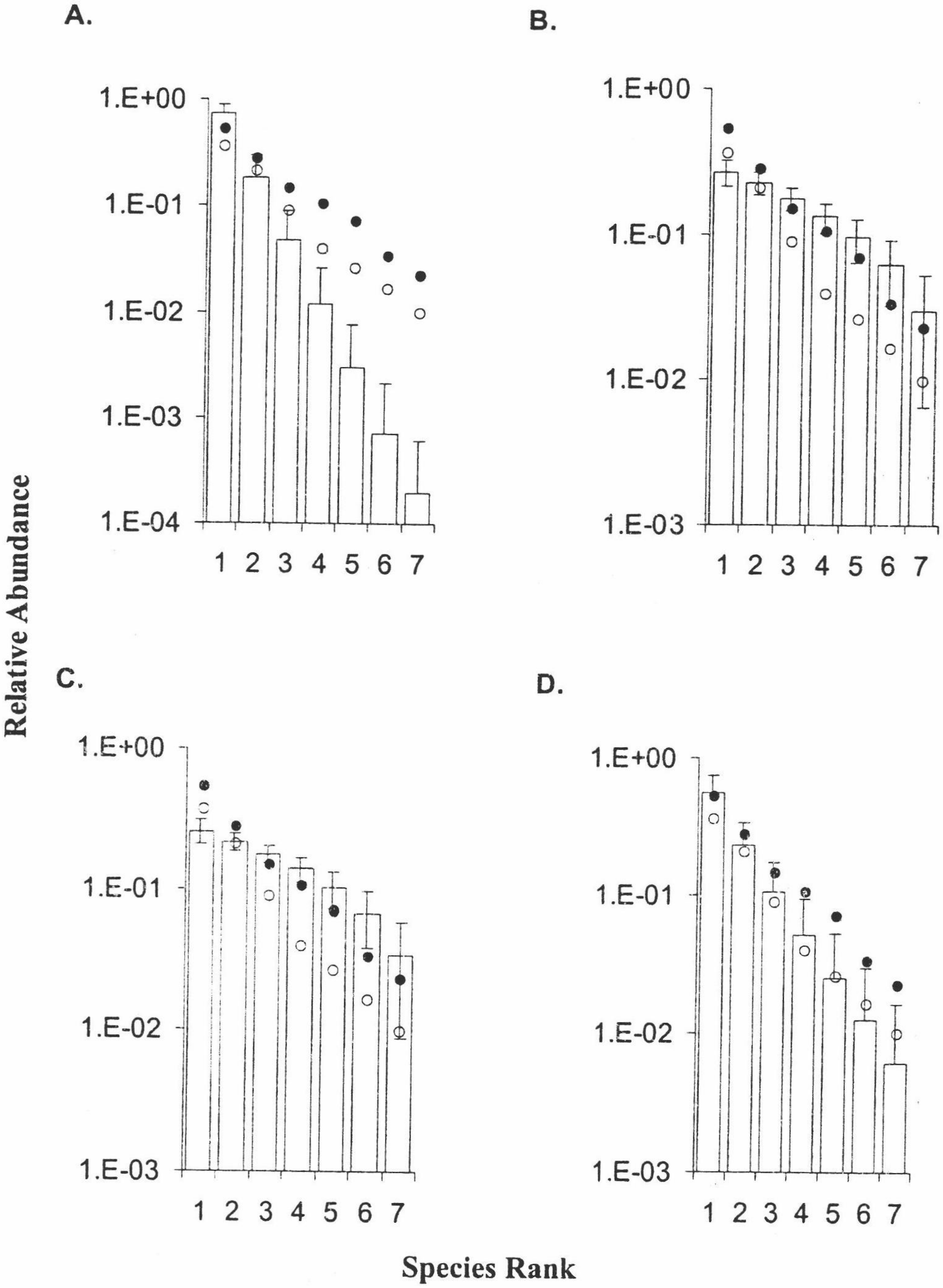

Figure 4.10. Comparisons of the relative biomass of species to predictions of the A) dominance preemption model, B) dominance decay model, C) random fraction model and D) random assortment model. Bars represent mean relative species abundance (± 1 standard deviation) of the seven most dominant species (ranked from most to least abundant). Filled circles represent the upper range of observed data from all transect positions. Open circles represent the lower range of observed data from all transect positions. A model is considered consistent with observed data if model predictions fall within the range of data for the first 6 species ranks.

microclimatic variables. It is likely that microclimatic and physical gradients occurred within our study sites. Factors such as air temperature, soil temperature, and light levels have been shown to decrease as distance from forest edges increases in old-growth Douglas-fir forests within the Pacific Northwest (Chen *et al.* 1995). For example, fluctuations in air temperature were wider between 60 and 120 m from the forest edge. Likewise changes in soil temperature were observed up to 60 m from the forest edge. Total flux in short wave radiation rapidly decreased 30-60 m into interior forest. An increase in relative humidity was observed as distance from the forest edge increased (Chen *et al.* 1995). In addition to microclimatic changes, changes in physical characteristics such as depth of leaf litter layer increase as distance from the forest edge increases in old-growth Douglas-fir forests (Hayes et al. unpublished data). Even factors associated with ecosystem productivity such as nitrogen and available carbon have been shown to change across forest edge gradients (Hayes et al. unpublished data).

Given these changes in physical factors across forest edges, it is not surprising that species composition also changes across forest edges. Taxa such as carabid beetles elicit distinct preferences for temperature, humidity, and light (Lindroth 1945; Lindroth 1969; Thiele 1977). Theile's synthesis of carabid studies suggests that the majority of forest dwelling carabids show affinity for habitat with high humidity and low illumination. The increase in abundance of carabid taxa such as *Scaphinotus* species, *Zacotus mathewsii*, and *Pterostichus* species across the edge forest gradient would be consistent with a behavioral preference for the increased relative humidity and the decreased light levels that reflect edge effects.

The changes I observed in predator species composition were largely defined by species that either increased or decreased in abundance across the forest edge. While in previous studies taxa have been shown to preferentially occupy and utilize edge habitats (Andren and Angelstam 1988; Donovan *et al.* 1997), I did not observe edge-specific responses, where abundance was highest at some intermediate distance across the transect, for most species. Whether an organism capitalizes on forest edges or is subjected to forest edges may be related to the relative scale of the edge effect and the size and dispersal ability of the organism (Kareiva and Wennergren 1995; Roland and Taylor 1997). Ground-dwelling arthropods with low dispersal ability may be overwhelmed by the spatial scale of edge effects and may be unable to respond to the variability associated with the edge. This has important conservation implications for ground-dwelling arthropods and other small-scale dispersers. Because I did not observe any edge specific response, these results suggest that for epigaeic arthropods, forest edges may represent a marginalized transition zone between clearcuts and old-growth forest rather than a novel habitat type. For species that require abiotic conditions associated with old growth forests, edges may effectively reduce available habitat as well as limit movement within "source" patches of remaining old growth forest (Pulliam 1998).

The negative impacts I observed on forest specialist species such as *Scaphinotus marginatus* was consistent with other studies of the impacts of forest harvesting and fragmentation. Niemela *et al.* (1993) reported that mature forest specialists including *Scaphinotus marginatus* disappeared from recently logged areas and were only found in sites that had been regenerating for 27 years. Likewise, my results substantiate the predictions of landscape harvest models that clear-cut harvesting reduces the diversity of old-growth related species under a checkerboard harvesting scenario that maximizes edge (Franklin and Forman 1987). This result is particularly significant given that clear-cut harvesting in this pattern was widely used in forestry within this region until the 1990's.

While these results suggest that forest edges do have significant impact on the species composition of predator communities within as little as 25 m or as much as 100 m, I was not able to detect differences in patterns of species abundance across edge-forest transects. Furthermore, the observed pattern in species abundance across transects was most consistent with the Random Assortment model of resource partitioning. Taken together, these results suggest that community structure of ground-dwelling predators along these edge transects may be consistent with a community that is not at equilibrium, or a 'disturbed' community. Impacts of clear-cutting and fragmentation have been likened to natural disturbances (Lenski 1982) that disrupt competitive exclusion between resource-limited species (Connell 1978). For example, diminished foraging success of a forest dwelling carabid in clearcuts was attributed to negative effects of interspecific competiton with congeneric species (Lenski 1984). Because community structure across forest-edges appears to be consistent with disturbed or unsaturated communities, the long-term impacts of edges on species interactions may be highly uncertain. Perhaps more disconcerting is that community structure of interior forest sites was consistent with non-equilibrium or disturbed communities which further stresses the risk of edge-effects to interior specialists. Given that disturbed communities may be more susceptable to the invasion and establishment of exotic species , forest edge-effects may put specialist species in a position of double jeopardy where they face habitat loss and introduced competitive effects simultaneously.

The use of species abundance models as indicators of disturbance has been criticized because they yield little information as to the magnitude or extent of disturbance (Watt 1998). Furthermore, results of other studies using species-abundance models as indicators of disturbance in fragmented forests have been conflicting. For example, in contrast to my findings, Hill *et al.* (1995) suggested disturbed communities correspond to the log-series while unlogged communities are reflected by the log-normal distribution. My results may be consistent with criticisms that species abundance models are not universal indicators of disturbance (Nummelin 1998). However, both Hill *et al.* (1995) and Nummelin (1998) interpreted resource-partitioning through statistical-based partitioning models and are subject to the methodological and interpretational pitfalls mentioned previously. This study directly addressed the extent of edges caused by clearcuts, and suggests a possible mechanism by which edge-effects alter predator community structure. Furthermore, I found predator community structure to be consistent with a model of random assortment regardless whether abundance is expressed as numerical abundance or biomass. This suggests that the patterns I observed are robust to artifacts of using species abundance patterns to measure resource-partitioning (Pagel *et al.* 1991).

Chapter 5

CONCLUSIONS

The goal of this study was to determine the extent of edge-effects resulting from clearcut harvesting on the distribution and community structure of epigaeic arthropods. From this work, I suggest that edge-effects on species composition extend up to 100 m into old-growth Douglas-fir forests (Chapter 2). Likewise, I have identified individual species that are affected by forest edges and quantified their responses (Chapter 2).

This information is critical to develop the generalities of ecological theory into applied tools for land-managers and conservation biologists alike. For example much of what we know regarding fragmentation stems from 'patch occupancy' metapopulation models (Hanski and Thomas 1994; Tilman *et al.* 1994). Such models treat habitat remnants as homogeneous in terms of habitat quality, and thus ignore within patch effects such as forest edges. Clearly such an assumption is violated in real forest fragments. It is also apparent that not all species are negatively affected by edges (Chapter 2). As a consequence, models of fragmentation must include species-specific information within habitat patches if they are ever to be applied to real-life scenarios. Taken together with predictions from existing models of fragmentation, my results show that the effective size of habitat patches may be smaller than what is represented on survey maps or LANDSAT images. As a result, extinctions predicted from landscape fragmentation models may be even more frequent when the effective size of fragments is incorporated.

Clearcut harvesting within the Pacific Northwest has undoubtedly increased the amount of forest edge on the landscape (Franklin and Forman 1987; Spies *et al.* 1994). However, determining the likelihood of extinctions resulting from forest harvest from the data I have presented may also be premature. Edge effects are geometrically confounded with the size of forest remnants. As a result, size of fragments and their distribution on the landscape also need to be considered (i.e. metapopulation models cannot be ignored). The connection between the within-patch and between-patch effects of fragmentation highlight the need for species specific information on movement within and between patches. However, given the large-scale on which current forest harvesting operations occur (10's of ha), it is doubtful that epigaeic arthropods would be able to compensate through dispersal.

Interestingly, I found that while species composition clearly changed across forest edges, community structure of the dominant functional group, arthropod predators, appeared remarkably consistent regardless of distance from the forest edge. Furthermore, the community structure of predator taxa was consistent with disturbed or unsaturated communities (Chapter 4). These results imply that predators as whole are not prey-limited across this gradient. This conclusion is even more robust given that temporal variation in predator activity across a season was small (Chapter 3). Given that disturbed communities may be more variable in composition (Didham *et al.* 1998) and may be more susceptible to invasion by exotic species, it follows that the long-term impacts of forest edges may be highly stochastic. Such a daunting prospect again highlights the need for detailed information regarding life-history of these organisms and their specific roles within the community and ecosystem.

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APPENDIX

List of predator taxa collected at the H. J. Andrews Experimental Forest between 22-May-1998 and 31-July-1998.

Family	Species	Author	Total Collected
Antrodiaetidae	*Antrodiaetus (spp.)*		128
Cantharidae	*Podabrus conspiratus*	Fall	2
Cantharidae	*Podabrus piniphilus*	(Eschscholtz)	10
Carabidae	*Agonum spp.*		1
Carabidae	*Carabus taedatus*	Fabricius	101
Carabidae	*Cychrus tuberculatus*	Harris	9
Carabidae	*Lebia perita*	Casey	2
Carabidae	*Leistus ferruginosus*	Mannerheim	1
Carabidae	*Notiophilus sylvaticus*	Eschscholtz	21
Carabidae	*Omus dejeani*	Reiche	17
Carabidae	*Promecognathus crassus*	LeConte	65
Carabidae	*Pterostichus (spp.)*		9
Carabidae	*Pterostichus amethystinus*	Mannerheim	3
Carabidae	*Pterostichus campbelli*	Bousquet	1
Carabidae	*Pterostichus cast-tuberc complex*		4
Carabidae	*Pterostichus castaneus*	(Dejean)	10
Carabidae	*Pterostichus herculaneus*	Mannerheim	1910
Carabidae	*Pterostichus inanis*	Horn	58
Carabidae	*Pterostichus inopinus*	(Casey)	38
Carabidae	*Pterostichus lama*	(Menetries)	125
Carabidae	*Pterostichus new spp.*	Labonte	10
Carabidae	*Scaphinotus angulatus*	(Harris)	36
Carabidae	*Scaphinotus angusticollis*	(Mannerheim)	418
Carabidae	*Scaphinotus marginatus*	(Fischer von Waldheim)	244
Carabidae	*Scaphinotus rugiceps*	(Horn)	178
Carabidae	*Syntomus americanus*	(Dejean)	3
Carabidae	*Trachypachus holmbergi*	Mannerheim	14
Carabidae	*Zacotus matthewsii*	LeConte	201
Histeridae	*Saprinus lugens*	Erichson	1
Lampyridae	*Ellychnia hatchi*	Fender	9
Lampyridae	*Phausis skelleyi*	Fender	4
Lycidae	*Dictyopterus simplicipes*	Mannerheim	2
Lycosidae	*Alopecosa kochi*	(Keyserling)	268
Lycosidae	*Pardosa (immature)*		15
Lycosidae	*Pardosa californica*	Keyserling	144
Lycosidae	*Pardosa dorsuncata*	Lowrie & Dondale	1791
Melyridae	*Amecocerus (spp.)*		32
Platypodidae	*Prostomis mandibularis*	(Fabricius)	2

APPENDIX (CONTINUED)

Scydmaenidae	*Eutheia (spp)*		1
Scydmaenidae	*Eutheia morae*	Marsh	4
Staphylinidae	*Ontholestes cingulatus*	(Gravenhorst)	1
Staphylinidae	*Staphylinus pleuralis*	LeConte	336
Staphylinidae	*Staphylinus saphyrinus*	LeConte	76
Thomisidae	*Xysticus (immature)*		86
Thomisidae	*Xysticus locuples*	Keyserling	1
Thomisidae	*Xysticus montanensis*	Keyserling	57
Thomisidae	*Xysticus pretiosus*	Gertsch	456
Throscidae	*Aulonothroscus validus*	(LeConte)	7
Vejovidae	*Uroctonus mordax*	Thorell	5