

AN ABSTRACT OF THE DISSERTATION OF

Jessica J. Rykken for the degree of Doctor of Philosophy in Entomology presented on June 9, 2004.

Title: Relationships Between Forest-floor Invertebrate Distribution, Movement, and Microclimate Under Alternative Riparian Management Practices

Abstract approved: *Redacted for Privacy*

Andrew R. Moldenke

Headwater streams and their riparian zones are a common, yet poorly understood, component of Pacific Northwest landscapes. I sought to describe the ecological significance of headwater stream riparian zones as habitat for forest-floor invertebrate communities, and to assess how alternative management strategies for riparian zones may impact these communities. I compared community composition of forest-floor invertebrates at five distances along 70 m trans-riparian (stream edge to upslope) gradients in three treatments: mature forests; clearcuts; and across riparian buffers of ~30 m width. In the buffer treatments, I looked for evidence of microclimatic edge effects, and also biological edge effects, as characterized by species distribution and movement patterns across the forest-clearcut boundary. Invertebrates were collected in pitfall traps, in five replicate blocks of three treatments each, in the Willamette National Forest, OR. Air and soil temperature, and relative humidity were measured at a subset of pitfall locations at each site. A pitfall grid was installed at one riparian buffer site for a mark-release-recapture study to record carabid beetle and lycosid spider movements across the buffer edge.

Ordination revealed a distinct "riparian" invertebrate community within 1 m of the stream edge in mature forest treatments, which was strongly related to a cool, humid microclimate. The stream appeared to influence microclimate at least 20 m upslope in the mature forest treatments. Invertebrate community composition in buffer treatments was far more similar to that of mature forests than was that of clearcuts, a pattern mirrored by microclimate. Microclimatic edge effects were not evident in the buffer, suggesting that the stream's cool, humid influence on microclimate may be modifying any warm, drying effects coming in from the forest-clearcut edge. While biological edge effects were not clear for invertebrate communities, individual species showed various responses to the buffer edge, depending on their habitat affinities and mobility. These results suggest that invertebrate distributions are strongly associated with microclimate, and that

riparian buffers of ~30 m width provide suitable habitat for many forest species. However, buffer edges may serve as barriers to dispersal for some forest interior species, or be permeable to invasion by open-habitat species, with possible consequences for long-term population and community dynamics within the buffer.

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**Relationships Between Forest-floor Invertebrate Distribution, Movement, and Microclimate
Under Alternative Riparian Management Practices**

by
Jessica J. Rykken

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RELATIONSHIPS BETWEEN FOREST-FLOOR INVERTEBRATE DISTRIBUTION, MOVEMENT, AND MICROCLIMATE UNDER ALTERNATIVE RIPARIAN MANAGEMENT PRACTICES

CHAPTER 1

INTRODUCTION

Riparian ecotones represent dynamic, diverse, ecologically complex interfaces, through which energy flows both latitudinally, between aquatic and terrestrial systems, and longitudinally, along dendritic watershed networks (Vannote et al. 1980, Naiman and Decamps 1997, Nakano and Murakami 2001). World-wide, research has documented the functional importance of riparian zones in providing shade and allochthonous input to streams (Vannote et al. 1980), having high levels of productivity, filtering nutrients and stabilizing stream banks (Naiman and Decamps 1997), and providing a mosaic of habitats for a high diversity or distinctive species composition of plants, vertebrates, and invertebrates (Doyle 1990, Lock and Naiman 1998, Pollock 1998, Brenner 2000, Antvogel and Bonn 2001, LaBonte 2002). Despite their ecological importance in the landscape, riparian zones are extremely susceptible to human-caused disturbance such as road building, altered flood regimes from dam building, introduction of exotic species, and forest fragmentation (Naiman et al. 1993, Gregory 1997, Naiman and Decamps 1997).

Douglas-fir forests of the Pacific Northwest comprise a landscape that is highly dissected by stream networks, and also is fragmented from intensive forest harvesting that has occurred over the last century. Headwater streams make up the highest density of streams in these forested watersheds, yet have received the least protection from the effects of forest fragmentation. Traditionally, their small size, and the absence of game fish, rendered headwater streams all but invisible in forest management plans. However, over the last decade, with the growing realization that headwater conditions can affect downstream habitat, and that riparian zones may provide critical habitat or corridors for terrestrial organisms, headwater streams and their riparian zones have been included in riparian management strategies on federal (USDA and USDI 1994) and state lands (Young 2000). One common strategy for stream and riparian protection has been the preservation of fixed-width forested "buffers" along many headwater streams in the Pacific Northwest. Currently on federal lands, riparian buffer widths based on "site potential tree height" serve as interim guidelines while watershed-scale aquatic conservation strategies are being implemented (Tuchman et al. 1996).

From a landscape ecology perspective, the implementation of riparian buffers along headwater streams represents the superimposition of a human-created ecotone (i.e., a forest fragment edge) onto a natural ecotone (i.e., the riparian zone). The simultaneous effects of riparian- and edge-related gradients at such a compressed scale will likely have unique interactions that may be difficult to predict. In upland systems, research on forest fragmentation has identified fragment size, isolation, shape, connectivity, and edge characteristics to be key factors affecting species responses (Saunders et al. 1991, Didham 1997). Microclimatic edge effects of 50 m or more have been documented in forest fragments (Chen et al. 1995, Murcia 1995), and direct biological effects (i.e., altered species distributions) have been measured as much as 100 m into the forest interior (Didham et al. 1998a, Work 2000). Forest fragmentation theory and evidence thus suggest that elongate, narrow riparian buffers may be comprised entirely of “edge” habitat, with virtually no unaltered interior habitat remaining. If this is the case, then riparian buffers may prove ineffective at providing habitat for many riparian- and/or forest-associated species.

The overall intent of this study was two-fold: (1) to assess the ecological “uniqueness” of headwater streams and their riparian zones in Douglas-fir forests, by exploring relationships between forest-floor invertebrate communities, microclimate, and microhabitat across these ecotones; and (2) to compare relationships between invertebrate distributions, movement, microclimate, and microhabitat under alternative riparian management treatments, including riparian buffers. I chose to focus on forest-floor invertebrates in this study because they are diverse and abundant, and perform many essential functions in forest ecosystem processes (e.g., decomposition, herbivory, nutrient cycling). Additionally, forest-floor invertebrates are relatively easy to sample, and they encompass a range of mobility, sensitivity to environmental gradients, and life history requirements. For all of these reasons, invertebrates have been used extensively in studies looking at the effects of forest fragmentation (Niemi et al. 1993a, Didham 1997, Work 2000), and in other ecological inventory and monitoring studies (Kremen 1992, Kremen et al. 1993, Pearson 1994, Rykken et al. 1997, Allegro and Sciaky 2003).

In Chapter 2, I look at patterns in forest-floor invertebrate community composition across three riparian management treatments: mature riparian forest; ~30 m-wide riparian buffer; and clearcut harvest to the stream edge with minimal or no forest buffer. First, I describe community composition in mature, forested riparian ecotones, and determine whether there is a “riparian” fauna associated with headwater streams that is distinct from upslope fauna. I then determine whether riparian forest buffers of ~30 m width are more effective than minimal or no buffers at preserving the forest invertebrate community associated with headwater streams. Lastly, I look

for evidence of biological “edge effects” on both invertebrate community composition and individual species distributions in riparian buffers.

Chapter 3 focuses on microclimate (air temperature, soil temperature, relative humidity), but looks at similar patterns as those in Chapter 2. Specifically, I characterize microclimatic gradients in mature riparian forests to determine the magnitude and extent of the stream’s influence on upslope microclimate. I then look for forest management effects on microclimate gradients, and characterize and quantify any edge effects on microclimate in the riparian buffer treatment. By looking at microclimate in mature forest and buffer treatments simultaneously, I hope to differentiate between gradients influenced by the stream (i.e., stream effects) versus those influenced by the forest edge (i.e., edge effects).

Biological edge effects, as characterized by individual species distributions and movements across the buffer edge, are the focus of Chapter 4. In this chapter, I use a spatial analysis technique to characterize the habitat relationships of several beetle and spider taxa, and I use mark-release-recapture methods to determine the mobility and movement patterns of these taxa. Using these data, I determine whether a species’ response to the forest edge (i.e., the permeability of the edge) can be characterized or predicted by considering both the habitat affinity of a species, and its mobility. Such information will be helpful in determining the consequences of fragment isolation for forest-associated species, and the “invasibility” of fragments by open-habitat associated species. I conclude with a summary of my results in Chapter 5, and discuss these in the broader context of riparian forest management.

CHAPTER 2

FOREST-FLOOR INVERTEBRATE DISTRIBUTIONS ACROSS HEADWATER STREAM RIPARIAN ECOTONES AND THEIR RESPONSE TO ALTERNATIVE FOREST MANAGEMENT PRACTICES

INTRODUCTION

Riparian zones are considered to be one of the most biologically diverse and ecologically complex components of Douglas-fir forests in the Pacific Northwest (Naiman et al. 1998, Pollock 1998). As ecotones between aquatic and upland terrestrial systems, riparian zones typically encompass steep environmental gradients, and are prone to frequent disturbance events such as flooding and debris flows. Consequently, riparian zones often comprise a heterogeneous mosaic of microhabitats, where biological diversity is assumed to be higher than in the surrounding upslope forests (Gregory et al. 1991, Naiman et al. 1993, Naiman and Decamps 1997). Indeed, such patterns of high diversity or distinctive species composition in riparian ecotones have been documented in plants (Nilsson et al. 1989, Naiman et al. 1998, Pabst and Spies 1998, Pollock et al. 1998), among vertebrates (Raedeke 1988, Lock and Naiman 1998, Doyle 1990, McComb et al. 1993), and invertebrates (Moring and Stewart 1994, Deharveng and Lek 1995, Andersen 1997, Hering and Plachter 1997, Brenner 2000, Antvogel and Bonn 2001, LaBonte 2002). The exchange of invertebrate biomass between terrestrial and aquatic foodwebs also has been documented as an important ecological process in riparian ecotones (Kawaguchi and Nakano 2001, Nakano and Murakami 2001). While most models of riparian diversity have been developed on mid- to high-order streams and rivers, headwater streams (i.e., 1st or 2nd order), which comprise upwards of 70% of the lotic network within a watershed (Meyer and Wallace 2001), have received little attention. Whether or not riparian zones associated with these small streams exhibit similar patterns of high diversity or distinctive species composition has not been well-documented.

In the heavily harvested landscapes of Pacific Northwest forests, riparian management strategies have reflected this gap in our knowledge of headwater stream and riparian ecology. Beginning in the mid-1970's, the degree of protection afforded a stream, in the form of a forested riparian "buffer," was determined by stream size and the presence of game fish (i.e., salmonids). Such buffers were expected to provide benefits to the aquatic biota, by shading the water and stabilizing the stream banks (Gregory 1997). In contrast, non-fish-bearing headwater streams received little to no protection at all. With the growing realization that headwater conditions can affect downstream habitat, and that riparian buffers not only serve to protect fish habitat, but also

may provide important breeding or foraging habitat and dispersal corridors for terrestrial organisms, new regulations regarding riparian buffers and reserves along streams, including non-fish-bearing headwaters, are being developed at both state and federal levels (USDA and USDI 1994, Young 2000, Forestry 2003). On federal lands in the Pacific Northwest, aquatic conservation strategies are being applied individually to entire watersheds, with interim guidelines for riparian buffer widths of one site potential tree-height (a minimum of ~30 m) along even ephemeral streams. In western Oregon, state riparian zone management guidelines for headwater streams call for leaving 6 m buffers within wider restricted harvest zones. In the region's highly dendritic landscapes, even modest riparian buffers have the potential to take a large amount of land out of timber production, and not surprisingly, the new riparian management strategies have raised some concern among forest managers.

Intensive harvesting practices have fragmented much of the forested landscape in the Pacific Northwest over the last century (Harris 1984). Although riparian management strategies have been implemented for only the last 30-40 years (on larger streams), riparian buffers may now represent one of the few intact forest remnants in a rotating patchwork of clearcuts and regenerating stands. As linear forest fragments, riparian buffers may provide critical habitat or refugia for forest species, or serve as connecting corridors between larger mature forest fragments (Harris 1984, Saunders et al. 1991, de Lima and Gascon 1999). However, the narrow, elongate shape and high edge-to-interior ratio characteristic of riparian buffers also may make them subject to a suite of biotic and abiotic "edge effects," potentially altering their species composition and diversity. Indeed, research documenting microclimatic edge effects penetrating up to 240 m into the forest (Chen et al. 1995), and direct biological effects as much as 100 m into the forest (Murcia 1995, Didham et al. 1998a, Work 2000) suggest that riparian buffers of 30-75 m each side of the stream (the range of widths presently implemented for non-fish-bearing streams under the federal Northwest Forest Plan) may comprise essentially all "edge" habitat. For forest species negatively affected by edge effects such as altered microclimate, riparian buffers could represent "sink" habitats, reducing population success at the landscape level (Pulliam and Danielson 1991).

As the region's scientists and managers work toward implementing effective and sustainable management strategies, there is clearly a need to learn more about the ecological significance of headwater stream riparian zones as habitat for forest species, and how forest diversity and function may be affected by various riparian management practices. It may be, for instance, that a minimal shrub buffer in the riparian zone along a headwater stream functionally protects stream and riparian terrestrial biota in a harvested unit. If this is the case, then it might

be argued that the economic revenue (from harvestable timber) lost by implementing forested buffers on headwater streams outweighs any increased ecological benefit for terrestrial biota. Alternatively, current riparian guidelines that call for buffers or reserves as one component of a management strategy may be critical to effectively maintaining the ecological integrity of headwater riparian systems.

This study addresses the effects of three alternative riparian management strategies on both microclimate and the distribution of forest-floor invertebrates along a gradient from stream edge, through the riparian zone, and into the adjacent upslope forest. Changes in microclimate related to riparian-upslope gradients and edge effects associated with forest fragmentation have been documented in regional studies (Chen et al. 1995, Brosofske et al. 1997), but the essential link to how these changes may affect forest and/or riparian biota remains weak. Forest-floor invertebrates are a critical group to consider in riparian systems because of their sheer diversity and abundance, as well as their functional importance in forest ecosystem processes (e.g., decomposition, herbivory, prey source, nutrient cycling). A range of mobility and sensitivity to environmental gradients (such as microclimate) among taxa also makes invertebrates ideal for studying patterns of habitat partitioning, dispersal between habitats, and community responses to human-caused disturbances such as fragmentation (Coulson and Butterfield 1985, Kremen et al. 1993, Niemalä et al. 1993a, Moring and Stewart 1994, Didham et al. 1998a). For these reasons, invertebrates have been used worldwide as biological indicators in ecological inventory and monitoring studies (McIver et al. 1990, Kremen 1992, Niemalä et al. 1993b, Pearson 1994, Rykken et al. 1997, Allegro and Sciaky 2003, Schowalter et al. 2003).

I compared invertebrate community composition and microenvironment relationships across three management treatments on headwater streams in western Oregon: old-growth forest with an intact riparian zone (control); preservation of a 30 m forested buffer on each side of the stream with clearcut harvest upslope; clearcut harvest with a minimal (i.e., a few scattered trees or only shrubs) or no buffer adjacent to the stream. Specifically, I had three objectives concerning riparian pattern, riparian management, and edge effects in low to mid-elevation forests of the western Cascade Range: to characterize "riparian" invertebrate communities associated with headwater streams in unmanaged (control) forests; to determine whether riparian forest buffers of 30 m width were more effective than minimal or no buffers at preserving the forest invertebrate community associated with headwater streams; and to assess the influence of "edge effects" on both the invertebrate community composition and individual species of riparian forest buffers. For all of these objectives, I looked for relationships between community composition, microclimate, and/or microhabitat variables to help explain observed distribution patterns.

METHODS

Regional setting

Study sites were in the Sweet Home Ranger District of the Willamette National Forest, on the western slope of the Cascade Range in Oregon, USA (Figure 2.1). The regional climate can be broadly characterized as having wet, mild winters—with snow accumulation at higher elevations—and warm, dry summers (Franklin and Dyrness 1988). Approximately 90% of the annual precipitation falls in winter (Harris 1984). Forest canopies at mid-elevations are dominated by Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), western redcedar (*Thuja plicata* Donn) and, at higher elevations, by Pacific silver fir (*Abies amabilis* (Dougl.) Forbes) (Franklin and Dyrness 1988). All sites within this study fell within the western hemlock zone, as classified by Franklin and Dyrness (1988). This vegetation zone comprises the majority of forest lands in western Oregon, and is economically significant for its timber production (Franklin and Dyrness 1988). Shrub and herb communities within these forests vary with elevation, soils, moisture availability, and other variables, but commonly include vine maple (*Acer circinatum* Pursh), rhododendron (*Rhododendron macrophyllum* G. Don), red alder (*Alnus rubra* Bong.), Oregon-grape (*Berberis nervosa* Pursh), salal (*Gaultheria shallon* Pursh), and sword fern (*Polystichum munitum* (Kaulf.) Presl).

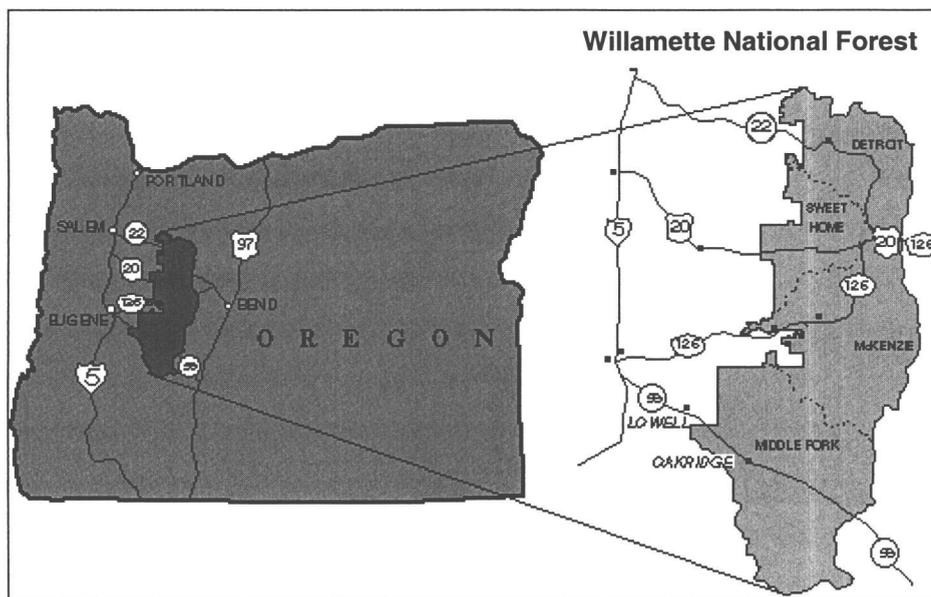


Figure 2.1 Location of study area (Sweet Home Ranger District) in the Willamette National Forest on the western slopes of the Cascade Range of Oregon, USA.

Site selection

I selected 15 first- or second-order headwater stream sites in low- to mid-elevation drainages (Table 2.1). Sites were divided among three treatment types: (1) old-growth forest on either side of the stream with contiguous forest upslope (control); (2) forested riparian buffer of approximately 30 m width on either side of the stream with clearcut harvest upslope; (3) clearcut harvest with minimal to no tree retention in the riparian zone. I first identified potential riparian buffer sites from aerial photos, and field-checked those sites with riparian buffers along headwater streams that were ≥ 25 m width (on either side of the stream) and ≥ 200 m long. I used all five riparian buffer sites that met these criteria. One mature forested site and one clearcut site was matched with each riparian buffer site to form a total of five replicate blocks with three treatments each. Because sites were not randomly selected, all inferences are limited to the actual sites considered in this study. Sites within a block were located within 4 km of each other, and in four blocks, two of the three treatments were located on the same stream. Each of the five blocks was located within a different sub-drainage of the district; three of these blocks were at higher elevations (1000-1268 m) and two blocks were at lower elevations (415-610 m). Forested control sites and forested portions of the buffer sites had never been harvested, with the exception of a light thinning upslope in the control site of the 2G block. Clearcuts had been harvested between 5 and 22 years previously, were burned 0-3 years post-harvest, and then replanted within a year after burning. All clearcut sites were in early stages of succession, with no developed canopy.

Sampling design

At each site, two 70 m sampling transects were oriented perpendicular to the stream (Fig. 2.2). Transects were offset from each other by at least 10 m, and located approximately in the middle of the harvested or forested unit, a minimum of 100 m from the upstream/downstream unit boundaries. At three sites, the transect length was shortened to 50-60 m in order to locate samples within 50 m of the upslope harvest unit boundary or from another headwater stream. Where two sites within a block occurred on the same stream, site transects were located ≥ 250 m apart.

Along each transect, I installed a pair of pitfall traps at each of five distances from the stream: 1, 5, 10, 20, and 50-70 m. Within a pair, traps were located approximately 10 m apart. Traps at different distances were offset on either side of the transect (Fig. 2.2) so that every trap was located at least 10 m from all other traps. With this configuration, the traps at 1-20 m from the stream all lay within the forest in the buffer treatment, and the traps at 50-70 m lay in the adjacent clearcut. At three sites, the dimensions of the forest or harvest unit on one side of the

Table 2.1. Site locations, physical characteristics, and management history.

Block	Treatment	Latitude	Longitude	Elevation (m)	Stream aspect	Avg. stream width (m)	Avg. buffer* width (m)	Harvest unit area (ha)	Harvest date(s)
2G	Buffer	N 44°20' 00.28"	W 122°17' 34.73"	1146	NW	2.9	26.3	10.9	1995
2G	Clearcut	N 44°19' 33.88"	W 122°15' 33.66"	1268	NW	1.2		8.5	1993
2G	Forest	N 44°21' 01.60"	W 122°18' 14.09"	1146	W	3.5			
BP	Buffer	N 44°24' 30.44"	W 122°23' 03.74"	512	SE	1.7	29.8	4.9	1994
BP	Clearcut	N 44°24' 05.70"	W 122°22' 43.05"	415	W	1.5		7.3	1989
BP	Forest	N 44°24' 05.43"	W 122°22' 29.59"	439	W	2.1			
MM	Buffer	N 44°27' 21.99"	W 122°17' 21.31"	1000	N	3.8	29.8	16.2	1994
MM	Clearcut	N 44°27' 45.34"	W 122°15' 34.90"	1097	SE	2.4		12.6	1978, 1995
MM	Forest	N 44°27' 13.95"	W 122°17' 12.51"	1097	NW	2.5			
SP	Buffer	N 44°33' 45.12"	W 122°10' 01.90"	1122	NE	1.5	28.6	5.3	1994
SP	Clearcut	N 44°33' 41.30"	W 122°09' 26.29"	1073	N	2.6		9.7	1986, 1999
SP	Forest	N 44°33' 51.80"	W 122°09' 46.00"	1073	E	3.4			
TC	Buffer	N 44°24' 47.17"	W 122°15' 43.19"	561	NW	5.1	34.3	19.0	1994
TC	Clearcut	N 44°24' 26.89"	W 122°16' 02.84"	561	W	1.2		14.6	1989
TC	Forest	N 44°24' 39.24"	W 122°15' 27.68"	610	W	3.6			

*Average buffer width on either side of the stream

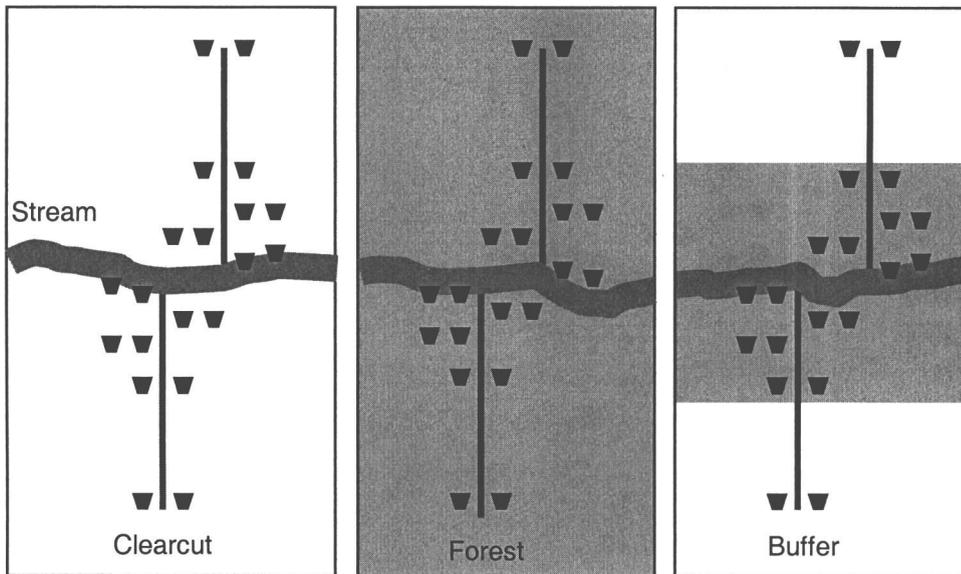


Figure 2.2 Pitfall trapping design on three riparian management treatments. Gray represents forest, white represents harvested area.

stream could not accommodate a transect of 50-70 m length, and in this case, all four traps at 50-70 m from the stream were located on the opposite transect. In all cases, a total of 20 pitfall traps were positioned at each site, divided equally among five distances from the stream.

Invertebrate sampling

I sampled invertebrates with plastic pitfall traps measuring 11 cm diameter at the mouth, and 13.5 cm deep (a standard quart-sized tub). I dug each trap into the soil, so that the mouth was flush with the surface of the ground. Inside each trap, I placed a smaller (5 cm deep) plastic cup containing equal parts water and propylene glycol (pet-safe antifreeze) to serve as a preservative for trapped invertebrates. Using this method, I could fill and empty the smaller interior cup during each sampling period, without dislodging the outer trap and thereby causing unnecessary disturbance to the soil. In an effort to exclude small vertebrates (i.e., small mammals, amphibians) from the traps, as well as keep nimbler invertebrates inside the traps once caught, I fit an aluminum funnel with a 2-3 cm opening at the bottom into the top of the trap. Each pitfall trap was covered with a flat aluminum roof (15 x 15 cm), and supported by 3 nails to keep out rain and organic debris, while allowing invertebrates access.

Six invertebrate sampling events occurred between August, 2000 and July, 2002 (Table 2.2). During the May/June, 2001 sampling period, snow prevented me from reaching the MM block. With one exception, each sampling event was approximately 14 days long. Between sampling events, a tight-fitting lid closed the traps.

Table 2.2 Invertebrate pitfall trapping dates between 2000 and 2002.

Range of trapping dates (to reach all blocks)	Duration of each sample (days per block)
16 Aug-18 Sep, 2000	23-27
18 May-7 Jun, 2001	14-15
17 Jun-6 Jul, 2001	14-16
31 Jul-17 Aug, 2001	14
13 Sep-1 Oct, 2001	14
31 May-5 Jul, 2002	13-15

Pitfall trapping has been used extensively in landscape-scale studies comparing the distributions, activity, and density of ground-dwelling arthropods (Uetz 1976, Coulson and Butterfield 1985, Hella and Muona 1985, Epstein and Kulman 1990, Niemalä et al. 1993a, Humphrey et al. 1999). The method is favored by many arthropod ecologists because it is relatively simple and inexpensive to set up and maintain the traps, several areas can be sampled simultaneously, traps generally catch large numbers of animals, and traps can integrate arthropod activity over several days or weeks at a time (Spence and Niemalä 1994, Topping and Sunderland 1992). However, the method has been simultaneously criticized for many reasons: there is often a trap bias toward larger, more mobile species, and even among these, phenology, sex, hunger, or time of day may affect activity levels (Adis 1979, Andersen 1995, Baars 1979a, Topping and Sunderland 1992); climate and the complexity of surrounding vegetation or substrate can affect trap efficiency (Adis 1979, Greenslade 1964); trap material, size, shape, and arrangement, and type of preservative are known to affect catches (Adis 1979, Digweed et al. 1995); and species have even been observed to vary in their “trappability” once at the trap edge (Halsall and Wratten 1988). In sum, trapping efficiency can be highly variable between species, seasons, and habitats, and consequently caution must be used when interpreting data and making inferences from studies using pitfall data. In this study, pitfall data gathered for two growing seasons were expected to provide a measure of relative “activity-density” (Thiele 1977) within species across riparian gradients and management treatments, rather than a true estimate of diversity or abundance.

Focal taxa and specimen identification

The focal invertebrate taxa I chose for this study—spiders, beetles, millipedes, gastropods—were intended to represent a broad range of functional groups (herbivores, detritivores, predators) and mobility/dispersal capabilities. I included taxa that fit some of the

criteria previously proposed for effective indicators of habitat heterogeneity and ecological integrity: populations could be sampled adequately with a simple pitfall trapping design; higher taxa occupy a broad spectrum of environmental conditions, while individual genera or species may be narrower habitat specialists; and the order or family is relatively well-known taxonomically and the natural history well-documented (Kremen et al. 1993, Pearson 1994). Not all focal taxa fit all of these criteria, however. For instance, I included gastropods because they were a group of significant concern among federal land managers in the Pacific Northwest. Although over 40 gastropod species appeared on the Survey and Manage list associated with the Northwest Forest Plan (USDA and USDI 1994), there was little known regarding the distribution or habitat associations of many of these species, and it was therefore difficult to manage for them. I included millipedes, among which there are many undescribed species, because, as detritivores, they comprise an important functional group in the forest-floor food web.

Focal taxa comprised members of nine orders and 34 families:

1. Class Arachnida

Order Araneae (spiders)—Antrodiaetidae, Dipluridae, Mecicobothridae,
Gnaphosidae, Salticidae, Thomisidae, Lycosidae, Agelenidae

2. Class Insecta

Order Coleoptera (beetles)—Carabidae, Cicindelidae, Scydmaenidae,
Staphylinidae (only Pselaphinae), Curculionidae

3. Class Gastropoda (snails and slugs)

Order Basommatophora—Carychiidae

Order Stylommatophora—Arionidae, Bradybaenidae, Haplotrematidae,
Helicarionidae, Polygyridae, Punctidae, Pupillidae, Valloniidae, Zonitidae

4. Class Diplopoda (millipedes)

Order Chordeumatida—Caseyidae, Rhiscosomididae, Conotylidae, Striariidae

Order Julida—Paeromopodidae, Parajulidae

Order Polydesmida—Nearctodesmidae, Xystodesmidae, Polydesmidae

Order Polyzoniida—Hirudisomatidae

Order Polyxenida—Polyxenidae

I identified most adult specimens to species, when reliable taxonomic keys were available. Mature specimens, as well as immature gastropods, were identified to the lowest taxonomic level possible. I lumped several unidentifiable species into the two carabid genera *Harpalus* and *Amara*, and counted the genera as two “species” in the analyses. Taxonomic

references for various taxa are listed in Appendix 1. Representative specimens of all identified taxa were verified by expert systematists and taxonomists. Voucher specimens of all taxa reside in the Oregon State Arthropod Collection, Oregon State University, Corvallis, OR.

Microclimate sampling

In 2002, I installed one microclimate data logger (GPSE 301 203 (THT-HR) Humidity and Dual Temperature Datalogger) each at 1, 10, 20, and 50-70m from the stream (near pitfall trapping stations), along one randomly selected transect per site. At each sampling station, I measured soil/litter temperature approximately 2-3 cm below the substrate surface, and ambient air temperature and percent relative humidity approximately 20 cm above the substrate surface, at all sites where pitfall trapping occurred. The sensors measuring ambient air temperature and relative humidity were protected from rain and dew under a large, inverted cup that hung from a wire arm attached to the top of a stake driven into the ground. Ideally, air temperature and relative humidity should have been measured 1-2 cm from the ground surface, where the invertebrates are active, however, adequate ventilation was required below the cups to prevent the creation of an artificial microclimate. At the end of the sampling season, I placed all microclimate loggers into climate-controlled chambers for calibration. Air and soil temperatures were accurate to within 0.3°C, and relative humidity was accurate to within 4%.

Microclimate parameters were sampled at six sites (two blocks) simultaneously. I sampled microclimate at all five blocks in late spring/early summer (between May 31 and July 13; average of 12 sampling days per block), and again in late summer (between August 27 and September 23; average of six sampling days per block). Although the microclimate sampling (2002) and most of the pitfall trapping (2001) were not synchronous, general microclimatic patterns among treatments were observed to be similar in a pilot study in 2001 (when just 2 blocks were sampled) and in 2002.

Microhabitat sampling

I estimated percent cover of herbaceous vegetation, moss, bare mineral soil, and coniferous and hardwood leaf litter in a 1 x 1 m plot next to each pitfall trap (20 per site). I characterized the top 5 cm of the forest floor at one randomly chosen corner of this plot as organic (including leaf litter) and/or mineral soil.

To characterize shrub cover, I set up a 10 x 2 m sampling plot at each sampling distance on each transect (10 per site). The sampling plot was oriented parallel to the stream, and

encompassed both pitfall traps at a given distance. Within each plot, I counted the number of live woody stems > 1 m tall and < 10 cm diameter at breast height (DBH) by species.

Trees and snags were assessed in plots measuring 20 x 4 m, encompassing and extending the shrub plots described above (10 per site). I halved the plot size to 20 x 2 m for plots at 1 m from the stream because the full plot would have extended into the stream. I counted and measured the DBH of all live woody stems > 10 cm DBH by species, if any part of the stem fell within the plot. I also measured the DBH of standing dead woody stems > 10 cm DBH and > 1 m tall (snags). I converted DBH measurements into basal area (m²/ha) for analyses.

I used a line-intercept method to measure large woody debris (LWD; i.e., all stumps and downed wood > 10 cm in diameter, of any length) that crossed a 10 m transect line running along the center of the shrub plot, parallel to the stream. For each piece of LWD, I measured its horizontal length touching the transect line, and its average vertical "width." LWD elevated > 50 cm off the ground was excluded. I assigned a decay class (1-5) to each stump or piece of LWD, with 1 representing a recently fallen tree with bark and some limbs present, and 5 representing a tree that is barely discernible from the substrate (Maser and Trappe 1984). Horizontal and vertical measurements for each piece of LWD were multiplied, and summed to derive an estimate for the quantity of LWD in each decay class in the plot.

Data analysis: methods

Within each site, I calculated mean abundances for each invertebrate species across the four traps at a given distance from the stream. Each of the five distance-samples within a site was termed a "trap zone" (15 sites x 5 distances = 75 trap zones). Trap zone mean abundances per species were averaged over all six sampling periods (August 2000-July 2002; only five sampling periods for trap zones in block MM). Trap zones were used as sample units in all ordinations, and as repeated measures (by distance) in parametric tests comparing differences between treatments (where each of the 15 sites represented an independent experimental unit).

Diversity measures were calculated to characterize the invertebrate communities at different distances from the stream and between treatments. They were based on the accumulated totals of species occurring in each trap zone or site over the five sampling periods in which all blocks were sampled. To measure diversity, I used a simple count of species richness (S) and the Shannon-Wiener diversity index (H; Shannon and Weaver). To measure functional and broad taxonomic diversity at each trap zone, I calculated proportions of total species within three functional groups (predator, detritivore, herbivore; see Appendix 2 for species classifications),

and three taxonomic groups (beetle, spider, gastropod). Millipedes were omitted from the taxonomic groups as they were synonymous with detritivores in this study.

For all community analyses, I deleted rare species that occurred in less than 5% of the samples, to reduce noise in the data set. Species average abundances also were log-transformed and then relativized by species maximum (thus equalizing rare and common species) in order to reduce variability among sample units (rows) and species (columns) in the data matrix. Such transformations are well-suited to pitfall trap data where trap catches are often strongly influenced by the complexity of the surrounding substrate and species size or behavior, rather than actual species density distributions. I checked for outlier sample units and species that were more than two standard deviations away from the average distance of each point from all other points. Outliers ranged from -2.01 to 2.8 SD away from the average, but because deleting them (singly or in combination) had no noticeable effect on the analyses, I retained them all.

Environmental variables (representing single values such as elevation, or averages for trap zones or sites) were log-transformed if the difference between minimum and maximum values was greater than one order of magnitude and/or if skewness was greater than 1.0. I converted the measurement of aspect (of a site) from degrees (1-360) to an index of "heat load" through the following equation: $\text{heat load index} = (1 - \cos(\theta - 45))/2$ where θ is the aspect in degrees (McCune and Grace 2002). The index ranges from 0 (coolest northeast slope) to 1 (warmest southwest slope). Microclimate data (air and soil temperature, relative humidity) were calculated in the following way: for each trap zone ($n = 60$), I first averaged the 3 pm value (i.e., the maximum daily temperature or the minimum relative humidity) over the two hottest consecutive days of the sampling period; next, for each trap zone, I averaged these maximum or minimum values over the two microclimate sampling seasons (early summer and late summer, 2002). These variables were meant to represent extremes in microclimate, which might be limiting to the activity of some invertebrates.

I used PC-ORD software (McCune and Mefford 1999) to perform all multivariate community analyses. I looked for patterns in community composition with increasing distance from the stream and across different management treatments, and attempted to relate these patterns to various measured environmental variables, by using non-metric multidimensional scaling (NMS; Kruskal 1964, Mather 1976) to ordinate trap zones (samples) in species space, and then correlating variables of interest with axes in the ordinations. Non-metric multidimensional scaling is a robust and effective ordination method for ecological data, which is typically non-normally distributed, and has a high proportion of zero values (Clarke 1993, McCune and Grace 2002). The method uses an iterative search for the best position of n entities (samples or species)

on a reduced number of k dimensions (axes) that minimizes the “stress” of the resultant k -dimensional ordination. An ordination with low stress (< 20) has maximal correspondence between ranked distances in the original n -dimensional space and ranked distances in the reduced k -dimensional space. I used the quantitative version of Sørensen distance to measure dissimilarity, and used a random starting configuration for all ordinations. Forty runs with real data were performed for each ordination, and the run with the lowest stress was used for analysis. I selected three-dimensional solutions for all ordinations, as additional axes provided only small reductions in stress, but fewer dimensions increased stress to unacceptable levels (McCune and Grace 2002). I set a stability criterion of 0.00001, with the solution ending after 10 iterations within this stability (McCune and Grace 2002). For each question being addressed, I rotated the ordination to align the primary variable of interest (distance from the stream or management treatment) along the horizontal axis (axis 1). I used joint plots to display the strongest correlations (Pearson’s r) between quantitative community or environmental variables and the ordination axes. The proportion of variance represented by each axis in an ordination was measured by calculating the coefficient of determination (r^2) between distances in the original n -dimensional space with those in the three-dimensional ordination space.

I used blocked multiple-response permutation procedures (MRBP; Biondini et al. 1988), to test for community differences between pre-defined groups (i.e., distances from the stream, or management treatments). This non-parametric procedure provides a measure of within-group homogeneity ($A = 1$ means that all entities within the group are identical), and a p -value associated with the null hypothesis of no difference between groups. Euclidean distance was used, and medians were aligned to zero for all blocks, in order to focus the analysis on within-block differences among distances or treatments (McCune and Grace 2002).

As a complement to the MRBP, I used Indicator Species Analysis (Dufrene and Legendre 1997) to examine associations of individual taxa with particular pre-defined groups. Groups were based on the question of interest, and/or strong patterns revealed in the NMS ordinations (i.e., microclimate). This method calculates an indicator value (IV, ranging from 0-100) for each species in each group, based on the relative abundance and frequency of the species in each group (McCune and Grace 2002). A perfect indicator taxon for a group ($IV = 100$) would be one that occurs only in that group, and occurs in all sample units within that group. The statistical significance of the IV_{\max} across groups for each species was evaluated by a Monte Carlo test using 1000 randomizations, with a null hypothesis that IV_{\max} is no larger than would be expected by chance alone.

Data analysis: approach

I addressed the three main research questions in the following way:

Community patterns in unmanaged forested riparian zones: I used NMS to ordinate 25 forested sample units (5 blocks x 1 treatment (forest) x 5 distances = 25 trap zones) in species space. I also used MRBP to look for community compositional differences between distance groups (1, 5, 10, 20, and 50-70 m from the stream; n = 5 trap zones for each group), and I used indicator species analysis to look for taxa strongly associated with particular distances from the stream or pre-defined groups based on microclimate.

Community patterns compared in forested, buffered, and clearcut riparian zones: I used NMS to ordinate 75 trap zones (5 blocks x 3 treatments x 5 distances) in species space. Because the trap zones at 50-70 m in the buffer treatment were located in clearcuts adjacent to the forested buffers, they were treated (and coded) as clearcut trap zones in the ordination and in the Indicator Species Analysis. I used indicator species analysis to look for taxa strongly associated with treatments or microclimate groups. To test for community compositional differences between buffer, forest, and clearcut treatment groups, I used MRBP with sites (rather than trap zones) as within-group entities (n = 5 sites for each treatment group). Site abundances for each taxon were calculated by averaging across 1, 5, 10, and 20 m trap zones for each site. Because some environmental variables (e.g., tree basal area, shrub density) were better assessed at the site scale to determine treatment differences, I also performed an ordination on the 15 sites as sample units, with each sample unit representing an average site abundance for each species (as in the MRBP), and environmental variables for each site representing averages of measurements between 1 and 20 m.

I compared diversity measures (S, H) between 1 and 20 m from the stream across all treatments, using a randomized complete block design with a repeated measures analysis. The repeated measures models assume that diversity measurements made at different sites are independent, but measurements made at different distances within the same site are correlated. An unstructured model for the covariance matrix was used, allowing covariances for all combinations of distances to be different. I used PROC GLM in SAS, Version 8 (1999) for these analyses. For all tests, I used a significance level of $\alpha = 0.05$.

Edge effects on community patterns in the riparian buffer treatment: I used NMS to ordinate 40 sample units (5 blocks x 2 treatments (buffer and forest) x 4 distances (1-20 m from the stream)) in species space. By ordinating both forest and buffer trap zones in species space, and

loading the maximum variation associated with distance from the stream onto one axis, I hoped to qualitatively compare transects of trap zones at consecutive distances from the stream in buffer and forest sites. I assumed that consistent dissimilarities in transect length and position between buffer and forest transects in the same block would indicate the influence of edge effects on community composition in the buffer. I also used MRBP to look for treatment differences in community composition, again using sites as within-group entities ($n = 5$ sites for each group).

Lastly, I looked for evidence of edge effects on selected individual species by qualitatively assessing their distribution patterns between 1 and 20 m from the stream in forest, buffer, and clearcut treatments. To select species, I used the results of an indicator species analysis comparing forest and clearcut groups to identify abundant species ($n > 100$ individuals) that were strong indicators ($IV > 50$) of either clearcut or forest treatments (or, in the case of *P. crenicollis*, a strong riparian indicator). I also included abundant generalist species that had high frequencies ($> 70\%$) and relatively equal abundances in both clearcut and forest groups. I used Friedman's non-parametric procedure for randomized blocks to compare mean abundances per trap zone of selected invertebrate species (averaged over all distances from the stream) across forest, buffer, and clearcut treatments. This helped to determine the robustness of the patterns observed in the distribution plots.

RESULTS

Across all treatments, I captured 16,233 invertebrates in the 34 target families, comprising 118 genera and 203 species (species list with mean abundances by treatment in Appendix 2). The most abundant species, the wolf spider *Pardosa dorsalis*, made up 13.7% of the total catch. As is commonly the case with invertebrate data, a few species were very abundant ($> 50\%$ of captures were comprised of 10 species) and many species were uncommon or rare (47% of species had ≤ 10 captures).

Community patterns in unmanaged forested riparian zones

I identified 124 invertebrate species in the mature forested sites, and used all species for calculating diversity measures, but eliminated 27 rare species (occurring in only a single sample unit) for multivariate community analyses. The NMS three-dimensional solution represented a total of 91.9% of the variation in the original data. The final solution had a stress of 8.47 (Monte Carlo test, $p = 0.020$), achieved after 63 iterations. Two of the three axes are shown in Figure 2.3. I rotated the ordination to maximize the correlation of distance from the stream with axis 1, this resulted in 11.7% of the original variation being loaded onto axis 1, and 66.2% onto axis 2.

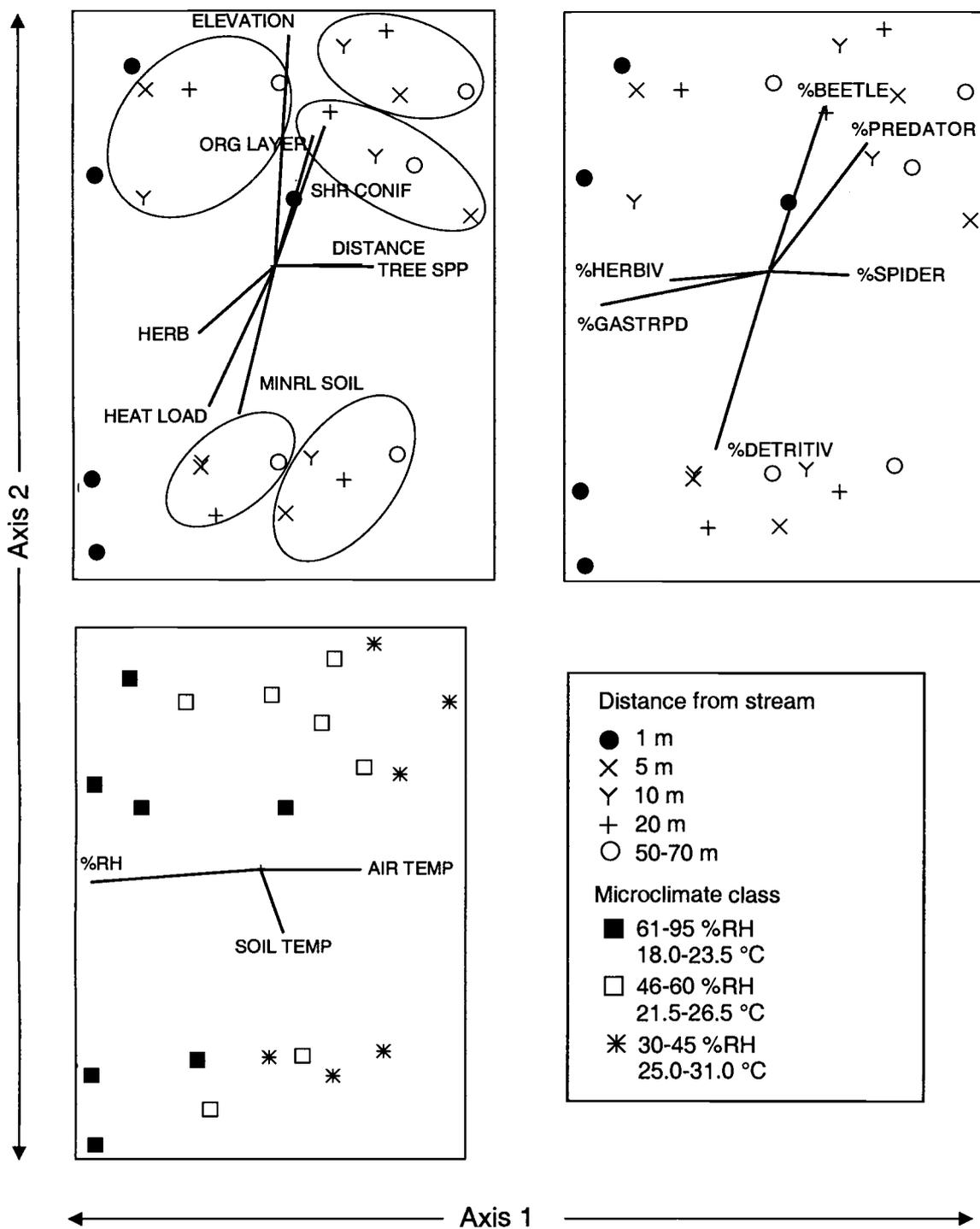


Figure 2.3 NMS ordination of forested sample units (trap zones; n = 25) in species space, only two dimensions of the 3-dimensional solution are shown. Vectors indicate the strength (minimum r^2 of 0.25, vector length proportional to strength) and direction of correlations between environmental or community diversity variables (see Table 2.4 for code definitions) and axis scores. In (a), ellipses surround sample units at 5-70 m from the stream within separate blocks. In (c), trap zones at 5m were eliminated from the ordination plot because microclimate was not measured at these trap zones. The ranges of relative humidity and air temperature were divided into three classes and overlain as a categorical variable in (c).

Elevation was very strongly correlated with axis 2 ($r = 0.943$), and separated sample units into two distinct groups of higher elevation (~1100 m) and lower elevation (~500 m) trap zones (Fig. 2.3). Although distance from the stream was not as strongly correlated with axis 1 ($r = 0.575$), four out of five of the trap zones at 1 m from the stream did cluster to one end of the axis (filled circles; Fig. 2.3a,b). Trap zones between 5 and 70 m from the stream within a block clustered together in distinct groups (Fig. 2.3a), suggesting strong block effects. Within three of the blocks, trap zones at increasing distances from the stream were ordered consecutively along axis 1. Overall, however, trap zones at 5 to 70 m did not cluster together into distinct distance-groups. Block effects were accounted for with MRBP, which revealed a significant difference among distance groups, with the community at 1 m distance different from all others (Table 2.3). The remaining four distance-groups (5, 10, 20, 50-70 m) were not significantly different from each other (Table 2.3).

Table 2.3 Results from MRBP testing for differences in community composition among various distance-groups.

Distance-groups tested	Chance-corrected within-group agreement (A)	p-value
All groups (1-70 m)	0.030	0
All groups except 1m (5-70 m)	0.011	0.124
1 m vs. 5 m	0.056	0.015
1 m vs. 10 m	0.046	0.020
1 m vs. 20 m	0.069	0.017
1 m vs. 70 m	0.100	0.015

Other environmental variables that correlated strongly ($r^2 > 0.25$) with axis 2 included: percent cover of mineral soil and heat load index which both increased at lower elevations, while the depth of the organic layer and the density of coniferous shrubs both increased at higher elevations (Table 2.4). Tree species richness was positively correlated with axis 1, and herb cover was strongly negatively correlated with both axis 1 and axis 2. ($r = -0.542$ and -0.507 respectively). Of the microclimate variables, relative humidity was very strongly negatively correlated with axis 1, while air temperature was strongly positively correlated with the same axis, suggesting that trap zones closer to the stream are cooler and more humid than trap zones further from the stream. Soil temperature increased at lower elevations, perhaps related to an increased heat load index associated with aspect. Because relative humidity and air temperature

showed stronger associations with axis 1 than did distance-from-stream (suggesting a greater influence on community composition), I divided the range of relative humidity and air temperature into three groups: cool/humid, medium temp./humidity, and warm/dry (Figure 2.3c). The cool/humid group included all of the 1 m trap zones and two of the 10 m trap zones. At the other end of the microclimate scale, the warm/dry group included all but one of the 70 m trap zones, and two 20 m trap zones.

Among community diversity variables (Fig. 2.3b), the proportion of detritivore species (millipedes) increased at lower elevations, while the proportion of beetle and predator species increased at higher elevations. The abundances of three relatively common millipede species, *Harpaphe haydeniana haydeniana*, *Caseya dendrogona*, and *Keypolydesmus anderisus*, were strongly negatively correlated ($r < -0.600$) with the axis 2. Abundant at higher elevations, six species of pselaphine beetles and five species of carabid beetles had strong positive associations ($r > 0.500$) with axis 2. The proportion of gastropod and herbivore species (gastropods plus weevils) increased closer to the stream in the cool/humid microclimate, while the proportion of spider species increased in the warmer/drier microclimate. Three snail species (*Ancotrema sportella*, *Punctum randolphi*, *Striaria pugetensis*) were strongly negatively correlated ($r < -0.500$) with axis 1.

Table 2.4 Selected environmental and community diversity variables and their strongest correlation (Pearson's r) with one of the two axes displayed in the NMS ordinations of forest-only trap zones (Fig. 2.3), and of forest, buffer, and clearcut trap zones (Fig. 2.5). Correlations > 0.5 are in bold/italic. Last column lists environmental correlations from NMS ordination of 139 species and 15 sites, with invertebrate abundances and environmental measures averaged over all distances within a site (ordination plot not shown; final solution had a minimum stress of 6.53 (Monte Carlo test, $p = 0.0196$) achieved after 74 iterations; cumulative $r^2 = 0.925$).

Table 2.4

Variable	Variable code	Forest only (Fig. 2.3) r (axis)	All treatments (n=75 trap zones; Fig. 2.5) r (axis)	All treatments (n=15 sites) r (axis)
<i>Trees</i>				
Tree species richness	TREE SPP	0.612 (1)	-0.228 (1)	0.073 (2)
Total live tree basal area	LIVE BA	0.345 (1)	-0.492 (1)	-0.572 (1)
Conifer basal area	CONIF BA	0.338 (1)	-0.407 (1)	-0.554 (1)
Hardwood basal area	HARD BA	-0.237 (2)	-0.312 (2)	-0.341 (2)
Snag basal area	SNAG BA	0.365 (2)	0.261 (2)	-0.445 (1)
Average tree DBH	AVG DBH	0.145 (1)	-0.177 (1)	-0.572 (1)
<i>Shrubs</i>				
Shrub species richness	SHRUB SPP	0.287 (2)	-0.146 (2)	-0.541 (2)
Shrub total density	SHRUB TTL	0.497 (2)	-0.245 (2)	0.088 (1,2)
Shrub/conifer density	SHR CONIF	0.731 (2)	0.375 (2)	0.439 (2)
Shrub/hardwood density	SHR HARD	0.337 (2)	-0.332 (2)	0.181 (1)
<i>Ground cover</i>				
% Herb cover	HERB	-0.542 (1)	-0.408 (2)	0.613 (1)
% Moss cover	MOSS	-0.289 (1)	-0.668 (1)	-0.766 (1)
% Mineral soil cover	MINRL SOIL	-0.754 (2)	0.403 (1)	0.689 (1)
% Leaf/needle litter cover	LITTER	-0.311 (2)	-0.386 (2)	-0.615 (2)
Depth organic layer	ORG LAYER	0.703 (2)	0.458 (2)	-0.666 (1)
<i>Large woody debris</i>				
LWD total (all decay classes)	LWD TTL	0.132 (2)	0.300 (2)	0.092 (2)
LWD (decay class 4-5)	LWD 45	0.232 (1)	0.051 (1)	-0.282 (1)
<i>Other</i>				
Distance from stream	DISTANCE	0.575 (1)	0.592 (1)	NA
Heat load index	HEAT LOAD	-0.733 (2)	-0.506 (2)	-0.574 (2)
Elevation	ELEVATION	0.943 (2)	0.924 (2)	0.809 (2)
<i>Community diversity</i>				
Invertebrate species richness	INVERT S	-0.090 (1)	0.524 (1)	
Shannon-Wiener diversity	INVERT H	-0.404 (2)	-0.309 (2)	
% Detritivore/millipede species	%DETRITIV	-0.812 (2)	-0.606 (2)	
% Herbivore species	%HERBIV	-0.606 (1)	-0.336 (2)	
% Predator species	%PREDATOR	0.690 (2)	0.611 (2)	
% Beetle species	%BEETLE	0.782 (2)	0.726 (2)	
% Gastropod species	%GASTRPPD	-0.791 (1)	-0.680 (1)	
% Spider species	%SPIDER	0.540 (1)	0.786 (1)	
<i>Microclimate</i>				
Air temperature	AIR TEMP	0.629 (1)	0.805 (1)	0.745 (1)
Soil temperature	SOIL TEMP	-0.501 (2)	0.724 (1)	0.865 (1)
Relative humidity	%RH	-0.822 (1)	-0.799 (1)	-0.533 (1)

Indicator Species Analysis revealed two species that were strongly negatively correlated with axis 1; the carabid beetle *Pterostichus crenicollis* and the snail *Striaria pugetensis* were strong indicators of the distance-group 1 m from the stream (Table 2.5). For the remaining distance-groups, only *Cryphoea exlinae* (an agelenid spider) showed any strong fidelity to a particular distance from the stream (20 m). Among the three microclimatic groups, *P. crenicollis* and *S. pugetensis* were indicative of the cool/humid group (Table 2.5), while there were six indicator species (four beetles, two spiders) for the warm/dry group. Three species within a single diverse genus in the family Carabidae, *Pterostichus*, provided indicator species for all three microclimate groups (Table 2.5).

Table 2.5 Indicator taxa for five distances from the stream (1-70 m), and for three microclimate classes (see Fig. 2.3 for ranges). Indicator Value (IV, ranges from 1-100) for each taxon based on combined values of relative abundance and frequency from Indicator Species Analysis. Only taxa with IV > 25 and $p \leq 0.05$ are shown. Letters in parentheses after taxon name indicate whether the taxon is a beetle (B), gastropod (G), or spider (S).

Indicator taxon	Distance from stream		Microclimate	
	Ind. Value (p-value)	Group indicated	Ind. Value (p-value)	Group indicated
<i>Striaria pugetensis</i> (G)	49.1 (0.049)	1 m	57.1 (0.020)	Cool/humid
<i>Pterostichus crenicollis</i> (B)	64.0 (0.001)	1 m	75.1 (0.003)	Cool/humid
<i>Cryphoea exlinae</i> (S)	51.5 (0.020)	20 m	-----	-----
<i>Pterostichus inopinus</i> (B)	-----	-----	56.1 (0.026)	Med. temp/humidity
<i>Pterostichus herculeus</i> (B)	-----	-----	81.0 (0.001)	Warm/dry
<i>Scaphinotus angusticollis</i> (B)	-----	-----	52.5 (0.038)	Warm/dry
<i>Rhyncholus brunneus</i> (B)	-----	-----	42.0 (0.045)	Warm/dry
<i>Steremnius carinatus</i> (B)	-----	-----	46.9 (0.018)	Warm/dry
<i>Antrodiaetus pugnax</i> (S)	-----	-----	43.6 (0.030)	Warm/dry
<i>Zelotes fratris</i> (S)	-----	-----	50.0 (0.021)	Warm/dry

Species diversity (including all rare species), as measured by species richness (S) and the Shannon-Wiener diversity index (H), was similar at all distances from the stream (Fig. 2.4).

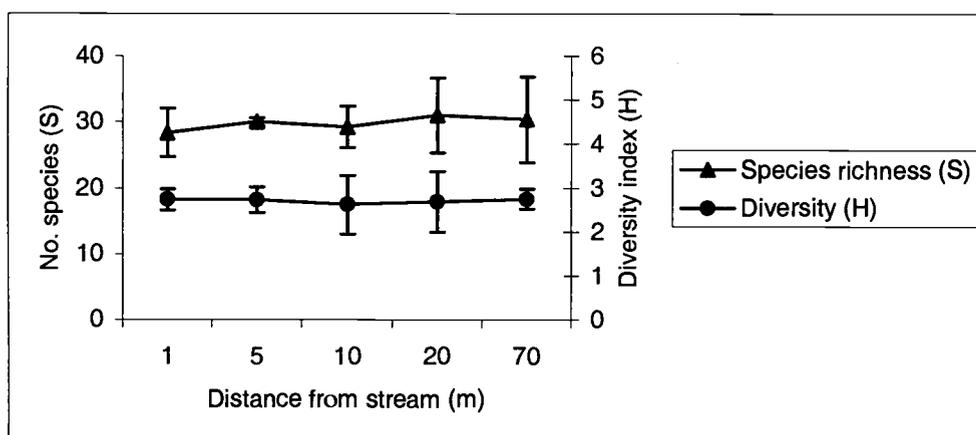
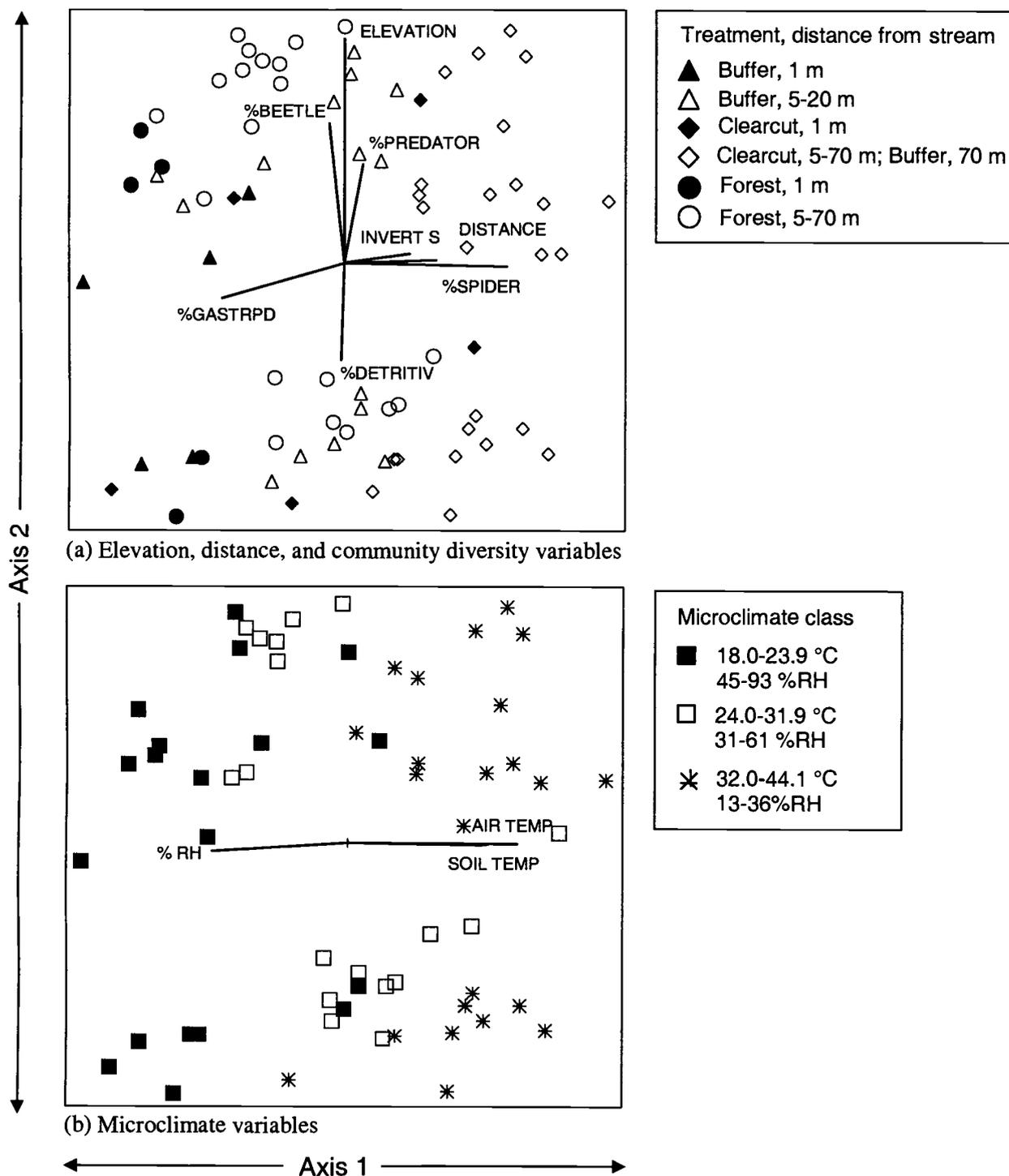


Figure 2.4 Average invertebrate species richness (S) and Shannon-Wiener diversity (H) at increasing distances from the stream in forest sites \pm 95% confidence interval ($n = 5$). Note x-axis is not to scale, y-axes are different scales.

Community patterns compared in forested, buffered, and clearcut riparian zones

I identified a total of 203 invertebrate species from all management treatments, but eliminated 69 rare species that occurred in three or fewer trap zones for all multivariate community analyses. The NMS three-dimensional solution represented a total of 83.9% of the variation in the original data. The final solution had a stress of 13.37 (Monte Carlo test, $p = 0.020$), achieved after 168 iterations. The two most informative axes are represented in Figure 2.5. When I visually rotated the ordination to align treatment “groups” with axis 1, this axis represented 17.9 % of the total variation, while axis 2 was loaded with 50.8 % of the original variation. Again, elevation was strongly associated with axis 2 ($r = 0.924$), with trap zones of higher and lower elevation blocks sorting into two distinct regions of species space along the axis (Fig. 2.5). Distance from the stream was positively correlated with axis 1 ($r = 0.592$). Along axis 1, trap zones at 1 m distance from the stream (filled symbols) in all three treatments clustered at one end (with two exceptions, both clearcut trap zones), while a mix of buffer and forest trap zones filled the middle of the ordination space, and clearcut trap zones clustered at the other end of axis 1 (Fig. 2.5). Among high elevation blocks, forest and buffer trap zones more than 1 m from the stream were segregated somewhat vertically (i.e., along axis 2), while at lower elevations, there was more mixing of trap zones among these two treatments. It should be noted that three of the 5-20 m buffer trap zones closest to the clearcut end of the ordination at high



(a) Elevation, distance, and community diversity variables

(b) Microclimate variables

Figure 2.5 NMS ordination of 75 sample units (trap zones) from buffer, clearcut, and forest treatments in species space, only two dimensions of the 3-D solution are shown. Vectors indicate the strength (minimum r^2 of 0.25) and direction of correlations between variables and axis scores. In (a), trap zones at 70 m from the stream in the buffer treatment are coded as "clearcut" as they lie in a clearcut adjacent to the buffer. In (b), 5 m sample units were omitted and the ranges of air temperature and relative humidity were divided into three classes and overlain as a categorical variable.

elevation represented one buffer site that had been subject to severe blowdowns. MRBP revealed significant community compositional differences between the three treatment groups (buffer vs. clearcut vs. forest; $A = 0.043$, $p = 0.004$). Pairwise comparisons between treatment groups confirmed what the ordination suggested, that forest and buffer groups were not significantly different from each other ($A = -0.006$, $p = 0.834$), while the clearcut group was significantly different from both the forest group ($A = 0.087$, $p = 0.016$) and the buffer group ($A = 0.072$, $p = 0.016$).

At the trap zone scale, there were fewer strong environmental associations with the axes than in the forest-only ordination (Table 2.4, column 4). Again, the heat load index increased at lower elevation trap zones, a function of aspect. Moss cover was negatively correlated with axis 1, indicating increased cover near streams and in forested conditions. At the site scale (ordination not shown, but revealed a similar pattern of clearcut sites clustered at one end of axis 1, and a mix of forest and buffer sites at the other end), there were numerous strong environmental correlates (Table 2.4, column 5). Not surprisingly, live tree basal area, conifer basal area, and average tree DBH were all strongly negatively correlated with axis 1 (i.e., fewer/smaller trees in the clearcut than in buffer/forest). Herb cover and mineral soil cover were strongly associated with the clearcut end of axis 1, while moss cover, litter cover, and depth of the organic layer were both strongly correlated with the forest/buffer end of the same axis. Heat load index and microclimate variables showed similar relationships with axes as in the ordination with 75 trap zones.

Relative humidity showed a strong negative association with axis 1, while both air and soil temperature increased along the axis from streamside to clearcut trap zones. As microclimatic variables were again strongly associated with axis 1, I divided the 75 trap zones into three groups based on air temperature (primarily) and relative humidity (Fig. 2.5b), using broader ranges than those in the forest-only ordination. Twenty of 22 trap zones in the warm/dry group were from clearcut treatments, 9 of 19 trap zones in the cool/humid group were from forest treatments, and 9 more were from buffer treatments.

Community diversity variables (at the trap zone scale) showed very similar associations to those found in the forest-only ordination (Figure 2.5a). The proportion of gastropod species increased with increasing relative humidity along axis 1. The proportion of detritivore species increased at lower elevations, while the proportion of beetle and predator species increased at higher elevations. Invertebrate species richness was positively correlated with axis 1, and the increased proportion of spider species in the clearcuts may have contributed to this overall diversity. The abundances of three lycosid spider species, one thomisid species, and two gnaphosid species were strongly positively associated ($r > 0.500$) with axis 1, while the carabid

beetle, *Pterostichus crenicollis*, and a millipede, *Nearctodesmus insulanus*, were strongly associated ($r < -0.500$) with the streamside/forested (negative) end of axis 1.

Over 20% of the 134 taxa used in this community analysis were found to be significant indicator species for a particular treatment group. Because buffer and forest trap zones were mixed together in the ordination, and these treatment groups were not different in the MRBP analysis, I combined them together into a single treatment group (forest/buffer; $n = 45$ trap zones), which was contrasted with the clearcut group ($n = 30$ trap zones). *P. crenicollis*, together with four other carabid beetles were significant indicators of the buffer/forest group (Table 2.6). Additionally, one pselaphine beetle, two agelenid spider species, and a "jumping slug," *Hemphillia dromedarius*, were indicators of the buffer/forest group. Clearcut indicator species included five carabid beetle species, one weevil, and 13 spider species distributed among five families (Table 2.6). Indicator species analysis performed on the three microclimate groups revealed three of the indicator species for the cool/humid group (the beetles, *P. crenicollis* and *Sonoma conifera*, and the agelenid spider, *Cybaeus cascadius*) to be shared with the forest/buffer group (Table 2.6). In addition, another pselaphine beetle, a haplotrematid snail, and the millipede, *N. insulanus*, were indicators of the cool/humid group. Of the sixteen significant indicators for the warm/dry group, all but two were also clearcut indicators. There were no significant indicators for the medium temperature/humidity group.

Diversity measures used in parametric statistics included all rare species. Repeated measures analysis of species richness (S), using univariate analysis of variance tests, indicated that there was no interaction between distance and treatment ($F_{6,24} = 0.15$, $p = 0.98$). Within treatments, mean species richness did not differ with distance from the stream ($F_{3,24} = 1.94$, $p = 0.15$). However, when all distances were averaged, there was evidence of a significant treatment effect ($F_{2,8} = 5.97$, $p = 0.03$; Fig. .26). Mean species richness in the clearcut (mean = 38.5; 95% CI:33.1,43.9) was significantly higher than in the forest (mean = 29.7; 95% CI:24.3,35.0; t-test for difference: $t_8 = 3.35$, $p = 0.01$) and the buffer (mean = 32.2; 95% CI:26.8, 37.5; t-test for difference: $t_8 = -2.4$, $p = 0.04$), however, the buffer and forest were not different from each other (t-test for difference: $t_8 = 0.95$, $p = 0.37$). For Shannon-Wiener diversity (H), repeated measures analysis based on multivariate analysis of variance was used. There was no significant interaction between distance and treatment (Wilk's Lambda = 0.36, $F_{6,12} = 1.33$, $p = 0.32$), and no distance-from-stream effect (Wilk's Lambda = 0.78, $F_{3,6} = 0.55$, $p = 0.67$). Treatment effects on Shannon-Wiener diversity, averaged over all distances, were also not significant ($F_{2,8} = 0.53$, $p = 0.61$; Fig. 2.6).

Table 2.6 Indicator taxa for two treatment groups (forest/buffer and clearcut), and for three microclimate classes (based on air temperature and relative humidity, see Fig. 2.5 for ranges). Indicator Value (IV) for each taxon based on combined values of relative abundance and frequency from Indicator Species Analysis. Only taxa with $IV > 25$ and $p \leq 0.05$ are shown. Letters in parentheses after taxon name indicate whether the taxon is a beetle (B), gastropod (G), millipede (M), or spider (S).

Table 2.6

	Management treatment		Microclimate	
	Ind. Value (p-value)	Group indicated	Ind. Value (p-value)	Group indicated
<i>Pterostichus crenicollis</i> (B)	35.2 (0.025)	Forest/buffer	49.0 (0.002)	Cool/humid
<i>Pterostichus inopinus</i> (B)	36.9 (0.045)	Forest/buffer	-----	-----
<i>Scaphinotus angusticollis</i> (B)	30.4 (0.039)	Forest/buffer	-----	-----
<i>Scaphinotus angulatus</i> (B)	52.8 (0.011)	Forest/buffer	-----	-----
<i>Sonoma conifera</i> (B)	29.2 (0.043)	Forest/buffer	30.7 (0.017)	Cool/humid
<i>Sonoma parviceps</i> (B)	-----	-----	30.1 (0.003)	Cool/humid
<i>Zacotus matthewsii</i> (B)	34.6 (0.010)	Forest/buffer	-----	-----
<i>Cybaeus eutypus</i> (S)	51.1 (0.025)	Forest/buffer	45.3 (0.001)	Cool/humid
<i>Cybaeus cascadius</i> (S)	46.1 (0.042)	Forest/buffer	-----	-----
<i>Hemphillia dromedarius</i> (G)	37.0 (0.004)	Forest/buffer	-----	-----
<i>Ancotrema sportella</i> (G)	-----	-----	40.9 (0.025)	Cool/humid
<i>Nearctodesmus insulanus</i> (M)	-----	-----	38.0 (0.001)	Cool/humid
<i>Harpalus spp.</i> (B)	40.0 (0.001)	Clearcut	33.4 (0.003)	Warm/dry
<i>Microlestes nigrinus</i> (B)	55.2 (0.001)	Clearcut	31.0 (0.006)	Warm/dry
<i>Omus dejeani</i> (B)	40.8 (0.005)	Clearcut	39.6 (0.005)	Warm/dry
<i>Otiorhynchus rugostriatus</i> (B)	34.1 (0.001)	Clearcut	31.2 (0.006)	Warm/dry
<i>Pterostichus lama</i> (B)	59.4 (0.001)	Clearcut	40.9 (0.013)	Warm/dry
<i>Pterostichus herculaneus</i> (B)	-----	-----	38.5 (0.041)	Warm/dry
<i>Trachypachus holmbergi</i> (B)	25.1 (0.003)	Clearcut	-----	-----
<i>Alopecosa kochii</i> (S)	68.3 (0.001)	Clearcut	57.9 (0.001)	Warm/dry
<i>Callilepis pluto</i> (S)	73.3 (0.001)	Clearcut	61.1 (0.001)	Warm/dry
<i>Cybaeus simplex</i> (S)	43.1 (0.002)	Clearcut	-----	-----
<i>Evarcha prozyskii</i> (S)	25.0 (0.008)	Clearcut	-----	-----
<i>Habronattus jucundus</i> (S)	30.0 (0.001)	Clearcut	25.7 (0.003)	Warm/dry
<i>Micaria pulicaria</i> (S)	30.0 (0.001)	Clearcut	-----	-----
<i>Pardosa californica</i> (S)	43.5 (0.001)	Clearcut	28.6 (0.026)	Warm/dry
<i>Pardosa dorsuncata</i> (S)	39.8 (0.002)	Clearcut	50.8 (0.001)	Warm/dry
<i>Pardosa dorsalis</i> (S)	58.3 (0.001)	Clearcut	41.2 (0.004)	Warm/dry
<i>Xysticus montanensis</i> (S)	65.0 (0.001)	Clearcut	65.8 (0.001)	Warm/dry
<i>Zelotes fratris</i> (S)	87.1 (0.001)	Clearcut	79.3 (0.001)	Warm/dry
<i>Zelotes josephine</i> (S)	33.3 (0.001)	Clearcut	-----	-----
<i>Zelotes puritanus</i> (S)	66.7 (0.001)	Clearcut	64.9 (0.001)	Warm/dry
<i>Ozyptila pacifica</i> (S)	-----	-----	31.8 (0.001)	Warm/dry

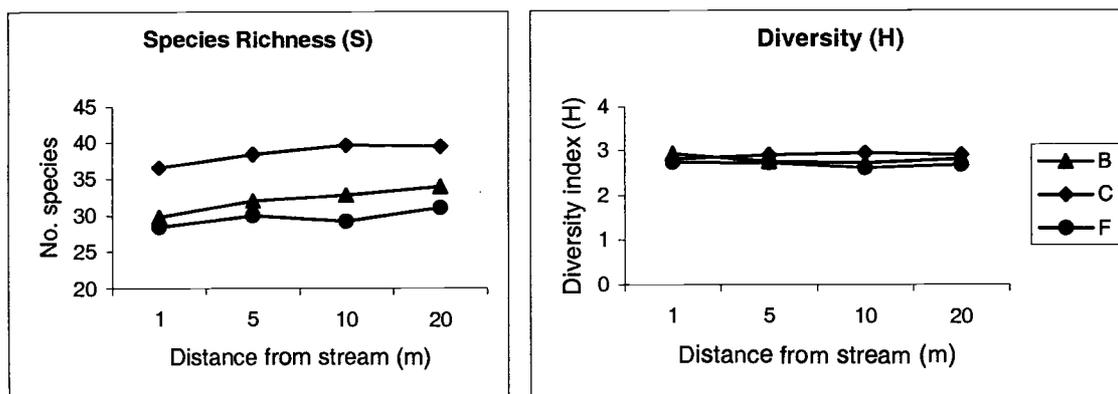


Figure 2.6 Mean values for invertebrate species richness (S) and Shannon-Wiener diversity (H) at increasing distances from the stream across three treatments (B=buffer, C=clearcut, F=forest; n = 5). Note x-axis is not to scale.

Proportional abundances of the four major invertebrate groups varied between treatments (Fig. 2.7). Beetles made up almost 60% of captures in the forest treatment (between 1 and 20 m from the stream) and only 36% in the clearcut. The reverse trend was seen with spiders, which made up over half the captures (51%) in the clearcut but only 17% in the forest. Beetle and spider abundances in the buffer treatment were intermediate between forest and clearcut levels. Millipedes and gastropods comprised about a quarter of the total invertebrate abundance in forests and buffers, but only 13% in clearcuts.

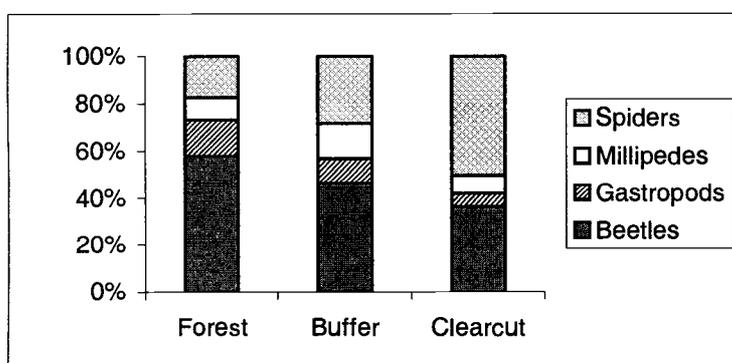


Figure 2.7 Proportional abundances of four major invertebrate groups in three management treatments (between 1 and 20 m from the stream).

Edge effects on community patterns in the riparian buffer treatment

I identified 141 invertebrate species in the buffer and forest treatments, and eliminated 39 rare species occurring in fewer than three trap zones for community analyses. A comparison of community composition in buffer and forest treatment groups using MRBP (with sites as within-

group entities), found no difference between treatments ($A = -0.003$, $p = 0.734$). The NMS ordination of trap zones from these two treatments (1-20 m from the stream) represented a three-dimensional solution and 85.5% of the variation in the original data. The final solution had a stress of 12.33 (Monte Carlo test, $p = 0.020$), achieved after 95 iterations. Two of the three axes are shown in Figure 2.8. I rotated the ordination to maximize the correlation of distance from the stream with axis 1 ($r = 0.790$), this resulted in 7.5% of the original variation being loaded onto axis 1, and 59.2% onto axis 2. Elevation, again, was strongly associated with axis 2 ($r = 0.947$). In both forest and buffer treatments, trap zones at 1 m from the stream clustered to the "left" end of the ordination. As in the previous ordination including three treatments (Fig. 2.5), the buffer trap zones more than 1 m from the stream at higher elevations clustered to the "right" end of axis 1, with the majority of forest trap zones more than 1 m from the stream occupying intermediate positions along the same axis (Fig. 2.8). At lower elevations, buffer and forest trap zones were more mixed together. Air temperature showed some correlation with axis 1 ($r = 0.491$), as did relative humidity ($r = -0.417$), although these associations were not as strong as in previous ordinations.

Based on results from the control riparian forest analyses that suggested that communities at 1 m from the stream were distinct from communities at all other distances, and communities at all other distances were not different from each other (Fig. 2.3, Table 2.3), I created a simple visual model showing both stream effects and potential edge effects on communities along two transects of trap zones at consecutive distances from the stream (Fig. 2.8, upper right). In this model, the forest transect had a large horizontal distance (dissimilarity) between trap zones at 1 m and 5 m from the stream, but the 5, 10, and 20 m trap zones were all relatively close (similar) to each other. In contrast, the buffer transect had much larger horizontal distances (dissimilarities) between trap zones at 5, 10, and 20 m from the stream, suggesting that physical or biological influences from the clearcut adjacent to the 30 m-wide riparian buffer were affecting the invertebrate community composition up to 20 m from the buffer edge (10 m from the stream). Note that relevant distances or dissimilarities between sample units in this model are along the horizontal axis (1) only, as this was the axis most strongly associated with distance from the stream. When I isolated and compared pairs of forest and buffer transects from each block in the ordination, no clear patterns emerged to suggest strong edge effects (Fig. 2.8). In all blocks except 2G, the distance between 1 and 5 m trap zones on both forest and buffer transects exceeded the distances between any other consecutive pairs of trap zones, suggesting stream effects. The differences in communities between 5 and 20 m from the stream on the buffer

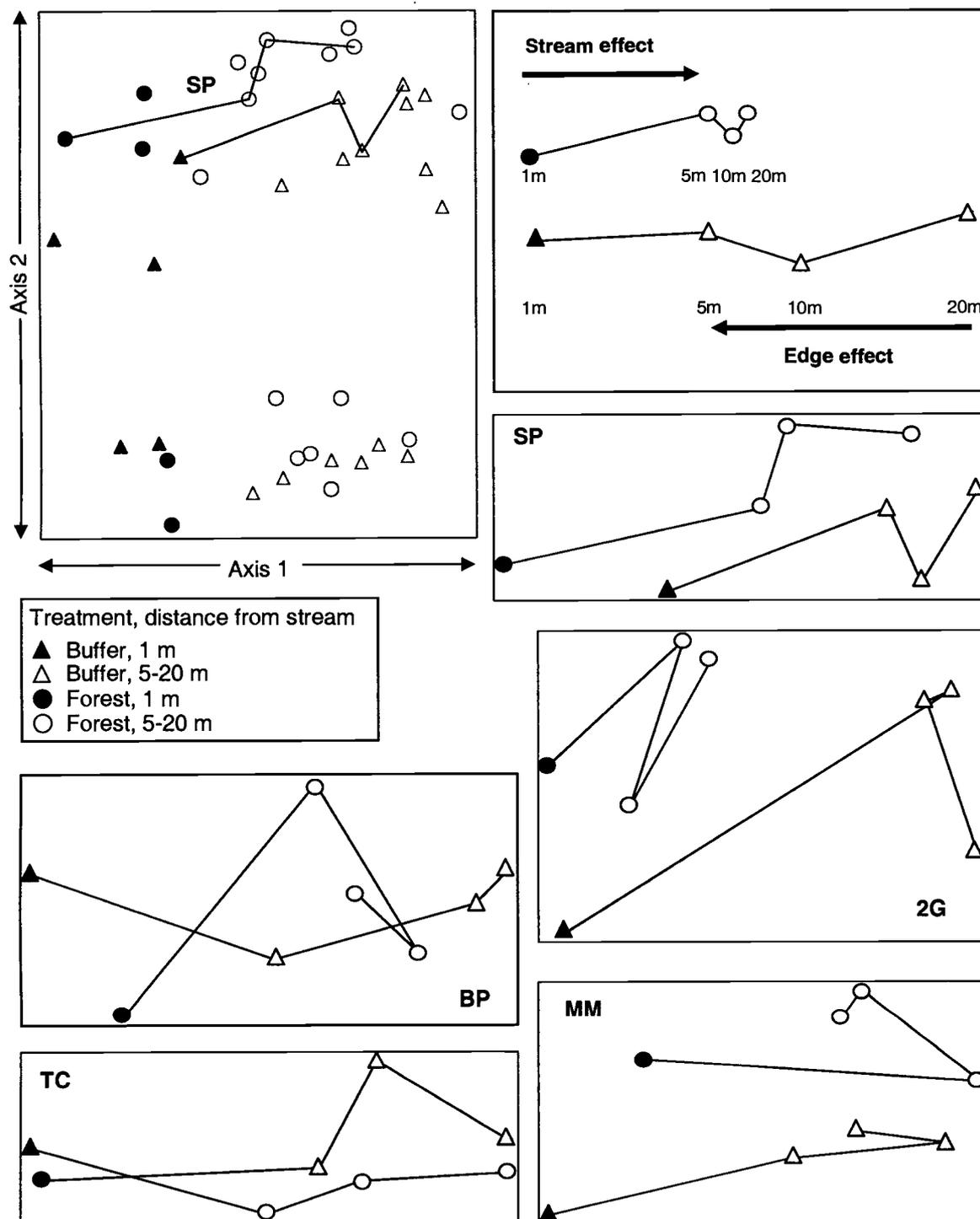


Figure 2.8 NMS ordination of 20 buffer and 20 forested sample units (trap zones) in species space, only two dimensions of the 3-D solution are shown. Vector diagrams isolate and compare forest and buffer trap zones for each block (SP, 2G, BP, TC, MM). Each vector joins trap zones at consecutive distances from the stream (1-20 m) within a site, representing a "transect." Buffer and forest transects from block SP are shown in main ordination (upper left) for reference. A hypothetical example portraying possible stream effects and edge effects is shown in upper right (see Results for explanation).

transects were not noticeably greater than those on the forest transects, except in BP. In this block, the relatively large distance between sample units at 5 and 10 m from the stream on the buffer transect, suggests an edge effect on communities at 10-20 m from the stream. In three of the blocks (SP, 2G, BP), the buffer transect extended further to the right side of the ordination than the forest transect, indicating that the trap zones farther from the stream (and closer to the buffer edge) occupied a region of species space associated with warmer/drier conditions than those in the intact forest. This was especially the case for the buffer site in the SP block, which was subjected to severe windthrow damage, and both microclimate and community composition appeared to be affected by the large gaps in the canopy.

Individual species distribution patterns between 1 and 20 m from the stream in buffer and forest treatments showed a variety of responses (Fig. 2.9). Among clearcut indicators, the lycosid spider, *Alopecosa kochii*, was absent outside of the clearcut treatment, while the lycosid spider, *Pardosa dorsalis*, showed obvious penetration into the buffer, with consistently higher mean abundances in the buffer than in the forest, all the way up to the stream edge. The eurytopic millipede species, *Harpaphe haydeniana*, showed similar mean abundances at all distances from the stream (the sharp peak at 10 m in the buffer resulted from an anomalous convergence of almost 137 millipedes in a single trap during one sampling period), across the three treatments.

Responses to the buffer edge also varied among the two forest indicators. *Scaphinotus angusticollis* had lower mean abundances throughout the buffer than in the forest, but especially at the buffer edge (20 m from the stream). *Cybaeus cascadius*, an agelenid spider, was most abundant in the forest, but also occurred in similarly low numbers in the clearcut and the buffer (except at 10 m). For the weevil, *Steremnius carinatus*, which appeared to be associated with upslope forests, mean abundance increased at the buffer edge relative to the forest and clearcut at the same distance, indicating it may be a species especially well adapted to edge conditions. For the stream edge/forest indicator, *Pterostichus crenicollis*, mean abundances in the forest were higher between 1 and 10 m from the stream than in the buffer, but all treatments showed a similar distribution pattern along the distance transect, with very high mean abundance at 1 m from the stream, and a steep decline beyond this distance.

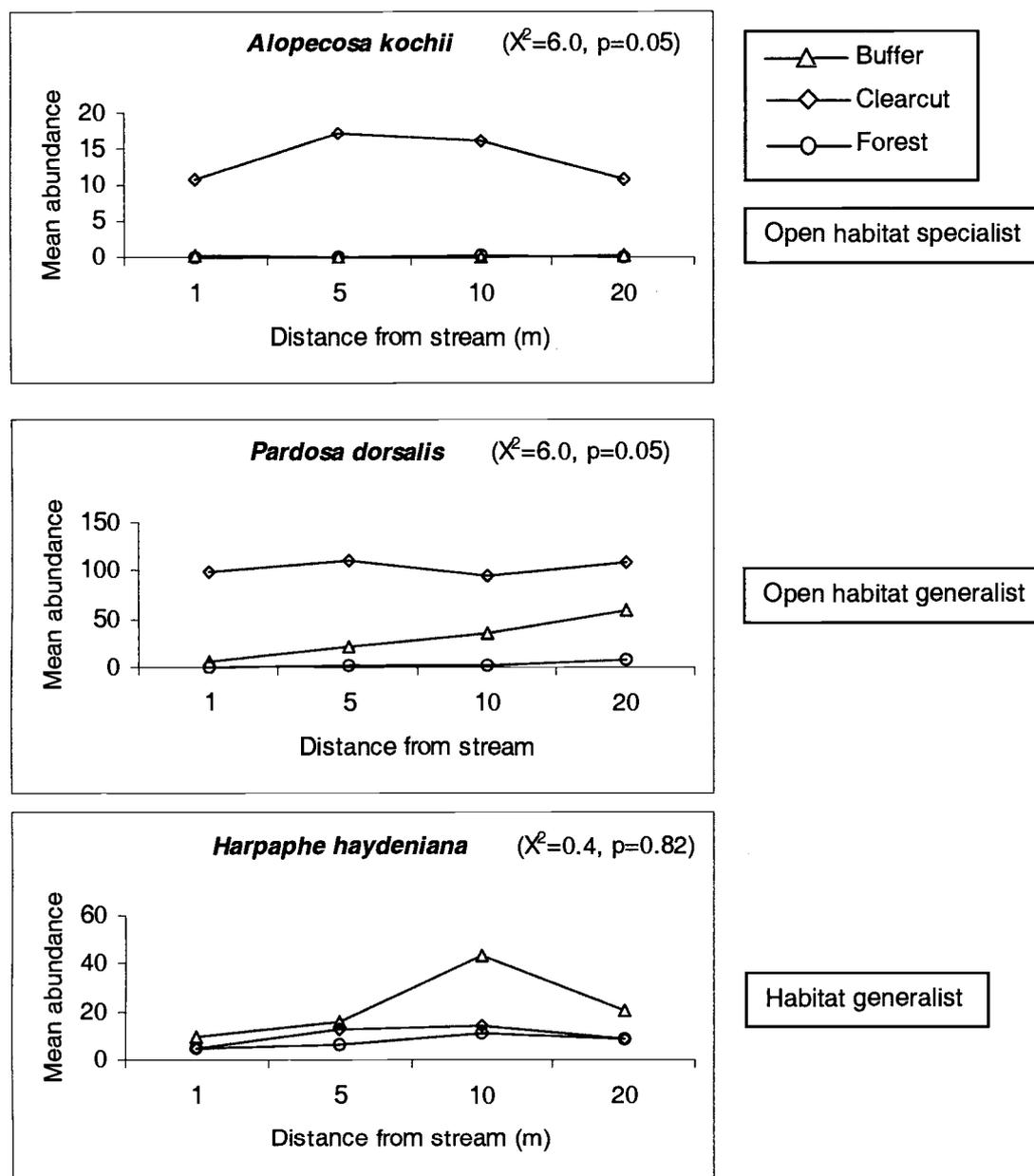


Figure 2.9 Mean abundance per trap zone of selected species at increasing distances from the stream, across buffer, clearcut, and forest treatments. Chi-squared statistic from Friedman's Test and associated p-value indicates strength of treatment effect (mean abundances averaged over all distances within a treatment).

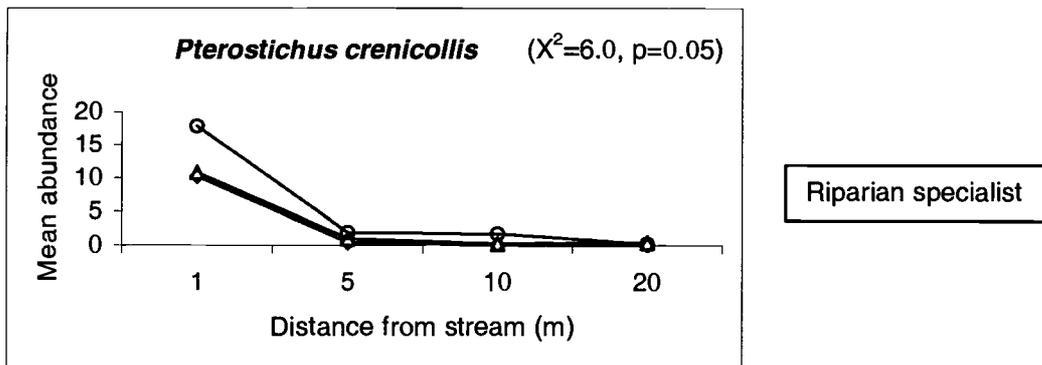
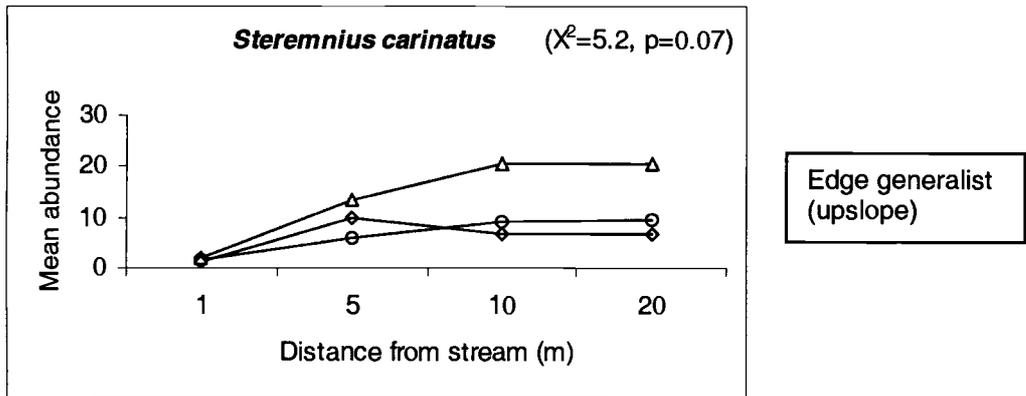
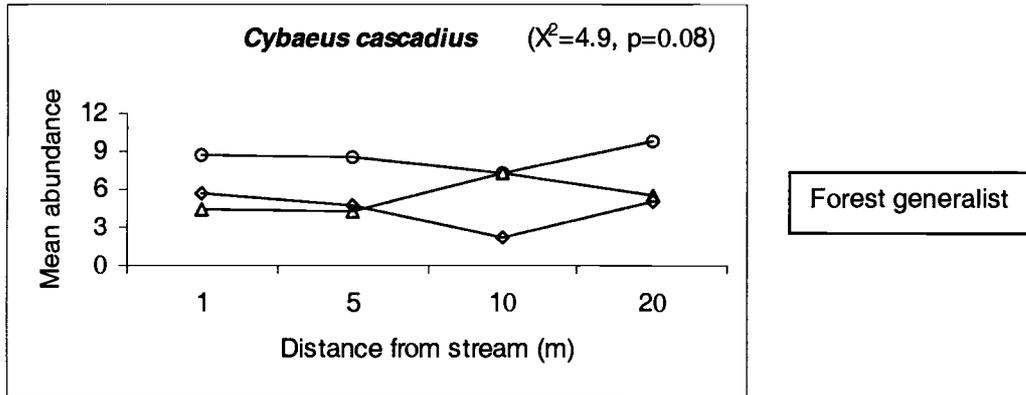
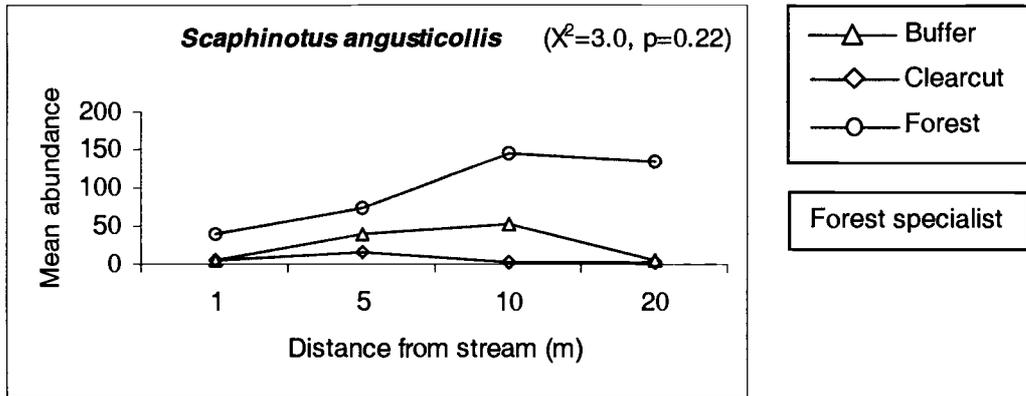


Figure 2.9 (continued)

DISCUSSION

Two variables, elevation and block, had stronger than expected influence on invertebrate community composition. Of the 203 species considered in this study, 34% were restricted to high (1000-1200 m) elevation sites, and 19% were restricted to low (400-600 m) elevation sites. While altitudinal limits for species distributions are commonly observed (Thiele 1977, Olson 1994, Reynolds and Crossley 1997, Touyama and Yamamoto 1997), the physical or biological drivers behind these distribution patterns are difficult to discern. Climate and its effects on vegetation composition and structure often have been proposed as factors regulating faunal distributions along elevational gradients (Thiele 1977, Currie 1991, Olson 1994, Butterfield 1996). In this study, air temperature and relative humidity during the growing season showed little association with the axis strongly correlated with elevation in the ordinations, and thus are not likely to be controlling altitudinal distributions. Higher sites were covered in snow for several months in winter, while lower sites were generally snow-free, however, I was not able to record microclimate variables through the winter. Shrub density, species diversity, and herb cover were strongly associated with elevation, and may have influenced forest-floor invertebrate communities by varying habitat structure, food sources for herbivores, or affecting soil moisture. Block effects also were influential. Although each block of sites was located in a different sub-drainage of the greater South Santiam River watershed, it is surprising that five blocks within a total area of less than 400 km² would show such distinct differences in community composition. Whether these distribution patterns reflect naturally disjunct populations of invertebrate species, or are an artifact of forest fragmentation effects at a larger scale than that considered in this study (Spence et al. 1996) cannot be determined here.

The ecological significance of headwater stream riparian zones in a forested landscape

Previous studies have documented a distinct invertebrate fauna associated with stream riparian ecotones in mid- to high-order streams and rivers, especially on gravel bars, floodplains, and other habitats close to the water's edge. For instance, Hering (1998) and Hering and Plachter (1997) found carabid beetles specializing on aquatically derived prey such as chironomid, caddisfly, and stonefly larvae, while Zulka (1994) recorded adaptations by riparian carabid species to periodic flooding events. The federally threatened tiger beetle, *Cicindela puritana* G. Horn, historically existed in metapopulations along the banks of the Connecticut River, where larvae require sandy substrate to excavate burrows (Omland 2002). Other studies have documented habitat partitioning by carabid and lycosid assemblages alongside rivers and in floodplain forests (Spence 1979, Moring and Stewart 1994, Sustek 1994a, Andersen 1997,

Antvogel and Bonn 2001). Brenner (2000), working just 30 km south of my study sites, found twice as many individuals and a higher diversity of beetles in the riparian zone of a 3rd-order stream than in the adjacent upslope forest habitat. In this study, the diversity of species did not differ significantly with distance from the stream, however, the community composition at 1 m from the stream appeared to be distinctive from all other distances, with the carabid beetle *Pterostichus crenicollis* and the snail *Striaria pugetensis* being the best indicators of this streamside community. Patterns of invertebrate distribution through the riparian ecotone were more strongly associated with microclimatic gradients than with distance from the stream, and it seems likely that streamside “riparian” species in these forests were responding to the cool, humid microclimate associated with headwater streams rather than to any particular riparian microhabitats (e.g., gravel bars, floodplains). While headwater stream margins are not the only places providing cool temperatures and high humidity in these forests during the dry summer months, they are an important resource along with seeps and other damp, shaded areas.

Affinity of some species for a cool, humid microclimate has been reported among carabid beetles (Thiele 1977, Andersen 1985, Wenninger and Fagan 2000) and lycosid spiders (Moring and Stewart 1994). Soil moisture, which I did not measure directly, but often observed to be higher next to the stream, also is known to be important for determining invertebrate distributions (Lowrie 1973, Epstein and Kulman 1990, Andersen 1997, Sustek 1994a, Deharveng and Lek 1995, Antvogel and Bonn 2001). Niemalä et al. (1988) described the carabid, *Agonum mannerheimi* Dejean, to be a forest specialist strongly tied to seeps and small marshes in mature coniferous forest. In this study, *P. crenicollis* and *S. pugetensis* also were strong indicators of a cool, humid microclimate in forested sites. The low number of indicators for the streamside and cool, humid microclimate classes may be because species strictly associated with a cool, humid microhabitat are rare (in abundance and distribution), and/or restricted to high or low elevations. Such species would make poor regional-scale indicators because of their sparse and geographically-limited distributions.

Functional and taxonomic diversity also varied with distance/microclimate and with elevation. Millipedes, the only detritivores included in the study, comprised a higher proportion of species at lower elevations, while predator species, primarily beetles, increased in proportion at higher elevations. Herbivores, especially gastropods, increased in proportion in cooler, humid sample units closer to the stream, corresponding with an increased cover of herbaceous vegetation. Interestingly, of the four snail-feeding carabids in the tribe Cychrini, none were strongly correlated with the cool, humid end of the ordination. Spiders comprised a higher proportion of species in the warm/dry trap zones further away from the stream. This may have

been influenced by the appearance of species such as *Zelotes fratris*, an indicator for the warm/dry group, and *Pardosa dorsalis*, both species typically associated with open habitats such as clearcuts (Jennings et al. 1988, McIver et al. 1990).

Evaluating management alternatives for headwater stream riparian zones

Invertebrate communities in riparian buffers of ~30 m width were far more similar to those in intact riparian forests than were those in clearcut riparian zones. At lower elevations especially, there was no discernible difference in community patterns at various distances from the stream between the buffer and forest treatments. Also, invertebrate communities at 1 m from the stream in the buffer and forest treatments, as well as in two sites in the clearcut treatment, were more similar to each other than to communities at other distances within the same treatment, supporting the notion that near-stream assemblages are a distinct set of forest fauna. Again, microclimate explained much of the variation associated with treatment differences, with a gradient of cool, humid conditions at the stream edge, to intermediate conditions at further distances from the stream in forest and buffer treatments, to the warmest, driest microclimate in the upslope clearcut treatment. Comparably strong associations of carabid beetle distributions and microclimatic variables across a forest-grassland transect were observed by Magura et al. (2001). Among indicator species, there was a high correspondence between clearcut and warm/dry microclimate indicators, and these far outnumbered the indicators of either the forest/buffer or cool/humid groups. These results support Niemälä's (1997) estimation that old-growth forest specialists make up only 10% of the forest-floor arthropod fauna. There was far less correspondence between indicator species of the forest/buffer group and the cool/humid group, perhaps because the forest/buffer trap zones comprised a relatively broad range of microclimate.

Expected functions of riparian buffers

In order to assess the ecological value of riparian buffers as part of a headwater riparian management strategy, it is critical to have a clear understanding of what functions the buffers are intended to serve. For instance, a primary aim may be to protect aquatic resources (such as salamanders or downstream salmonids) by providing shade and erosion control for the headwaters. An additional management goal may be to protect the unique terrestrial riparian fauna associated with headwater streams. Results from this study suggest that the ecotone harboring a distinctive "riparian" invertebrate fauna along headwater streams may be less than 5 m wide, and that a minimal shrub/small tree buffer along the stream edge may provide as much

protection for some riparian species as a 30 m buffer (e.g., *P. crenicollis*; Fig. 2.9). However, if riparian buffers are intended to provide long-term refugia or dispersal corridors for not only riparian, but also forest specialists, then the buffers must be evaluated as forest fragments, and characteristics such as size (width) and edge effects must be considered.

Riparian buffers as refugia for riparian/forest species

Riparian buffers are essentially long, narrow forest fragments, which, if connected upstream and downstream with other tracts of mature forest, also may represent dispersal corridors. Research from both temperate and tropical regions has documented the two main effects of forest fragmentation on invertebrate diversity and distributions. Isolation (both spatial and temporal) of forest fragments can affect the dispersal of forest specialists to other forest patches (Niimalä et al. 1993b, Niimalä 1997, Didham et al. 1998a, de Lima and Gascon 1999), while habitat modification can affect the long-term survival of populations within a forest fragment (Halme and Niimalä 1993, Niimalä et al. 1993b, Davies and Margules 1998, Didham et al. 1998a, Carvalho and Vasconcelos 1999). The extent of habitat modification will depend on fragment shape, size, and edge effects (Didham 1997). Typical edge effects may include: physical modifications to the forest habitat such as changes in microclimate; direct biological effects such as the disappearance of forest specialists at fragment edges, or the invasion of open-habitat species into forest fragments; and indirect biological effects such as the potential intra-guild interference that an invading predator may exert on an existing forest predator community (Murcia 1995, Lang 2003).

Studies focusing exclusively on physical edge effects associated with microclimate have documented changes in variables such as air temperature and relative humidity extending from 30 to 240 m into the forest (Chen et al. 1995). Given that the riparian buffers considered in this study measured an average of 30 m wide on either side of the stream, one might conclude that they contained no unmodified forest habitat at all. Indeed, the elongate, narrow shape and resulting high edge-to-interior ratio of riparian buffers makes them comparable to European hedgerows in their vulnerability to physical (and biological) edge effects (Bedford and Usher 1994, Sustek 1994b). However, riparian buffers differ from hedgerows in a fundamental way, because, by definition, they encompass (or lie adjacent to) a stream, and often an associated valley. The microclimatic "stream effect" which provides cool, humid conditions some distance upslope, may thus serve as a modifying influence on the opposing warm, dry conditions contributed by the clearcut-influenced "edge effect" in a riparian buffer that is only 30 m wide. Brosfoske (Brosfoske et al. 1997), working in relatively small forested streams, found that the

microclimatic stream effect exerted gradients (in air and soil temperature, relative humidity) that extended 30 to 60 m from the stream, where they reached upland forest interior values. These results, and comparable findings in this study (Chapter 3), suggest that at 20 m from the stream in a riparian buffer (where the outermost buffer “edge” sampling station was located) the microclimate may approximate upland forest interior values, and perhaps provide suitable conditions for forest species and communities.

Direct biological edge effects, exemplified by the disappearance of forest specialists, the attraction of “edge species,” or the invasion of open-habitat species into forest fragments, have been documented in both forest and agricultural settings, and measured to penetrate from 5 to 200 m into a forest fragment (Halme and Niemälä 1993, Bedford and Usher 1994, Pajunen et al. 1995, Spence et al. 1996, Work 2000, Magura et al. 2001). Heliola et al. (2001), on the other hand, describing the distribution of carabids across a forest-clearcut edge, found no evidence of direct biological effects. Magura et al. (2001) classified carabid species into five categories based on their distribution across a forest-grassland transect: habitat generalists, open habitat-associated species, forest generalists, forest specialists, and edge-associated species. I found examples of all such patterns among the species considered in Fig. 2.9, as well as riparian specialists, and open habitat generalists (Fig. 2.10). Of course, most invertebrate species distributions defy strict categorization, so that even the “forest specialist” *Scaphinotus angusticollis* occurred in low numbers in the clearcut treatment within 5 m from the stream, perhaps representing either remnant or dispersing individuals.

Patterns in univariate community measures—such as species richness and diversity—across ecotones or between harvest treatments appear to defy generalization. For instance, Bedford (1994) and Magura (2001) found higher beetle and spider diversity at the edge between forest and open land in comparison to that in forest or open land alone, while Didham et al. (1998b) and Davies and Margules (1998) found that beetle richness did not change from the interior to the edge of a forest fragment, with forest species being replaced by open habitat species. Spence et al. (1996) measured intermediate species richness at the edge, the highest numbers of species in the clearcut, and lowest in the forest. In my study, species richness and diversity did not vary significantly with distance from the stream (or edge) in any of the treatments. However, overall species richness was higher in the clearcut treatment than in the buffer or forest treatments. Such a pattern of increased species richness in clearcuts over forests has been attributed to both a persistence of forest generalists and a high diversity of open-habitat species such as diurnal hunting spiders (e.g., lycosids and gnaphosids; McIver et al. 1990, Pajunen et al. 1995, Niemälä 1997). The overall usefulness of using diversity measures to detect

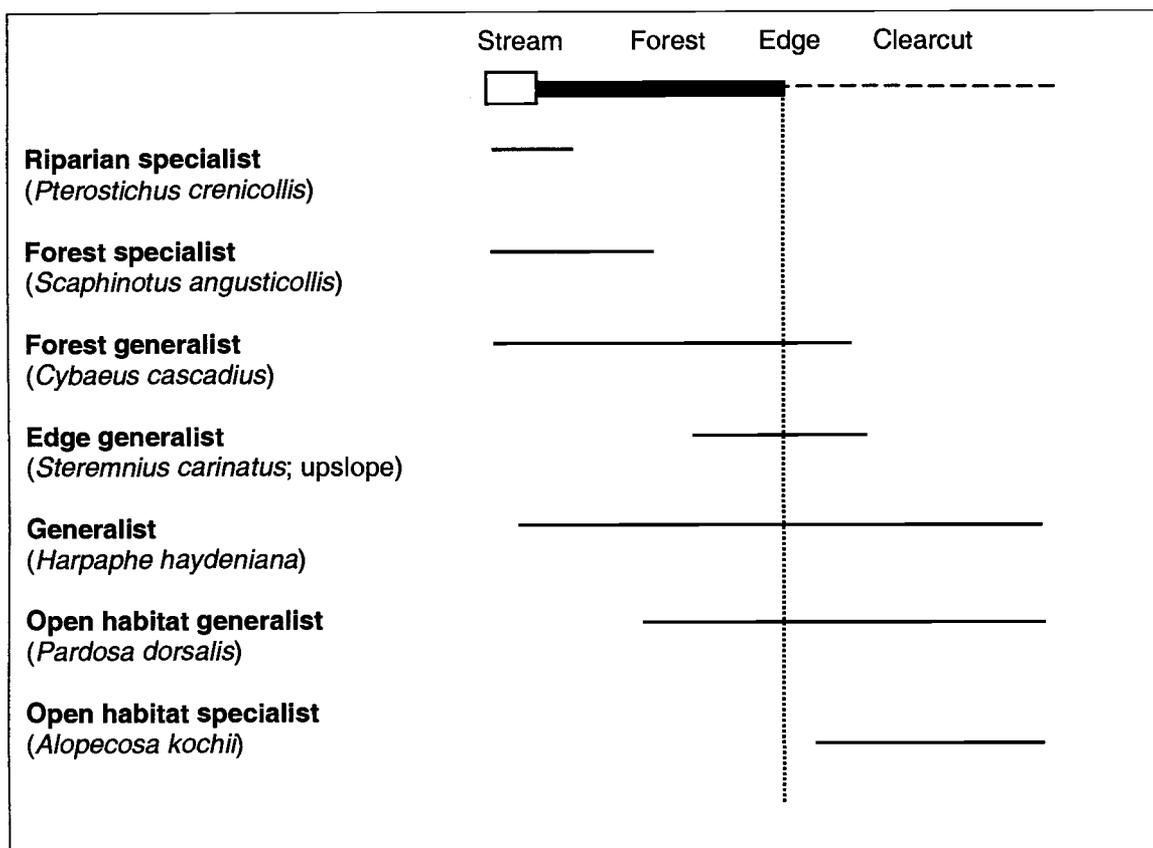


Figure 2.10 Characteristic distribution patterns (represented spatially by lines) of species groups across a riparian forest-clearcut edge. Plots of mean abundance with distance-from-edge in different treatments for species listed as examples are shown in Fig. 2.9.

effects of disturbance or habitat heterogeneity has been debated by some (Belaoussoff et al. 2003), and it is often the case that effects of habitat fragmentation on species abundance are more apparent than on diversity measures (Davies and Margules 1998). Edge effects could be inferred when comparing proportional abundances of the four major taxa (spiders, beetles, gastropods, millipedes) among the three treatments. Buffer treatments had proportionally more spiders, and fewer beetles and gastropods than forest treatments, and thus showed a pattern intermediate between forest and clearcut treatments.

Multivariate edge effects at the community level were not clearly discernible. Invertebrate communities in forest trap zones and in buffers not subjected to blow-downs were quite similar. In most of the blocks, stream effects associated with a cool/humid microclimate appeared to exert a stronger influence on community distributions than clearcut-influenced edge effects. In sum, results suggested that while individual species responded to the buffer edge in various ways (some species perhaps responding to microclimatic edge effects), diversity at the

edge was not obviously affected, and species responses were not strong enough (perhaps because species numbers were so variable and distributions so patchy) to affect responses at the community level.

Invertebrates as biological indicators

Although many invertebrate attributes (e.g., abundance; diversity of species, size, dispersal traits, functional roles, life cycles, responses to environmental gradients) make them ideal indicator organisms for assessing habitat heterogeneity and ecological integrity (Rosenberg et al. 1986, Kremen et al. 1993, Pearson 1994, Oliver and Beattie 1996b), some of these same attributes can make invertebrates an especially challenging group to research. In this study, limited or patchy distributions of many species at high versus low elevations, or among different sub-drainages, made forest-floor invertebrates less than ideal "global" indicators of habitat type or treatment. Madson (1998) similarly found that differences in invertebrate species composition between sampling blocks in western Oregon overwhelmed any forest thinning treatment differences. The dominance structure of most invertebrate communities, with a few very common species, and the vast majority of species being uncommon or incidental occurrences, also contributes to this difficulty in finding ubiquitous indicators. Additionally, assumptions associated with standard parametric statistical analyses are usually not met by individual species distributions. Consequently, multivariate community analysis is a more robust tool for discerning invertebrate distribution patterns. Even with ordination techniques, however, rare species are typically deleted as "noise" in the data set (McCune and Grace 2002), thus potentially interesting information will be lost.

The choice of focal taxa and level of resolution for identification may affect the quality of results. In this study, I made an effort to work mostly with groups with a relatively well-known and stable taxonomy. In selecting a limited number of "surrogate" beetle and spider groups, I ignored taxonomically challenging groups that may have been effective riparian indicators (e.g., Ptiliid beetles) or forest indicators (e.g., Linyphiid or Erigonid spiders). Oliver and Beattie (1996a) similarly found that using surrogate taxa to measure species richness and turnover across habitat types compromised the level of accuracy in detecting differences. However, they concluded that the benefit of increased survey efficiency using surrogate invertebrate taxa was an acceptable trade-off for lower accuracy. Another strategy to increase efficiency and approach taxonomically difficult groups in invertebrate diversity studies has been to use morphospecies (Oliver and Beattie 1996b, Dangerfield et al. 2003), or coarser level resolution (i.e., genus or family) for sample identification. While species-level taxonomy is likely to result in some

redundancy in information at the cost of time and taxonomic effort, in my study, this level of resolution revealed three species within the genus *Pterostichus* to be strong indicators of three separate microclimatic groups, and two species of lycosid spiders to vary greatly in the degree to which they invaded a forested riparian buffer. The benefits of using species level resolution will likely vary according to the types of questions being asked, and the taxonomic groups being considered.

Despite the ecological and taxonomic challenges posed by invertebrates, they represent, both numerically and functionally, such an important component of biodiversity that they cannot be ignored when evaluating patterns of diversity in the landscape. Although their small size and general “invisibility” make them easy to overlook when developing landscape level forest management strategies, the distribution and movement of invertebrates across the landscape, and their response to human disturbances, disclose patterns that provide important insights into more general ecosystem processes.

Management implications

For a riparian management strategy to be effective, its expected functions must be clearly articulated. The configuration (including position, width, contiguity) of riparian protection in the landscape can then be designed accordingly, based on the best available data. For instance, data from this study suggest that, from a forest-floor invertebrate’s perspective, the riparian ecotone associated with headwater streams is no more than several meters in width. This pattern of a “spatially compressed” riparian zone and fauna in headwater basins, as compared to larger drainages with a more distinctive riparian fauna, was also documented for amphibians by Sheridan and Olson (2003). In some cases, a minimal shrub buffer may be adequate to preserve the community composition associated with this narrow ecotone. However, other forest specialists, more prone to edge effects, such as *Scaphinotus angusticollis*, require a forested buffer, and moreover, may benefit from riparian buffers with a lower edge-to-interior ratio. For example, in a dendritic hedgerow network in France, Petit and Burel (1993) found reproducing populations of carabid beetles were concentrated in intersections, or “nodes.” Likewise, confluences of small streams may provide good core areas for larger, “rounder” riparian forest refugia that encompass more than one headwater stream, and may be less susceptible to windthrow (Cissel et al. 1998). However, this configuration may come at the expense of losing connectivity with upstream and downstream forest fragments.

While not directly addressed in this study, the spatial and temporal isolation of forest fragments in the landscape should also be considered. Collinge et al. (2001) found that

threatened valley elderberry longhorn beetles associated with fragmented riparian woodlands displayed metapopulation dynamics, and isolation of populations beyond their dispersal capabilities threatened species survival. In a study on the effects of temporal isolation on carabid populations, Petit and Burel (1998) determined that present distributions of carabids in a hedgerow network were more influenced by the landscape of 40 years ago, than by recent modifications, suggesting that they were able to survive in isolation for some time. This time lag in response of a species to human disturbance may provide a window of opportunity for landscape restoration such as forest regrowth, and/or reconnection of forest fragments. In contrast, Niemalä et al. (1993a) reported that populations of several carabid species considered to be forest specialists did not recover in regenerating clearcut sites even 27 years after logging, and McIver et al. (1990) estimated that a minimum of 30 years were required for a forest spider community to reestablish in the wettest clearcut sites.

It is apparent that whether a riparian buffer serves as a source or sink (Pulliam and Danielson 1991) for riparian/forest specialists will depend both on characteristics of the buffer itself (shape, size, isolation, edge-to-interior ratio), and on the population dynamics and dispersal capabilities of each species (Den Boer 1990). In this study, riparian buffers were approximately five years old, and thus some invertebrate populations within them may still represent forest "remnants" with no dispersal potential. Among carabid beetles, many forest specialists have lost use of their wings, and thus are poor dispersers (Halme and Niemalä 1993, Lattin 1993), while colonizers of open habitats such as clearcuts typically display strong dispersal traits such as the "ballooning" behavior of small spiders (Foelix 1996). Even if riparian buffers do not provide viable breeding habitat for some forest specialists, they may still serve an important function as corridors for dispersal between larger forest fragments upstream and downstream. For example, hedgerow studies in Europe showed that windbreaks of 15-30 m width were used by some carabids to travel through arable land, even if the hedgerows were not used as breeding habitat (Sustek 1994b, Charrier et al. 1997).

An effective riparian management strategy will encompass a range of ecological functions, and balance the habitat needs of invertebrate, vertebrate, and plant taxa. Flexibility in the configuration and design of riparian protection strategies, according to local conditions and goals, will likely be a key factor for success (Gregory 1997). For instance, the Aquatic Conservation Strategy in the federal Northwest Forest Plan (USDA and USDI 1994, Tuchman et al. 1996), calls for individual assessments of watersheds, and allows for a variety of management options including: no riparian protection, fixed-width buffers, restricted harvest areas; and the creation of larger patch reserves (Sedell et al. 1994, Cissel et al. 1998). Elsewhere, riparian

buffers of various widths and thinning densities have been proposed and implemented (Kelsey and West 1998, Olson et al. 1999), and an abundance of literature documents the effects of varying buffer width on breeding and dispersing populations of vertebrates (Machtans et al. 1996, de Lima and Gascon 1999, Hagar 1999, Pearson and Manuwal 2001, Vesely and McComb 2002, Cockle and Richardson 2003). Landscape scale studies with invertebrates, such as this one, that address riparian management and conservation issues will be an integral addition to this database, and will help to inform land managers of more effective riparian management options.

CHAPTER 3

MICROCLIMATE PATTERNS ASSOCIATED WITH ALTERNATIVE RIPARIAN MANAGEMENT TREATMENTS IN THE WESTERN OREGON CASCADE RANGE

INTRODUCTION

As ecotones between aquatic and upland terrestrial systems, riparian zones typically encompass steep environmental gradients and a heterogeneous mosaic of microhabitats (Risser 1995, Naiman and Decamps 1997), and are considered to be one of the most ecologically complex and dynamic components of Douglas-fir forests in the Pacific Northwest (Gregory et al. 1991, Naiman et al. 1998). Riparian forests provide important functions in the landscape: they directly affect stream quality by providing shade and allochthonous material such as leaf litter and wood, as well as controlling bank erosion (O'Laughlin and Belt 1995, Naiman and Decamps 1997); they provide habitat for terrestrial flora and fauna, including riparian specialists (Raedeke 1988, McComb et al. 1993, Naiman et al. 1993, Pollock 1998, Antvogel and Bonn 2001); and their dendritic networks in the landscape may serve as movement or dispersal corridors for propagules, individuals, or air masses (Naiman and Decamps 1997, Chen et al. 1999, de Lima and Gascon 1999). Especially in the dry summer months typical of the temperate "rain forests" of the Pacific Northwest, streams and their associated riparian zones provide a critical microclimatic resource to many species, in the form of a cool, moist microenvironment (Harris 1984). Small, often intermittent, headwater streams comprise the vast majority of the lotic network in these forests, yet little research exists relating the size and topography of a stream to the magnitude or extent of its influence on riparian and upslope microclimate (but see Brososke et al. 1997, Olson et al. 2000). It is important to have a clearer understanding of the function of headwater streams as a distinct microclimatic resource because these small streams and their riparian zones are particularly vulnerable to harvest disturbance (Sheridan and Olson 2003).

Management strategies for headwater streams and their riparian zones have developed since riparian buffers were first implemented along larger streams to shade and protect fish habitat in the 1970s (Gregory 1997). With the realization that smaller, non-fish-bearing streams and their riparian zones also provide important functions in the landscape, a variety of aquatic and riparian conservation strategies have been implemented on entire watersheds and on streams of all sizes on federal, state, provincial, and private lands in the Pacific Northwest. On the smallest streams in Oregon, these management practices include leaving no buffer, leaving minimal intact streamside buffers within wider zones of restricted timber harvest, and preserving intact buffers up to the size of local site potential tree-heights (USDA and USDI 1994, Gregory 1997, Young

2000). Leaving the narrowest of buffers alongside headwater streams has the potential to take a large amount of land out of timber production in the region's highly dendritic landscapes, yet even the widest buffers currently used essentially comprise long, narrow forest fragments, which may be susceptible to strong edge effects and thus not effective in preserving interior riparian conditions (Laurance and Yensen 1991).

Physical edge effects involving changes in variables such as air temperature, soil temperature, relative humidity, airflow, and light intensity at forest edges have been widely-documented (Matlack 1993, Chen et al. 1995, Davies-Colley et al. 2000, Newmark 2001). An altered microclimate at the forest edge has, in turn, been associated with biological effects such as changes in forest vegetation density and structure (Williams-Linera 1990, Young and Mitchell 1994, Camargo and Kapos 1995, Davies-Colley et al. 2000), changes in the diversity and distribution of plant and animal species (Didham et al. 1998a, Gehlhausen et al. 2000, van Wilgenburg et al. 2001), and the altering of ecological processes such as nutrient cycling (Klein 1989, Chen et al. 1999, Geiger et al. 2003). While forest edges may be considered a transition zone between forest interior and open habitat conditions, some forest edges have recorded more extreme values and diurnal variation in microclimate than the habitats on either side (Chen et al. 1993), and "edge-philic" species that are strongly associated with such conditions may be a component of edge communities (Work 2000). Both physical and biological edge effects have been documented to penetrate from 2.5 to over 200 m into the forest interior depending on edge orientation, edge age, daily or seasonal cycles, and local weather conditions (Williams-Linera 1990, Matlack 1993, Chen et al. 1995, Gehlhausen et al. 2000, Work 2000). Together, these observations suggest that a riparian buffer of 30-75 m width (or 60-150 m, if on both sides of the stream), the approximate range currently prescribed along non-fish-bearing headwater streams in Oregon, may comprise essentially all "edge" in terms of both abiotic and biotic modifications.

A critical difference between riparian buffers and similarly shaped upslope forest fragments is that riparian buffers encompass (or lie adjacent to) a stream, and often an associated valley. This unique juxtaposition of stream, forest, and cleared habitat represents an anthropogenic ecotone (forest edge) superimposed on a natural ecotone (riparian zone). In a headwater setting, both ecotones are likely to be spatially compressed (Sheridan and Olson 2003), but still overlapping (Fig. 3.1). It may be that the cool/humid influence exerted by the stream on riparian and upslope microclimate (i.e., the stream effect) serves as a modifying influence on the opposing warm/dry conditions contributed by the clearcut-influenced edge effect from above. To date, most studies have focused on either the stream effect (e.g., Brosofske et al. 1997, Olson et al. 2000) or the forest-clearcut edge effect (e.g., Chen et al. 1995) on microclimate. I attempted

to characterize and quantify both effects simultaneously in small headwater streams in the western Cascade Range of Oregon. Documenting and interpreting such information will aid riparian management decisions and contribute to the specification of headwater riparian buffer reserves for preservation.

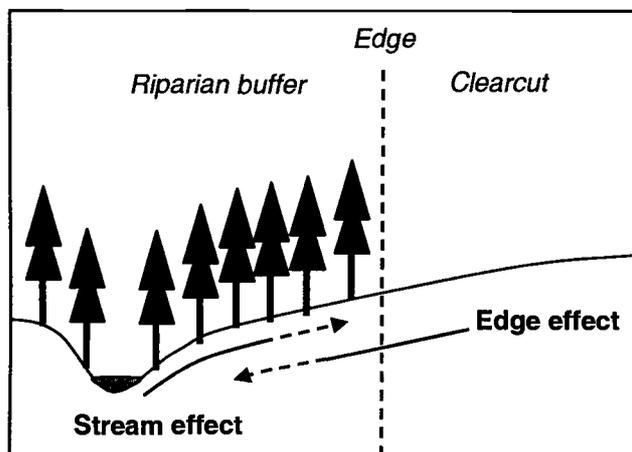


Figure 3.1 A hypothetical model of opposing daytime “effects” on microclimate exerted by the stream (i.e., cooler air and soil temperatures, higher relative humidity extending away from the stream) and by the clearcut adjacent to the riparian buffer edge (i.e., warmer air and soil temperatures, lower relative humidity extending towards the stream).

I compared trans-riparian patterns of three microclimate variables (air temperature, soil temperature, and relative humidity) between three riparian management treatments on headwater streams: mature forest riparian zone (control); clearcut harvest with a minimal or no buffer adjacent to the stream; and preservation of a ~ 30 m forested riparian buffer on each side of the stream with adjacent clearcut upslope. Specifically, my objectives were to: (1) characterize and quantify riparian microclimatic gradients associated with headwater streams in mature, unmanaged forests (i.e., describe the natural “stream effect”); (2) determine if similar microclimatic gradients were maintained in the clearcut and buffer treatments, including examination of clearcut-influenced edge effects in the buffer treatment; and (3) compare seasonal variability in microclimate variables along a trans-riparian transect from the stream edge, through the riparian buffer, and out to the clearcut.

METHODS

Regional setting

Study sites were in the Sweet Home Ranger District of the Willamette National Forest, on the western slope of the Cascade Range in Oregon, USA. The regional climate can be broadly characterized as having wet, mild winters—with snow accumulation at higher elevations—and warm, dry summers (Franklin and Dyrness 1988). Approximately 90% of the annual precipitation falls in winter (Harris 1984). Forest canopies at mid-elevations are dominated by Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), western redcedar (*Thuja plicata* Donn) and, at higher elevations, by Pacific silver fir (*Abies amabilis* (Dougl.) Forbes) (Franklin and Dyrness 1988). All sites within this study fell within the western hemlock zone, as classified by Franklin and Dyrness (1988). This vegetation zone comprises the majority of forest lands in western Oregon, and is economically significant for its timber production (Franklin and Dyrness 1988). Shrub and herb communities within these forests vary with elevation, soils, moisture availability, and other variables, but commonly include vine maple (*Acer circinatum* Pursh), rhododendron (*Rhododendron macrophyllum* G. Don), red alder (*Alnus rubra* Bong.), Oregon-grape (*Berberis nervosa* Pursh), salal (*Gaultheria shallon* Pursh), and sword fern (*Polystichum munitum* (Kaulf.) Presl).

Site selection

I selected 15 first- or second-order headwater stream sites in low- to mid-elevation drainages (Table 3.1). Five replicate sites were chosen to represent each of three treatment types: old-growth forest on either side of the stream with contiguous forest upslope (control); forested riparian buffer of approximately 30 m width on either side of the stream with clearcut harvest upslope; and clearcut harvest with minimal to no tree retention in the riparian zone. I first identified potential riparian buffer sites from aerial photos, and field-checked those sites with riparian buffers along headwater streams that were ≥ 25 m width (on either side of the stream) and ≥ 200 m long. Five riparian buffer sites in the study area met these criteria. One forested site and one clearcut site was matched with each riparian buffer site to form a total of five replicate blocks with three treatments each. Because sites were not randomly selected, all inferences are limited to the actual sites considered in this study. Sites within a block were located within 4 km of each other, and in four blocks, two of the three treatments were located on the same stream (separated by a minimum distance of 250 m). Each of the five blocks was located within a different sub-drainage of the U.S Forest Service district; three of these blocks were at higher elevations (1000-1268 m) and two blocks were at lower elevations (415-610 m). Forested control

Table 3.1 Site locations, physical characteristics, and management history.

Block	Treatment	Latitude	Longitude	Elevation (m)	Transect slope aspect*	Buffer edge aspect**	Avg. buffer width (m)***	Avg. stream width (m)	Harvest date(s)
2G	Buffer	N 44°20' 00.28"	W 122°17' 34.73"	1146	NW	NE	26.3	2.9	1995
2G	Clearcut	N 44°19' 33.88"	W 122°15' 33.66"	1268	NW			1.2	1993
2G	Forest	N 44°21' 01.60"	W 122°18' 14.09"	1146	W			3.5	
BP	Buffer	N 44°24' 30.44"	W 122°23' 03.74"	512	SE	NE	29.8	1.7	1994
BP	Clearcut	N 44°24' 05.70"	W 122°22' 43.05"	415	W			1.5	1989
BP	Forest	N 44°24' 05.43"	W 122°22' 29.59"	439	W			2.1	
MM	Buffer	N 44°27' 21.99"	W 122°17' 21.31"	1000	N	W	29.8	3.8	1994
MM	Clearcut	N 44°27' 45.34"	W 122°15' 34.90"	1097	S			2.4	1978, 1995
MM	Forest	N 44°27' 13.95"	W 122°17' 12.51"	1097	NW			2.5	
SP	Buffer	N 44°33' 45.12"	W 122°10' 01.90"	1122	NE	SE	28.6	1.5	1994
SP	Clearcut	N 44°33' 41.30"	W 122°09' 26.29"	1073	N			2.6	1986, 1999
SP	Forest	N 44°33' 51.80"	W 122°09' 46.00"	1073	E			3.4	
TC	Buffer	N 44°24' 47.17"	W 122°15' 43.19"	561	NW	NE	34.3	5.1	1994
TC	Clearcut	N 44°24' 26.89"	W 122°16' 02.84"	561	W			1.2	1989
TC	Forest	N 44°24' 39.24"	W 122°15' 27.68"	610	W			3.6	

*Aspect of the slope on which microclimate sampling transect was located

**Aspect of the edge of the buffer in which sampling transect was located

***Average buffer width on either side of the stream

sites and forested portions of the buffer sites had never been harvested, with the exception of a light thinning upslope in the control site of the 2G block. Clearcuts had been harvested between 5 and 22 years previously, were burned 0-3 years post-harvest, and then replanted within a year after burning. All clearcut sites were still in early stages of succession, with no development of a conifer canopy among saplings.

Sampling design and data collection

At each site, I collected microclimate data along a 70 m transect located on one randomly chosen side of the stream. Each transect ran perpendicularly from the stream edge into the upslope forest and/or clearcut; the compass orientation of the transects usually varied between treatments within a block (Table 3.1). In the buffer treatment, forest-clearcut edges were oriented to the NE, W, and SE. I placed four data loggers along each transect at 1 m, 10 m, 20 m, and 70 m from the stream (Fig 3.2; transect length was shortened to 50 m at one site to keep furthest sample at least 50 m from another headwater stream). Data loggers at 20 m from the stream were within 5-10 m of the forest edge in the buffer treatment. As the forest edge was generally “feathered” with trees and stumps intermixed for at least 10 m, the 20 m data logger usually fell just a few meters downslope of the boundary of the intact forest. At each data logger station, I

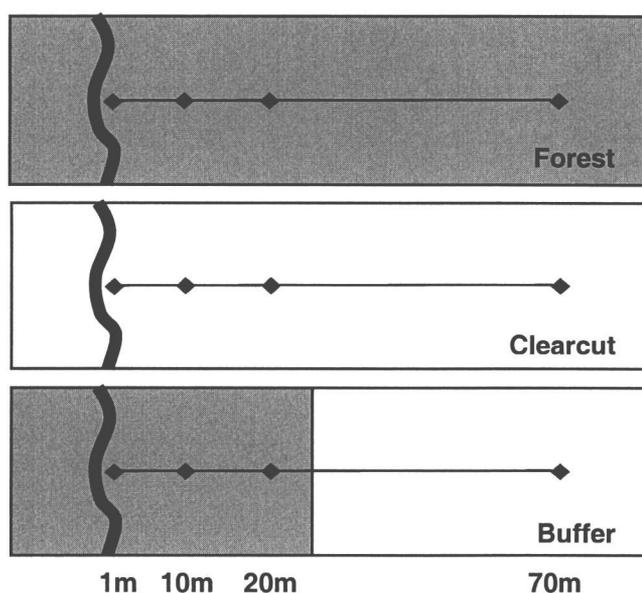


Figure 3.2 Sampling design for collecting microclimate data in three riparian management treatments. Gray = forest, white = harvested area, stream runs along left side. Data loggers (black diamonds) are located at 1, 10, 20, and 70 m from the stream edge on only one side of the stream at each site. Note that aspect of sampling transect may vary between treatments.

measured soil/litter temperature approximately 2-3 cm below the substrate surface, and ambient air temperature and percent relative humidity approximately 20 cm above the substrate surface. I measured microclimate parameters using GPSE 301 203 (THT-HR) Humidity and Dual Temperature Dataloggers. Temperature and relative humidity were measured every three hours, starting at 12:00 AM. The sensors measuring ambient air temperature and relative humidity were protected from rain and dew under a large, inverted cup that hung from a wire arm attached to the top of a stake driven into the ground. At the end of the sampling season, I placed all microclimate loggers into a climate-controlled chamber for calibration. Air and soil temperatures were accurate to within 0.3°C, and relative humidity was accurate to within 4%.

I had sufficient equipment to sample microclimate parameters at six sites (two blocks) simultaneously. I sampled microclimate at all five blocks in two sampling periods: late spring/early summer (between May 31 and July 13, 2002; average of 12 sampling days per block), and again in late summer (between August 27 and September 23, 2002; average of six sampling days per block).

Data analysis

I calculated "maximum" and "minimum" values for each microclimate variable (air and soil temperature, relative humidity) at each data logger station (15 sites x 4 loggers = 60 stations). In each block, maximum temperatures and minimum relative humidity were calculated by averaging the 3PM value over the two hottest consecutive days of the sampling period; minimum temperatures and maximum relative humidity represented the 6AM value over the two coolest consecutive days of the sampling period. Because the range and pattern of each microclimatic variable was similar between early summer and late summer seasons, I averaged both maximum and minimum values over the two sampling seasons. Maximum and minimum values were intended to represent extremes in microclimate, which might be limiting to the activity of some forest species.

All parametric analyses were performed with PROC MIXED in SAS, Version 8 (1999). Where assumptions of normally distributed residuals and homogeneity of variance were not met, I log-transformed the data. Reported results represent back-transformations to the original scale. In all tests, effects were considered statistically significant at a level of $\alpha = 0.10$.

Riparian forest microclimate: To investigate potential differences in the three microclimatic variables with increasing distance from the stream (1-70 m) in mature forest conditions I considered each data logger station (i.e., one distance at one site) to represent an experimental

unit. I fitted a model for a randomized complete block design (5 blocks) and used analysis of variance to test for a distance effect. Where the distance effect was significant, I determined the magnitude and extent of the microclimate gradient by comparing differences between consecutive distances from the stream (1 m vs. 10 m, 10 m vs. 20 m, 20 m vs. 70 m).

Riparian management and edge effects: To explore potential differences in the three microclimatic variables between management treatments (buffer, clearcut, forest) and between distances from the stream, I fitted a model for a split plot design, where each site represented the whole plot, and distances at 1-20 m from the stream comprised the split plots. Where the distance effect (averaged across treatments) was significant, I looked for differences between consecutive distances from the stream (1 m vs. 10 m, 10 m vs. 20 m) to determine the overall magnitude and extent of the microclimate gradient. Where the treatment effect was significant, I looked for differences between pairs of treatments. If the buffer was significantly different from the forest treatment, I looked for differences between these two treatments at comparable distances (i.e., buffer at 20 m vs. forest at 20 m) to determine the magnitude and extent of edge effects in the buffer. P-values and confidence intervals for all pair-wise comparisons were adjusted by the Tukey method for multiple comparisons.

Seasonal variability in microclimate across the buffer edge: I examined differences in microclimatic variability along a transect from stream edge (1 m) to the "interior" of the riparian buffer (10 m) to the buffer edge (20 m) to the clearcut (70 m), by subtracting the mean minimum from the mean maximum for each microclimate variable at each data logger station. Because minimum and maximum values were measured on different days during sampling periods (i.e., the two consecutive hottest days were not also the two consecutive coolest days), and then averaged between two sampling periods, I refer to the final measure used for variability as "seasonal," to differentiate it from diurnal variability. Seasonal variability thus encompasses the range of temperatures or humidity that non-dispersing invertebrates (perhaps in different life stages) must tolerate within the growing season. Data logger stations between 1 and 70 m from the stream were considered experimental units. Again, I fitted a model for a randomized complete block design and used an analysis of variance to examine potential distance effects on variability for each of the three microclimate variables. Where the distance effect was significant, I looked for differences in seasonal variability between consecutive distances from the stream. I also plotted the mean variability of microclimate variables in the forest treatment to provide a

visual reference for expected patterns in an unmanaged, "interior" forest, but did not include this treatment in the analysis.

RESULTS

Riparian forest microclimate

In the forested treatment, mean maximum air temperature (at 3PM) differed significantly with distance from the stream ($F_{3,12} = 14.68$, $p < 0.001$). A gradient of increasing air temperature with increasing distance from the stream was evident between 1 and 20 m from the stream (a cumulative increase of 5.35 °C), air temperature then leveled off between 20 and 70 m from the stream (Table 3.2, Fig. 3.3). The median minimum air temperature (at 6 AM) did not differ significantly with distance from the stream ($F_{3,12} = 1.62$, $p = 0.237$; Fig. 3.3).

There was weak evidence to suggest a difference in median soil temperatures with distance from the stream (maximum soil temperature: $F_{3,12} = 2.68$, $p = 0.094$; minimum soil temperature: $F_{3,12} = 2.60$, $p = 0.100$). While median maximum soil temperature remained relatively constant within 1 to 20 m from the stream, it was estimated to be 12% higher at 70 m than at 20 m (Table 3.2; Fig. 3.4). Median minimum soil temperature decreased by 6% from 1 m to 10 m from the stream, then leveled off between 10 m and 70 m (Table 3.2; Fig. 3.4).

Table 3.2 Estimates and tests of significance for differences in mean air temperature (°C) and relative humidity (%), or ratios of median soil temperature (°C), between consecutive distances from the stream in the forested riparian treatment ($n = 5$).

Variable	Time	Distance contrast	Estimate	±90% CI	t-statistic (12 d.f.)*	p-value
Air temp. (°C)	3PM	1 m vs. 10 m	-3.06	-5.11, -1.01	-2.66	0.021
		10 m vs. 20 m	-2.29	-4.34, -0.24	-1.99	0.069
		20 m vs. 70 m	-1.87	-3.92, 0.18	-1.63	0.129
Soil temp. (°C)	6AM	1m vs. 10 m	1.06	1.01, 1.11	2.17	0.050
		10 m vs. 20 m	0.96	0.92, 1.00	-1.59	0.138
		20 m vs. 70 m	0.97	0.93, 1.02	-1.02	0.329
	3PM	1 m vs. 10 m	0.93	0.85, 1.02	-1.39	0.190
		10 m vs. 20 m	1.05	0.95, 1.15	0.87	0.401
		20 m vs. 70 m	0.89	0.81, 0.98	-2.13	0.055
Rel. humidity (%)	3PM	1m vs. 10 m	14.65	4.69, 24.61	2.62	0.022
		10 m vs. 20 m	10.45	0.49, 20.41	1.87	0.086
		20 m vs. 70 m	4.05	-.591, 14.01	0.72	0.483

* t-statistic for relative humidity has 11 d.f.

Negatively associated with air temperature, mean minimum relative humidity (at 3PM) also differed significantly with distance from the stream in the forested treatment ($F_{3,12} = 10.83$, $p = 0.001$), but with a gradient of decreasing relative humidity with increasing distance from the stream (Fig. 3.5). Minimum relative humidity dropped 14.7% between 1 and 10 m from the stream, and dropped another 10.5% between 10 and 20 m (Table 3.2). Beyond 20 m, there was no difference. In the coolest part of the day (6AM), mean maximum relative humidity was similar (between 91 and 95%) at all distances from the stream ($F_{3,12} = 1.07$, $p = 0.397$; Fig 3.5)

Riparian management and edge effects

There was strong evidence for both a treatment effect ($F_{2,8} = 30.85$, $p < 0.001$) and a distance effect ($F_{2,24} = 14.83$, $p < 0.001$) on air temperature during the hottest part of the day (3PM). The median air temperature at 10 m from the stream (averaged across all treatments) was 20% higher than at 1 m, but did not differ between 10 and 20 m (Table 3.3, Fig. 3.3). The median air temperature in the clearcut (averaged across all distances) was 35% higher than in the buffer, and 49% higher than in the forest, however, there was no difference between the buffer and forest treatments (Table 3.3). Although not tested in the statistical analysis, it is apparent that in the clearcut beyond the buffer edge (in the "buffer" treatment), at 70 m from the stream, the mean air temperature was similar to that at 70 m from the stream in the clearcut treatment (Fig. 3.3).

During the coldest part of the day (6AM), there was also strong evidence for a treatment effect on mean air temperature ($F_{2,8} = 16.30$, $p = 0.002$), but no evidence for differences in air temperature with distance from the stream ($F_{2,24} = 0.50$, $p = 0.610$). At 6AM, the clearcut treatment was 2.30 °C and 2.72 °C cooler than the buffer and forest treatment, respectively, while the buffer and forest did not differ from each other (Table 3.3, Fig. 3.3). A visual assessment suggests that in the buffer treatment, at 70 m from the stream (in the clearcut), the mean air temperature dropped down to approximately the same as that in the clearcut treatment at 70 m from the stream (Fig. 3.3).

In the analysis of mean soil temperature, significant treatment*distance interaction effects (3PM: $F_{4,24} = 2.61$, $p = 0.061$; 6AM: $F_{4,24} = 5.45$, $p = 0.003$) implied that the effect of one factor (distance or treatment) on both maximum and minimum soil temperature depended on the level of the other factor. The plot of mean maximum (3PM) soil temperatures (Fig. 3.4) suggests that although the effect of treatment depended on the distance from the stream, there was a distinct pattern of increased mean soil temperature in the clearcut between 1 and 20 m from the stream when compared to the forest and buffer treatments. In fact, the F-value for the main effect of treatment ($F_{2,8} = 46.70$, $p < 0.001$) was approximately 18 times as large as the F-value for the

interaction effect. Such a large F-value suggests that, despite interaction effects, the main effect of treatment on mean maximum soil temperature is important to consider, and comparisons are reported (Table 3.4). As with air temperature, the mean soil temperature in the clearcut (averaged across all distances) was significantly higher (by 6.23 °C) than in the buffer, and also higher (by 7.10 °C) than in the forest, while there was no difference between the buffer and forest treatments (Table 3.4, Fig. 3.4). The F-value for the main effect of distance on mean maximum soil temperature was relatively low ($F_{2,24} = 5.16$, $p = 0.014$) and therefore distance cannot be considered independently of treatment.

Mean minimum soil temperature did not differ much between treatments or between distances from the stream (a range of 9.8 °C to 11.1 °C across all treatments/distances; Fig. 3.4). There appeared to be some trend of increasing minimum soil temperature with distance from the stream in the clearcut treatment, in contrast to more stable temperatures across the riparian zone in buffer and forest treatments. Minimum soil temperatures were considerably higher than minimum air temperatures across all treatments (Figs. 3.3, 3.4).

Microclimate patterns across treatments for minimum relative humidity (at 3PM), again, appeared to be negatively associated with maximum air temperature. There was a strong treatment effect on mean minimum relative humidity ($F_{2,8} = 19.96$, $p < 0.001$), as well as a strong distance effect ($F_{2,23} = 20.34$, $p < .001$). Relative humidity at 1 m from the stream (averaged across all treatments) was 17.6 % higher than at 10 m, but there was no difference in mean relative humidity between 10 and 20 m (Table 3.5, Fig. 3.5). Minimum relative humidity in the clearcut was 19.6% and 27.3% lower than in the buffer and forest, respectively, while the buffer and forest did not differ from each other (Table 3.5, Fig. 3.5). The mean minimum relative humidity at 70 m in the buffer treatment appeared to be very similar to that at 70 m in the clearcut treatment (Fig 3.5).

As with air and soil temperature, differences in mean relative humidity between treatments and distances were much smaller at 6AM than at 3PM (Fig. 3.5). While the overall effects were statistically significant (treatment: $F_{2,8} = 3.21$, $p = 0.095$; distance: $F_{2,23} = 6.60$, $p = 0.005$), Tukey-adjusted p-values suggested no difference between treatments. Differences between distances were too small to be accurately detected by the data loggers (Table 3.5).

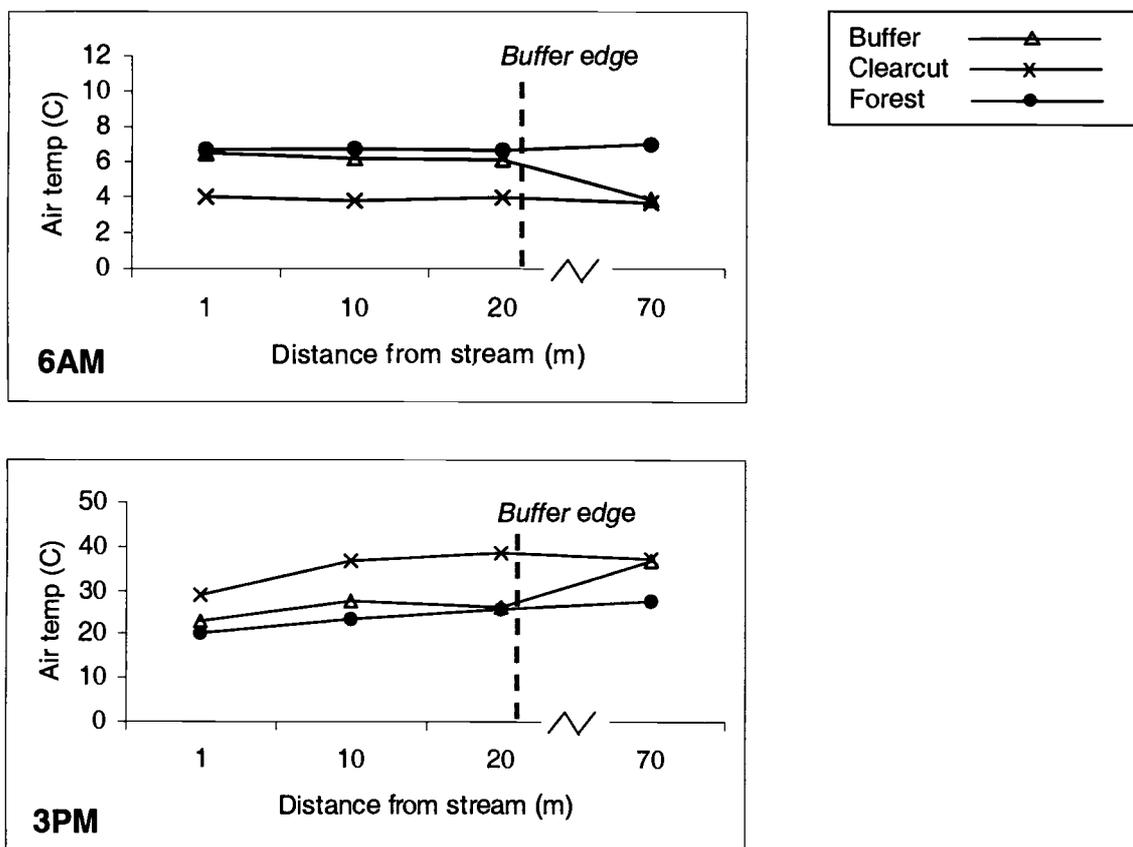


Figure 3.3 Mean minimum air temperature (at 6AM) and maximum air temperature (at 3PM) in buffer, clearcut and forest treatments, between 1 and 70 m from the stream ($n = 5$). Location of the forest edge in the buffer treatment is 25-30 m from the stream. (Note that x-axis is not to scale, and y-axes in two plots are different scales.)

Table 3.3 Estimates and tests of significance for differences in mean (6AM) or ratios of median (3PM) air temperature ($^{\circ}\text{C}$) between management treatments (B = buffer, C = clearcut, F = forest), and between consecutive distances (1-20 m) from the stream ($n = 5$). Contrasts are reported only if main treatment and/or distance effect(s) were significant.

Time	Contrast	Estimate	Tukey-adjusted $\pm 90\%$ CI	t-statistic (treatment, 8 d.f.) (distance, 24 d.f.)	Tukey-adjusted p-value
6AM	B vs. C	2.30	1.07, 3.52	4.48	0.005
	B vs. F	-0.42	-1.64, 0.80	-0.82	0.700
	C vs. F	-2.72	-3.94, -1.50	-5.31	0.002
3PM	B vs. C	0.74	0.65, 0.84	-5.70	0.001
	B vs. F	1.10	.097, 1.25	1.83	0.221
	C vs. F	1.49	1.31, 1.69	7.53	< 0.001
	1m vs. 10 m	.83	0.78, 0.92	-4.18	< 0.001
	10 m vs. 20 m	.96	0.87, 1.05	-0.93	0.630

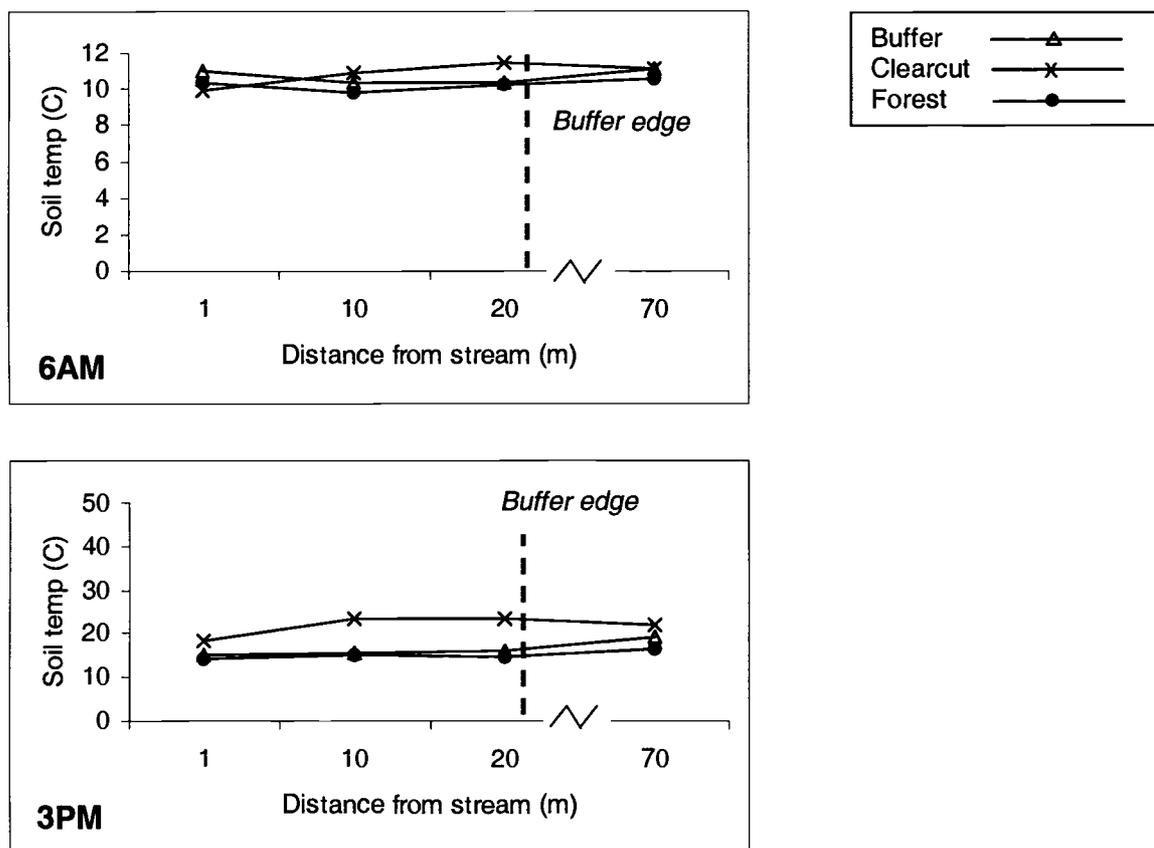


Figure 3.4 Mean minimum soil temperature (at 6AM) and maximum soil temperature (at 3PM) in buffer, clearcut and forest treatments, between 1 and 70 m from the stream ($n = 5$). Location of the forest edge in the buffer treatment is 25-30 m from the stream. (Note that x-axis is not to scale, and y-axes in two plots are different scales.)

Table 3.4 Estimates and tests of significance for differences in mean soil temperature ($^{\circ}\text{C}$) between management treatments (B = buffer, C = clearcut, F = forest; $n = 5$). Contrasts are reported only if main treatment and/or distance effect(s) were significant.

Time	Treatment contrast	Estimate	Tukey-adjusted $\pm 90\%$ CI	t-statistic (8 d.f.)	Tukey-adjusted p-value
3PM	B vs. C	-6.23	-8.14, -4.31	-7.77	< 0.001
	B vs. F	0.88	-1.03, 2.79	1.10	0.543
	C vs. F	7.10	5.19, 9.02	8.86	< 0.001

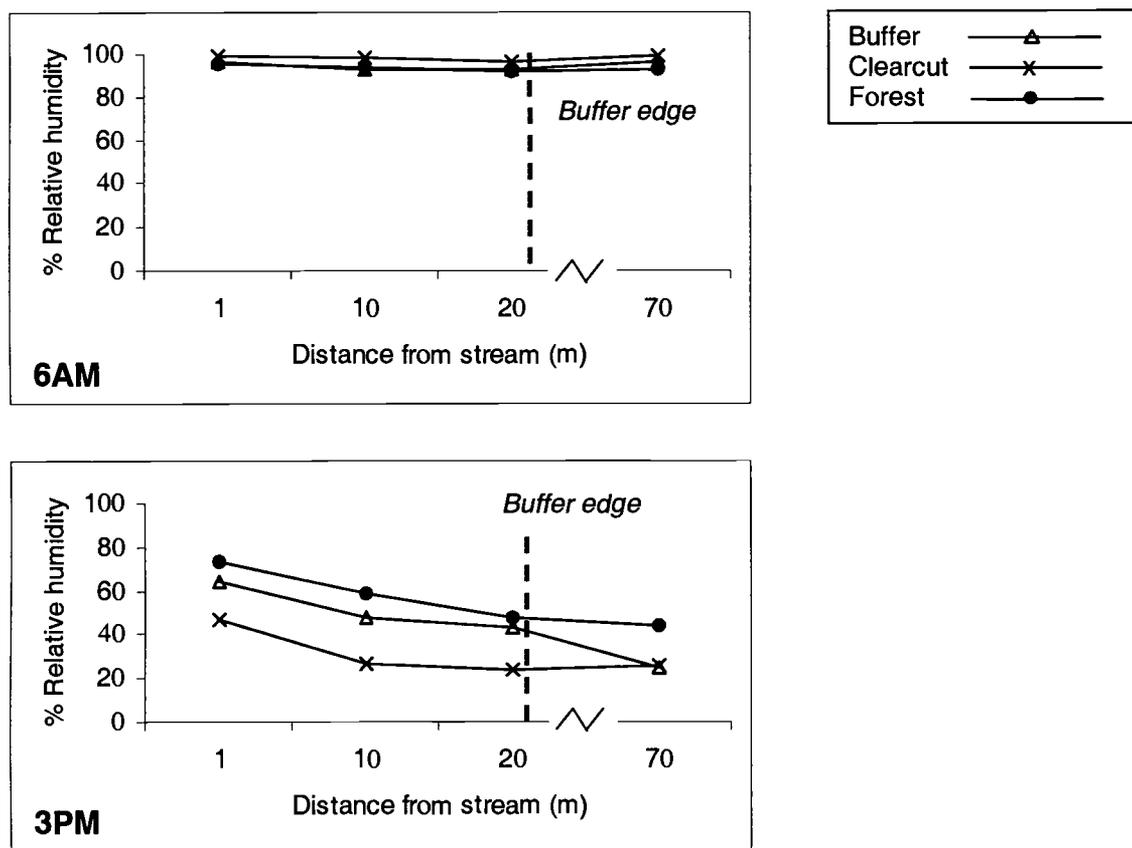


Figure 3.5 Mean maximum relative humidity (at 6AM) and minimum relative humidity (at 3PM) in buffer, clearcut and forest treatments, between 1 and 70 m from the stream ($n = 5$). Location of the forest edge in the buffer treatment is 25-30 m from the stream. (Note that x-axis is not to scale, and y-axes in two plots are different scales.)

Table 3.5 Estimates and tests of significance for differences in mean relative humidity between treatments (B = buffer, C = clearcut, F = forest) and between consecutive distances (1-20 m) from the stream ($n = 5$). Contrasts reported only if main treatment and/or distance effect(s) significant.

Time	Contrast	Estimate	Tukey-adjusted $\pm 90\%$ CI	t-statistic (treatment, 8 d.f.) (distance, 23 d.f.)	Tukey-adjusted p-value
6AM	B vs. C	-4.11	-8.85, 0.64	-2.07	0.159
	B vs. F	0.44	-4.30, 5.19	0.22	0.973
	C vs. F	4.55	-0.17, 9.27	2.30	0.113
	1 m vs. 10 m	1.86	0.05, 3.70	2.22	0.090
	10 m vs. 20 m	1.17	-0.59, 2.92	1.43	0.341
3PM	B vs. C	19.59	8.80, 30.39	4.33	0.006
	B vs. F	-7.69	-18.49, 3.12	-1.70	0.264
	C vs. F	-27.28	-37.89, -16.67	-6.13	< 0.001
	1 m vs. 10 m	17.64	9.37, 25.92	4.60	< 0.001
	10 m vs. 20 m	6.02	-2.06, 14.10	1.61	0.263

Seasonal variability in microclimate across the buffer edge

The magnitude of seasonal variability (mean maximum – mean minimum) in air temperature changed significantly ($F_{3,12} = 22.09$, $p < 0.001$) along the transect stretching from the stream edge (1 m), into the riparian buffer (10 m), across the buffer edge (20 m), and out to the clearcut (70 m; Fig.3.6). Variability in mean air temperature was 4.92 °C lower at 1 m from the stream than at 10 m, and 12.67 °C lower at the buffer edge than in the clearcut (Table 3.6). Air temperature variability was relatively constant within the buffer between 10 and 20 m from the stream. A similar pattern was observed in the forested treatment between 1 and 20 m from the stream, shown for reference in Figure 3.6.

Table 3. 6 Estimates and tests of significance for differences in the mean variability (mean max. – mean min.) of microclimate variables between consecutive distances from the stream in the buffer treatment ($n = 5$). Note that 1 m is at stream edge, 10 m is within riparian buffer, 20 m is at the buffer edge, and 70 m is in the clearcut adjacent to the buffer.

Variable	Distance contrast	Estimate	$\pm 90\%$ CI	t-statistic (12 d.f.)*	p-value
Air temp. (°C)	1 m vs. 10 m	-4.92	-8.73, -1.11	-2.30	0.040
	10 m vs. 20 m	1.09	-2.73, 4.90	0.51	0.621
	20 m vs. 70 m	-12.67	-16.48, -8.85	-5.92	< 0.001
Soil temp. (°C)	1 m vs. 10 m	-0.87	-3.14, 1.40	-0.68	0.508
	10 m vs. 20 m	-0.74	-3.01, 1.54	-0.58	0.575
	20 m vs. 70 m	-2.21	-4.48, 0.07	-1.73	0.109
Rel. humidity (%)	1m vs. 10 m	-14.09	-27.26, -0.92	-1.92	0.081
	10 m vs. 20 m	-4.60	-16.84, 7.64	-0.68	0.514
	20 m vs. 70 m	-21.80	-34.04, -9.56	-3.20	0.009

* t-statistic for relative humidity has 11 d.f.

Seasonal variability in mean soil temperature also changed significantly with distance from the stream ($F_{3,12} = 3.27$, $p = 0.059$). As with air temperature, soil temperature variability was highest in the clearcut (at 70 m), but the difference of 2.21 °C between the clearcut and the buffer edge (20 m) was barely significant ($p = 0.109$), and variability within the riparian buffer was similar between the stream edge, the interior of the buffer, and the buffer edge (Table 3.6; Fig. 3.6). The variability in soil temperature in the forested treatment appears to follow no consistent gradient within 1 to 20 m from the stream, and covers a similar range of variability as within the riparian buffer (Fig. 3.6).

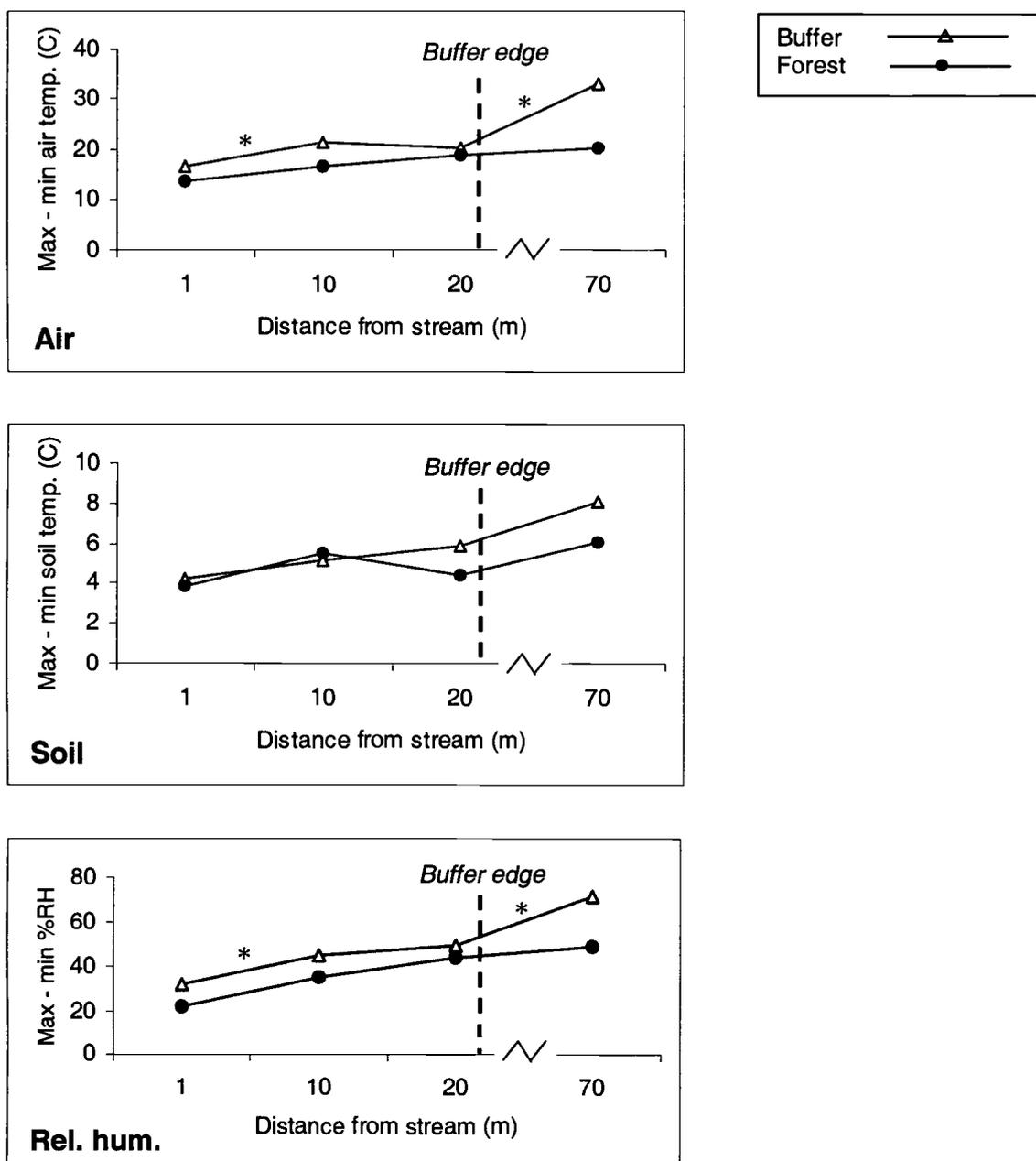


Figure 3.6 Mean variability (mean max – mean min) in microclimate variables (air temperature, soil temperature, relative humidity) with increasing distance from the stream in the buffer and forest treatments (n = 5). Location of the forest edge in the buffer treatment is 25-30 m from the stream. (Note x-axis is not to scale). Asterisk denotes a significant difference in mean variability between consecutive distances from the stream in the buffer treatment. The pattern of variability in the forest treatment is shown for reference only and was not included in the analysis.

The strong distance effect on the seasonal variability of mean relative humidity ($F_{3,11} = 10.90$, $p = 0.001$) mirrored the pattern of air temperature variability along the buffer transect (Fig. 3.6). Variability at 1 m from the stream was 14.1% lower than at 10 m, there was no difference in variability between the middle and the edge of the buffer, and variability was 21.8% higher in the clearcut than at the buffer edge (Table 3.6). Again, the pattern of variability in the forested treatment between 1 and 20 m from the stream showed a similar trend (Fig. 3.6).

DISCUSSION

Riparian forest microclimate: the “stream effect”

In mature, unmanaged forests, headwater streams exerted an influence on riparian microclimate, but the magnitude and extent of this stream effect was dependent on the variable and the time of day. It is important to keep in mind that the measurements of microclimate variables used in this study represented seasonal and diurnal extremes (maxima and minima), and therefore may not be directly comparable to average values reported in other studies. Nevertheless, for air temperature, a mean increase of more than 5°C over the first 20 m from the stream in mid-afternoon, was higher than the ~3°C increase previously measured on similarly-sized streams in western Washington Douglas-fir forests (Brososke et al. 1997). A similarly strong mid-afternoon effect on relative humidity, which dropped more than 25% over the first 20 m from the stream, was also greater than the ~11% decrease reported by Brososke et al. The 20 m extent of the stream effect on the variables measured in my study was less than the 31-47 m reported by Brososke et al., but greater than the average of 14 m reported for several variables by Olson et al. (2002) for managed stands of approximately 50 years old. As I had no data loggers between 20 and 70 m from the stream, I conclude that the actual extent of the stream effect for air temperature and relative humidity was somewhere between 20 and 70 m. For maximum soil temperature, values did not differ significantly with distance from the stream, so no stream effect can be inferred. At 6AM, when air temperatures was at its minimum, and relative humidity was at its maximum, stream effects disappeared for both variables.

As has been noted with edge effects, the magnitude and extent of the stream effect on microclimate appears to be inherently dynamic (Newmark 2001). Not only is the strength of the stream effect dependent on the variable and the time of day, which I tested, but it is also presumably influenced by changes in daily weather, the season, and factors such as topography, vegetation structure, and the size and permanence of stream flow, which I did not examine. The five forested streams used in this study included a range of elevations, slopes, and stream sizes; that their average stream effects on microclimate were of a significant magnitude and extent

strongly suggests that small headwater streams and their riparian zones provide a distinctly cooler, moister microenvironment aboveground within the surrounding upslope Douglas-fir forests in the dry summer months typical of the western Cascade Range.

Riparian management and forest-clearcut edge effects

Alternative management treatments implemented in the riparian zone had very different effects on riparian microclimate during the hottest part of the day. While gradients of increasing air temperature and decreasing relative humidity between 1 and 10 m from the stream were evident in all treatments, the clearcut treatment had significantly higher overall air temperature (11°C) and soil temperature (7°C), and lower relative humidity (27%) than the forest treatment. These numbers, though far higher than some differences reported by Chen et al. (1993; 1-2°C air, 2-6°C soil, 10-15% relative humidity), are not surprising, given that a clearcut receives far more direct solar radiation, higher wind speeds, and has higher rates of evapotranspiration than the interior of an adjacent forest (Chen et al. 1993, Geiger et al. 2003). Air and soil temperatures in the clearcut were most similar to the intact forest treatment at the stream edge (1 m), suggesting a relatively strong stream effect on temperature even in the clearcut. Three of the five clearcut streams were bordered by a high density of shrubs and a few trees, which likely influenced the microclimate. In the early morning, contrasts between the forest and the clearcut were reversed, with the clearcut showing significantly lower air temperature than the forest at all distances (due to higher losses of outgoing long-wave radiation; Geiger et al. 2003), while there was little discernible difference in soil temperature or relative humidity between any of the treatments. Again, all the above contrasts reflected extreme seasonal hot and cool weather conditions; treatment differences for all variables would likely have been lower during the afternoon on cool, cloudy days, and perhaps higher for soil temperature and relative humidity during warmer early mornings (Chen et al. 1993).

Despite the extreme conditions represented by the data in this study, no significant overall treatment differences were detected between the buffer and the forest for any microclimate variable, at either time of day. Plots comparing 3PM air temperature and relative humidity (Figs. 3.3, 3.5) suggest that perhaps there was some difference between the two treatments that may have ecological, if not statistical, significance. However, when the microclimate data were plotted separately for each block (not presented here), four of five blocks showed essentially no difference between forest and buffer treatments, while the buffer treatment in the fifth block, subjected to severe windthrow of trees, had higher air temperatures (and lower relative humidity) than even the clearcut treatment between 1 and 10 m from the stream. This

one block then, disproportionately influenced the buffer means in the plots, but did not affect the statistical tests. That there were no apparent edge effects in the intact riparian buffers is surprising, considering the abundance of evidence in the literature documenting strong edge effects on microclimate. Across forest fragment edges, changes in air temperature and relative humidity have been reported to extend 2.5 to 240 m into the forest, while changes in soil temperature have a narrower range (0 to 60 m; Williams-Linera 1990, Young and Mitchell 1994, Newmark 2001, Chen et al. 1995, Davies-Colley et al. 2000, Gehlhausen et al. 2000, Newmark 2001). Dong et al. (1998) reported that the air temperature directly over streams with riparian buffers of 17 to 72 m width increased 2-4°C between pre- and post-harvest conditions, and relative humidity decreased by approximately 8%. Although microclimate was not measured within the buffers, buffer width appeared to have little predictive value for estimating air temperature over the stream, suggesting that even the widest buffers were not wide enough to keep edge effects from penetrating all the way to the stream environment (Dong et al. 1998).

Many factors are known to influence the magnitude and extent of edge effects on microclimate in forest fragments, such as aspect (Matlack 1993, Gehlhausen et al. 2000), the age and vegetative "seal" of the edge (Williams-Linera 1990, Matlack 1993, Camargo and Kapos 1995), time of day (Newmark 2001), season (Young and Mitchell 1994), daily weather conditions (Chen et al. 1995, Davies-Colley et al. 2000), elevation, and slope (Chen et al. 1999). In my study, edges were relatively young (~5 years) and open; the five replicates for each treatment incorporated a broad range in edge aspect (for buffer sites: NE, W, SE), elevation (400 to 1200 m), and slope (steep to essentially flat); I contrasted microclimate at times of the day when extreme minima and maxima were expected to occur (Chen et al. 1993), and chose days representing the hottest and coolest days of the two sampling periods. Given these site conditions and measurement criteria, it is unlikely that I failed to detect edge effects due to biased or inappropriate sampling design. Edge effects less than 5 m may not have been detected by the 20 m loggers, but would likely be attributable to the "rough" edge associated with the buffer treatments (see Methods). One possible explanation for the absence of edge effects is that the magnitude and extent of the stream effects on microclimate, which extended out at least 20 m into the upslope in the unmanaged, forested sites, were modifying any warming/drying edge effects coming into the buffer from the adjacent clearcut (Fig. 3.1). In addition, the steep topography associated with most of the headwater streams may have protected riparian microclimate from stronger edge influences (Dong et al. 1998). Such a hypothesis further suggests that the magnitude and extent of edge effects are highly variable and not easily predictable, and that generalizations about edge effects should be treated with caution (Murcia 1995).

Seasonal variability in microclimate across the buffer edge

Patterns of seasonal variability for the three microclimate variables, along a transect from the stream edge, through the riparian buffer, to the adjacent clearcut, further supported that edge effects were not influential. While seasonal variability in air temperature and relative humidity were lowest at the stream edge and highest in the clearcut, variability within the riparian buffer (at 10 m) and at the buffer edge (at 20 m) were intermediate in value, and not significantly different from each other. A comparable pattern of decreasing variability between 10 m and 1 m from the stream for these two variables was also observed in the intact forest treatment, further suggesting that this near-stream pattern was attributable to a stream effect, rather than an edge effect. Upland edge studies, comparing microclimate measurements or their diurnal variability along transects from forest interior to cleared land, have reported the highest values for some parameters to be in the clearcuts, and for others, to be at the forest edge (Williams-Linera 1990, Chen et al. 1993, Davies-Colley et al. 2000). Extreme values and variability at the forest edge have been attributed to the presence of stable air masses, which increase air temperature and drying (Chen et al. 1999). Again, it may be that in this study, because the forest edge is associated with a riparian buffer, stream effects that tend to lessen the variability of some microclimate variables are extending upslope to modify effects that might otherwise increase variability at the edge.

Biological effects of changes in microclimate

Distributions of many species are closely associated with riparian habitats. Numerous and varied explanations for riparian associations have been reported, including a reliance on aquatically-derived prey (Hering 1998, Nakano and Murakami 2001), life history traits that are adapted to fluvial disturbance regimes (Zulka 1994, Naiman and Decamps 1997), and physiological adaptations to cool/moist microclimates (Thiele 1977, Andersen 1985, Antvogel and Bonn 2001, Kauffman et al. 2001). Field studies on forest-floor invertebrates, such as spiders and beetles, have related changes in activity levels and predation rates to changes in soil temperature, air temperature, and relative humidity (Neve 1994, Atienza et al. 1996, Honek 1997). Thiele (1977) reported that carabid beetles may be able to discriminate differences of 5% in relative humidity, while Honek (1997) calculated that catches of diurnal carabids in a fallow field increased 6.3% for every 1°C increase in mean daily air temperature. Thus, it might be hypothesized that relatively small changes in microclimate within a riparian buffer (e.g., within the range observed by Brosfoske et al. (1997) in post-harvest treatments) resulting from edge effects may have significant consequences for some riparian species, and these, in turn, may

affect higher trophic levels (van Wilgenburg et al. 2001) or ecosystem processes (Klein 1989). If ecological integrity is to be maintained in riparian areas, it is critical that edge effects on microclimate be minimized in riparian areas.

Management implications

The results of this study indicate that in the summer growing season, in the dry forested landscapes of the western Cascade Range, headwater streams and their riparian zones provide a cool/moist microclimatic gradient aboveground that extends at least 20 m from the stream. Such a distinctive microclimatic resource is likely to be important to many organisms as breeding or foraging habitat. In order to preserve this resource within a harvested landscape, it is also clear that harvesting to the stream edge will not be an effective management strategy, as large increases in soil and air temperature, and decreases in relative humidity, result. Data collected under the sampling and geographic constraints of this observational study, suggest that another management alternative, preserving a forested riparian buffer of ~30 m width on either side of the stream, is far more effective in preserving the original riparian forest microclimatic conditions than fragmentation models (e.g., the core-area model; Laurance and Yensen 1991) would predict. One reason for this may be that the stream influence on riparian forest microclimate modifies the opposing influence from the forest-clearcut edge. A 30 m-wide riparian buffer on headwater streams is certainly wider than that called for by many current management guidelines in the Pacific Northwest (Young 2000), yet approximates the minimum width suggested by various researchers studying riparian microclimate (e.g., 45 m by Brososke et al. 1997; 40 m by Davies-Colley et al. 2000) and riparian fauna (e.g., 40 m by Hagar 1999; 45 m by Pearson and Manuwal 2001; 30 m by Cockle and Richardson 2003). Unexpected events such as the windthrow of trees, especially in narrow buffers, should also be considered in riparian design.

While the magnitude and extent of edge effects documented in upslope forest fragment studies may not be directly applicable to riparian forest fragments, such research has brought to light the dynamic and variable nature of forest edges and their effects on forest microclimate. Factors such as aspect, elevation, slope gradient, and edge structure all need to be considered when designing effective aquatic/riparian conservation strategies. The adequacy of implementing fixed-width riparian buffers on all the streams of a particular region or jurisdiction has been questioned by many (Castelle et al. 1994, O'Laughlin and Belt 1995, Gregory 1997). More recently, managers have started to design aquatic/riparian management strategies at a watershed scale, in which they can combine many options. These options include: no protection on some streams; preserving riparian buffers of various widths on streams of different sizes and

topographic positions; allowing modified harvesting such as thinning in the riparian zone; or creating larger “patch” reserves that may encompass several streams and their junctions (Cissel et al. 1998, Olson et al. 2002). These kinds of management strategies require far more intricate planning, local knowledge, and ecological understanding than the “one size fits all” approach, and will rely on studies such as this one to provide data for designing effective riparian options.

CHAPTER 4

LINKING SPATIAL PATTERN TO ANIMAL MOVEMENT ACROSS A FRAGMENTED LANDSCAPE: AN ARTHROPOD'S VIEW OF FOREST EDGE PERMEABILITY

INTRODUCTION

Habitat loss and fragmentation pose significant threats to biodiversity and the integrity of functioning ecosystems world-wide (Saunders et al. 1991, Haila 1999, Klein 1989). In the Pacific Northwest, intensive harvesting of the region's coniferous forests over the last century has resulted in a heavily fragmented landscape (Harris 1984). During the last several decades, state and federal management practices on these forests have included the implementation of riparian "buffers" along larger fish-bearing streams and rivers, and more recently, along small headwater streams (Gregory 1997). On federal lands especially, these linear forest patches are expected to provide not only shade and erosion control for the stream, but also habitat or dispersal corridors for terrestrial species (Tuchman et al. 1996). Depending on their connection with contiguous forest upstream or downstream, riparian buffers may represent either isolated fragments or connecting corridors in the landscape.

Empirical research encompassing a wide variety of taxa has identified several key factors that affect species responses to fragmentation, these include: fragment size, isolation, shape, edge characteristics, and connectivity in the landscape (Laurance and Yensen 1991, Saunders et al. 1991, Didham 1997). Evidence, primarily from upland forest studies, suggests that the elongate shape and high perimeter-to-area ratio of riparian buffers may subject them to significant physical (e.g., microclimate) and/or biological edge effects (Brosofske et al. 1997, Murcia 1995), with potential negative impacts on the population dynamics and survival of forest species.

A considerable amount of research on biological edge effects, as characterized by animal distributions and movement across fragment edges, has focused on ground-dwelling arthropods, such as ground beetles (Carabidae) and wolf spiders (Lycosidae). These relatively mobile, predatory taxa exhibit a range of sensitivity to environmental gradients and are easy to sample with pitfall traps. Landscape-scale research on the effects of forest fragmentation on ground-dwelling arthropods has taken two main approaches. Work by Niemalä et al. (1993a), Spence et al. (1996), Didham et al. (1998a), Pajunen et al. (1995) and others has primarily addressed the effect of fragment size and/or isolation on arthropod spatial distributions in tropical and boreal forests. Such community level studies have inferred that some forest interior species may be negatively affected by physical and/or biological edge effects (e.g., avoidance of the edge due to

change in microclimate; forest invasion by open-habitat associated species), while forest generalists may readily cross the forest edge, utilizing both forest and open habitats (Halme and Niemalä 1993, Spence et al. 1996, Davies and Margules 1998, Carvalho and Vasconcelos 1999).

Another approach to determining species responses to forest fragment edges is based in the agricultural landscapes of western Europe. Here, networks of linear hedgerows and/or small patches of “set-aside” semi-natural areas comprise the majority of woodland fragments in a matrix of agricultural fields, and research has focused on carabids and lycosids as important predators of agricultural pests. Mark-release-recapture or radio-tracing techniques have been employed to characterize individual movement patterns across habitat edges, and to assess “edge permeability” for various mobile species. Such techniques have revealed that hedgerows may serve as habitat or movement corridors for some forest species (Burel 1989, Charrier et al. 1997, Joyce et al. 1999), other species may cross readily between habitats (Duelli 1990, Kennedy 1994, Martin et al. 2001), or, alternatively, hedgerows may act as barriers to movement for open-habitat species (Mauremooto et al. 1995, Thomas et al. 1998). These varied findings support the idea proposed by Stamps et al. (1987) and others that the permeability of an edge (i.e., whether it is “hard” or “soft”) to species movement is a function not only of the physical structure of the edge, but also of characteristics unique to the species such as dispersal ability and habitat requirements (Joyce et al. 1999, Collinge and Palmer 2002).

This study brought together these two approaches by integrating information on spatial distribution patterns of forest-floor arthropods across a fragmented forest landscape, with direct observations of individual movements within and across habitat types, in order to characterize the various ways that arthropod taxa may perceive and respond to forest fragment edges. The study was implemented at a single site encompassing a forested riparian buffer and an adjacent clearcut in a Douglas-fir forest of the western Oregon Cascade Range, USA.

I focused on four mobile (but flightless), predatory taxa that are relatively abundant at mid-elevations in the Oregon Cascade Range. The genus *Scaphinotus* (Carabidae) is a large group, comprised primarily of snail-feeding beetles. *Scaphinotus angusticollis* (Fischer von Waldheim) is endemic to the Pacific Northwest, and is thought to be a forest interior species (Work 2000). Data collected at nearby sites by the author confirms that within this region of the Oregon Cascade Range, *S. angusticollis* is restricted primarily to undisturbed forest (see Chapter 2). Another species, *S. marginatus* (Fischer von Waldheim), is known to have a more eurytopic distribution across forests and cultivated areas (LaBonte 2002, Laroche and Lariviere 2003), although it has been reported to be a forest specialist in lodgepole pine forests (Spence et al. 1996). A third species of ground beetle, *Pterostichus n.sp.*, has not yet been described, but is

fairly common in the region surrounding the study site, and is also presumed to have a eurytopic distribution based on the distribution of related species (personal observation). Lastly, lycosid spiders are known to be associated with open habitats such as meadows and clearcuts (Jennings et al. 1988, McIver et al. 1990, Pajunen et al. 1995).

The specific objectives of the study were to: (1) describe habitat affinities of the four arthropod taxa by relating spatial distribution to microhabitat and microclimate variables across a trans-riparian gradient of three habitat types (forested riparian buffer, edge, clearcut); (2) characterize relative mobility (displacement distances/rates) and activity patterns for the four arthropod taxa; and (3) investigate whether movement patterns of species across forest edges may be characterized or predicted based on their habitat affinity and mobility.

METHODS

Site description

The study site was located at 1150 m elevation (44° 20' 00.28" N, 122° 17' 34.73" W) within the Sweet Home Ranger District of the Willamette National Forest, on the western slope of the Cascade Range in Oregon, USA. The climate in this region can be broadly characterized as having wet, mild winters—with some snow accumulation at higher elevations—and warm, dry summers (Franklin and Dyrness 1988). Forest canopies at this elevation in the western hemlock zone are dominated by Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), and western redcedar (*Thuja plicata* Donn) (Franklin and Dyrness 1988). This vegetation zone comprises the majority of forest lands in western Oregon, and is economically significant for its timber production (Franklin and Dyrness 1988).

The study site comprised a first-order headwater stream with a 25 m-wide forested riparian buffer on either side, and a 7-yr old clearcut adjacent to the buffer. I placed a trapping grid on the northeast-facing bank of the stream so that the buffer edge would face southwest, and be exposed to the most extreme effects of the sun. The trapping grid encompassed an area from the stream edge, across the riparian buffer, and into the clearcut above (Figure 4.1). Between the forested buffer and the clearcut, I delineated a 7 m-wide transitional zone, containing both scattered trees and stumps, as “edge.”

Sampling design

I set up a 63 x 49 m pitfall sampling grid parallel to the stream (Fig. 4.1). Eighty trapping stations were arrayed at 7 m intervals along both axes, encompassing an area of 3087 m². At each trapping station (grid intersection), I placed two pitfall traps approximately 1 m apart, for a total of 160 traps. Traps consisted of plastic drinking cups (9 cm diameter at the mouth, 12 cm deep) buried into the ground so that the rim was flush with the forest floor. I fitted plastic funnels into the top of the traps to help exclude small vertebrates and to keep captured invertebrates from climbing out. Square metal roofs supported by nails kept debris and rain out of the traps. At the beginning of each trapping period, I placed a few small, moist strips of paper towel into an easily removable small cup nested in the bottom of the larger cup, in order to provide cover and moisture for trapped invertebrates. I sealed each trap with a tight-fitting lid between trapping periods.

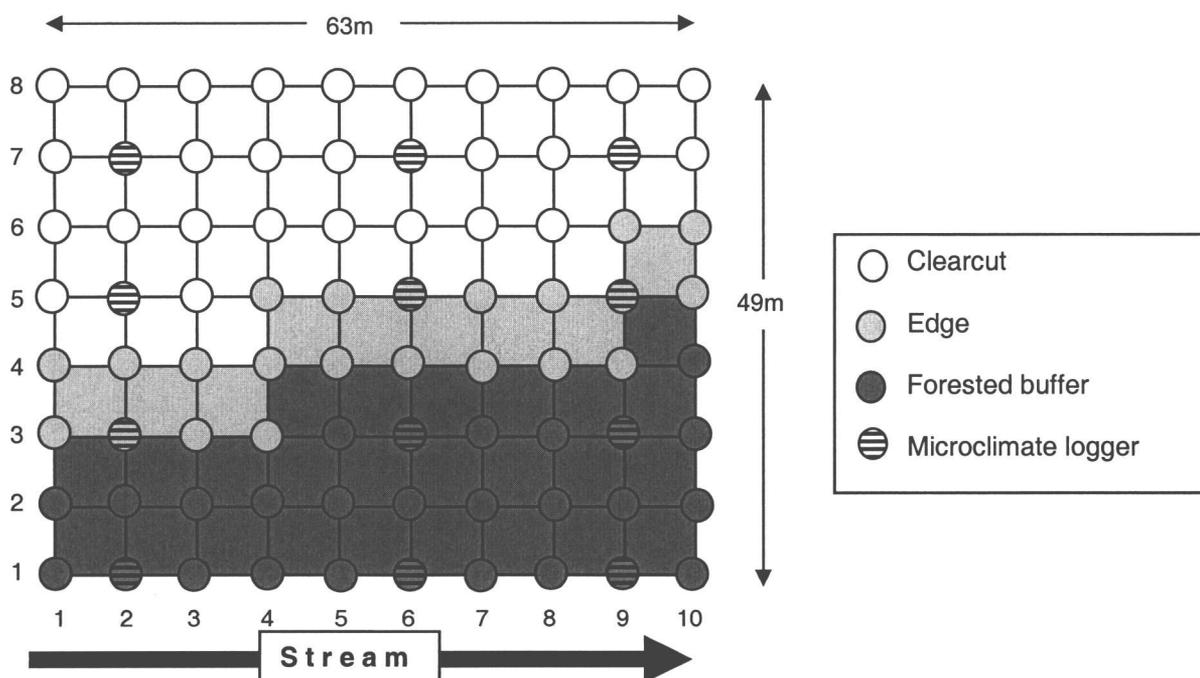


Figure 4.1 Trapping grid, with headwater stream along lower boundary. Buffer edge faces southwest. Each circle represents one trapping station with 2 pitfall traps. Dark gray circles ($n = 27$) are in forested buffer, light gray circles ($n = 22$) are in edge, and white circles ($n = 31$) are in clearcut. Trapping stations are spaced 7 m apart along both axes. Striped circles in each habitat represent trapping stations with microclimate loggers.

Trapping began on June 18, 2002. For a given two-day mark-release-recapture (MRR) trapping cycle, I opened all 160 traps in the morning of Day 1, and returned in the morning of Day 2 to begin counting and marking trapped arthropods. Because counting and marking took anywhere between 3 and 10 hours, I divided the grid transects perpendicular to the stream (1-10) into consecutive pairs (1&2, 3&4...9&10) and randomly chose the order of visitation to each pair. At each trapping station, I counted numbers of carabids and lycosids in both pitfall traps, marked them as described below, and recorded recaptures. I released animals at their capture site, and closed the lids of all traps so that marked animals had between 15 and 24 hours to disperse before the possibility of recapture. Trapping activities fell into three time periods: 10 trapping/MRR cycles in early summer (between June 18 and July 13); 8 trapping/MRR cycles in mid-summer (between August 8 and 28); and 4 trapping cycles in late summer/early autumn (between September 6 and October 9). I stopped marking arthropods after August 28, 2002, but continued to record recaptures in late summer/early autumn. I used arthropod counts from early and mid-summer for analysis of spatial pattern (see below). As snails and slugs represent a potential food source for two *Scaphinotus* species, I also kept track of gastropod counts in the traps for use in later analysis.

Marking arthropods

To mark carabid beetles, I first restrained them on 2.5 cm diameter wooden dowels with rubber bands as described by Thomas (1995). I applied a small patch of Paper Mate Liquid Paper® on each elytron, let it dry briefly, and then wrote a unique identifying number on the whitened patches (so that the number appeared twice on the beetle) with a fine-tipped permanent marker. Because the lycosid spiders were too quick and hairy to mark with unique numbers, I used six different colors of fluorescent marking powder for marking. Each color identified the grid row(s) where the spider was caught and released (rows 1 and 2 shared a color, as did rows 7 and 8; see Fig. 4.1). Thus, upon recapture, I knew from which grid row (y coordinate) the spider had come, but not which trap (x coordinate) in the row, nor did I know on what date the spider had last been captured and marked. The mark was applied by gently shaking the spider in a plastic bag containing one color of powder. Preliminary lab and field observations indicated that the powder stayed visible on some portion of the spider (usually the dorsal portion of the abdomen, where the spider apparently could not reach to groom) for a minimum of two days, and as long as two weeks.

I marked carabid beetles in the genus *Scaphinotus* (*S. marginatus*, *S. angusticollis*) and the genus *Pterostichus*. Because most Pacific Northwest *Pterostichus* species within a size class

are difficult to identify without magnification, I could not identify these beetles to species in the field with certainty. I used pitfall data from the previous two years (Chapter 2) to assume that the majority (if not all) of the *Pterostichus* individuals I marked were *Pterostichus n. sp.* Of the lycosid spiders I marked, less than 10% were *Alopecosa kochii* (based on size), and the rest were in the genus *Pardosa*. Again, based on previous data (Chapter 2), I assumed nearly all were *Pardosa dorsalis*. I grouped all lycosid spiders into one taxon for analysis.

Microclimate sampling

I set up microclimate data loggers at 12 trapping stations (Fig. 4.1), so that any point on the trapping grid was no more than 14.5 m from a data logger. I measured soil/litter temperature approximately 2-3 cm below the substrate surface, and ambient air temperature and percent relative humidity approximately 20 cm above the substrate surface. These microclimate parameters were measured with GPSE 301 203 (THT-HR) Humidity and Dual Temperature Dataloggers during all trapping activity between June 17 and August 28, 2002. Loggers measuring ambient air temperature and relative humidity were protected from rain and dew under a large, inverted cup that hung from a wire arm attached to the top of a stake driven into the ground. Ideally, air temperature and relative humidity should have been measured 1-2 cm from the ground surface, where the invertebrates are active, however, adequate ventilation was required below the cups to prevent the creation of an artificial microclimate, and for this reason I had to place the loggers at some distance (20 cm) above the ground surface. All loggers were calibrated in climate-controlled rooms at the end of the study, and determined to be accurate within 0.3°C for air and soil temperature, and within 4% for relative humidity.

Microhabitat sampling

Herbs and other ground cover: I measured percent cover (0%, 1-5%, or to the nearest 10%) of herbaceous vegetation in a 1 x 1m plot placed in a randomly selected cardinal direction adjacent to the stake marking each trapping station, for a total of 80 plots. I also measured percent cover of bare mineral soil, moss, and leaf litter (including both needles and leaves) within this plot. Percent cover values for each variable at each plot were used in spatial analysis.

Shrubs, trees, snags: I set up a 20 m² circular (2.52 m radius) sampling plot at each trapping station, for a total of 80 plots. The sampling plot was centered on the stake marking the trapping station, and encompassed both pitfall traps. Within each plot, I counted the number of shrubs, defined as live woody stems > 1 m tall and less than 10 cm diameter at breast height (DBH) by

species. Shrub density (no. stems/20m²) for each plot was used in spatial analyses. For each tree species (live woody stems > 10 cm DBH), I counted and measured the DBH if any part of the tree lay within the plot. I also measured the DBH of dead woody stems > 10 cm DBH and > 1 m tall (snags). For each plot, combined basal area (calculated from DBH) of live trees and snags (cm²) per m² was used in spatial analyses.

Large woody debris (LWD): I used a line intercept method to measure all stumps and downed wood > 10 cm diameter and ≥ 1m length that crossed either of two perpendicular 5.04 m transect lines, each centered on the same stake as in shrub/tree sampling plots described above (total of 80 plots). For each piece of LWD, I measured its horizontal length touching the transect line(s), and its average vertical width. I excluded LWD elevated > 50 cm off the ground. The value used for each plot in the spatial analyses was the total area (cm²) of wood measured under the transect lines, divided by the total length of the transect lines per plot (10.08 m), for an overall index of cm² wood/m. I assigned a decay class (1-5; Maser and Trappe 1984) to each stump or piece of LWD, with decay class 1 representing a relatively freshly fallen tree, and 5 representing decomposed wood with little of its original structural integrity.

Spatial analysis

To analyze spatial patterns of arthropods and habitat variables, and the spatial associations between them, I used Spatial Analysis by Distribution Indices (SADIE; Perry 1995, Perry 1998, Perry and Dixon 2002). I chose these methods over other geostatistical methods (e.g., variance:mean methods, wavelet analysis) for several reasons. SADIE is designed specifically for count data, and can therefore handle a high proportion of zero counts. In addition to producing overall indices of spatial pattern/association, SADIE methods also are able to produce spatially explicit maps of local aggregation and association that are relatively simple to interpret (Dale et al. 2002, Perry et al. 1999, Perry et al. 2002).

Spatial pattern: Using (x,y,z) data in the form of spatially-referenced counts, SADIE measures the degree of aggregation (patches or gaps) in the data by calculating the minimum total distance that individuals would have to move (by being “donated” by sample units with high counts, or “received” by sample units with low counts) so that abundance was equal in every sample unit over the entire sample area. This observed distance to regularity is denoted D; the larger it is, the more spatially clustered are the counts. Overall spatial pattern can be quantified by running a specified number of simulations, in which each run starts with a random permutation of the

observed counts among sample units, and results in a calculation of distance to regularity. By dividing D by the mean value of these randomized simulations, the program calculates an index of aggregation (I_a). If the counts are randomly arranged, $I_a = 1$, while $I_a > 1$ indicates arrangement of counts into clusters (patches or gaps), and $I_a < 1$ indicates regularity. This method also allows a formal test of the null hypothesis of spatial randomness, by comparing D with the tails of the distribution of the randomly permuted distances to regularity (a two-tailed test).

In addition to the overall index for aggregation, each sample unit is assigned a clustering index (based, again, on randomized permutations of observed data among sample units) which measures the degree to which the individual unit contributes to clustering, either by donating individuals as a member of a patch ($v_i > 1$) or receiving individuals as a member of a gap ($v_j < -1$). For a random distribution of the counts, v_i and v_j have an expected value of 1 or -1, respectively. These local indices can be used to build contour maps, where values of $v_i > 1.5$ (i.e., 50% above a value of v_i expected by chance alone) indicate patches, and values of $v_j < -1.5$ (50% below expectation) indicate gaps. Mean values of these indices can also be compared to corresponding values from the randomizations to provide formal tests of clustering into patches (V_i) versus gaps (V_j), and to give probabilities of deviating from the expectation of 1 or -1, respectively (Perry et al. 1999). It is important to realize that SADIE measures pattern associated with clustering, rather than raw counts, so that an isolated high count in one sample unit surrounded by very low counts has a low clustering index (v_i) when compared to a sample unit with a moderately high count surrounded by similar counts.

I summed arthropod counts for a given sample unit over the early summer and mid-summer trapping periods (June 18 to August 28, 2002; 18 trapping cycles total) for use in SADIE analysis, unless otherwise noted. These counts represent a measure of "activity" rather than static density distributions, as a single individual may be counted multiple times in the same or different sample units. Also, pitfall traps measure "activity-density" by design, as the more active an individual is, the more likely it is to be trapped (Thomas et al. 1998). Because integer counts are needed for SADIE, I rounded measures of some of the habitat variables (e.g., tree basal area, LWD index) to the nearest integer. All indices were derived using the maximum allowable 5967 randomizations. Contour maps were constructed using SURFER version 5.01 (1994, Golden Software Inc., Golden CO, USA).

Spatial association: SADIE can also be used to compare the spatial patterns (as measured above) for two sets of data. I used the method to compare associations between two taxa (beetles and gastropods), between males and females within a species, and between species and habitat

variables. An index for local spatial association, χ_k , measures the similarity between the clustering indices (v_i, v_j) of the two data sets at the k th sample unit. A large positive value of local association indicates a coincidence of patches or gaps in both data sets (association), while a large negative value indicates a patch from one data set coinciding with a gap from the other data set (dissociation). The method also calculates an overall mean measure of association (X), which is equivalent to the simple correlation coefficient between the clustering indices of the two sets of data. A positive X indicates some degree of association, while a negative X indicates dissociation between the two data sets. A randomization method is used, in which clustering indices in both data sets are randomly permuted (9999 times in this study) among their respective sample units, to test the significance of X under a null hypothesis of no association (or dissociation), after making adjustments for small-scale spatial auto-correlation in both sets of clustering indices (Dutilleul 1993, Perry and Dixon 2002). In this case, a large p-value (i.e., for significance at $\alpha = .05$, $p > 0.975$) indicates significant dissociation, and a small p-value ($p < 0.025$ indicates significant association). I used critical values for χ_k , derived under the null hypothesis of no association, as significant contour intervals in mapping.

Analysis of arthropod movement

Mark-release-recapture data allowed me to characterize movement patterns for four arthropod taxa across three habitat types: forested buffer, edge, and clearcut (Fig. 4.1). I treated the edge between the forest and clearcut as a separate entity because the forest boundary was not abrupt, and because the literature suggests that edges may encompass physical conditions and biological assemblages distinct from the habitats on either side (Matlack and Litvaitis 1999, Meiners and Pickett 1999, Work 2000). I built a spatially explicit model to determine the null expectation for the movement patterns of each taxon within and across habitat types, based on two pieces of information: (1) spatial distribution as determined by SADIE, and (2) mobility as estimated by the mean displacement between release and recapture.

From each of the sampling units (grid intersections) within a taxon's distribution (as revealed by SADIE), the model assumed that an arthropod could travel its assigned mean displacement distance in any one of four cardinal directions (along grid lines). Given these four possibilities for each sampling unit, I estimated the probability that the arthropod released at this point would move to another place within the same habitat, move outside the grid, move across the habitat boundary (e.g., clearcut to edge), or move across two habitat boundaries (e.g., clearcut through edge to buffer; see Fig. 4.2 below for all possible movement categories). Probabilities summed to one for each sampling unit. The model also assumed that if the taxon was restricted

to a particular habitat (i.e., forested buffer), then it could not cross the preferred habitat boundary, instead, it changed direction to move parallel to the preferred habitat boundary. Additionally, as the bottom edge of the grid was bounded by a stream that, for simplicity, was assumed to be a barrier to movement, arthropods were not allowed to move down through the bottom edge of the grid, but instead were deflected back into the buffer, to move parallel to the grid bottom.

The method for calculating the expected frequency distribution for a hypothetical eurytopic taxon (i.e., distribution throughout the entire sampling grid) is shown in Table 4.1. At each sample unit, I summed the probabilities (0 to 1) for each of 12 possible movement categories (Fig. 4.2), and then summed these over the 80 sampling units of the grid (possible range for each movement category is 0 to 80; column 2, Table 4.1). Because my mark recapture data did not include movements of arthropods over the outside boundary of the grid, I subtracted from 80 (the total sum of all probabilities) the sum of the probabilities associated with moving from any of the habitat types to the outside. I then calculated the proportions of the remaining nine movement categories within the grid over the adjusted total (column 3, Table 4.1). Finally, I multiplied each adjusted proportion by the total number of observed arthropods for that taxon, to arrive at an expected frequency distribution (column 4, Table 4.1).

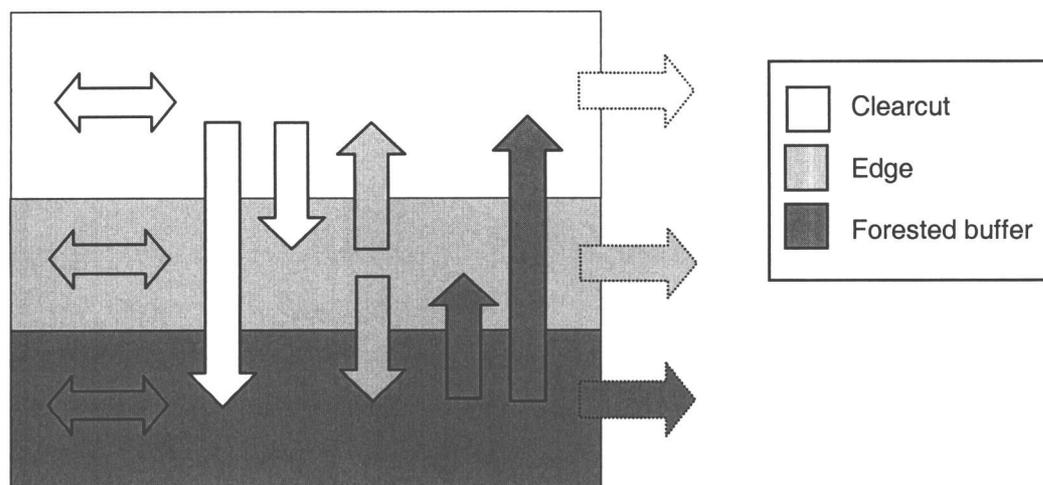


Figure 4.2 All possible movement categories for arthropods (see also Table 4.1, column 1). Movement within the same habitat indicated by horizontal arrows (on left); movement across habitat or grid boundaries indicated by vertical arrows. Movement across the outer grid boundaries (indicated by arrows bounded by dotted lines) was *not* included in the model.

Table 4.1 Summary of method used to derive expected frequency distribution for a hypothetical eurytopic species ($n = 50$ individuals) that has a mean displacement distance of 15 m. Probabilities from 80 sampling units were summed for each movement category (column 2). Sum of probabilities for clearcut to outside (11.75), edge to outside (3.875) and buffer to outside (5.375) was subtracted from grand total of probabilities (80 minus 21) to arrive at adjusted total (59). Proportions of adjusted total were calculated for each category (column 3), and then multiplied by total number of observed beetles (50) to arrive at expected frequency distribution (column 4). Finally, the expected frequency distribution (column 4) was qualitatively compared to the observed frequency distribution (column 5).

Movement category	Sum of probabilities (x)	Proportions of adjusted total (x/59)	Expected frequencies (x/59 * 50)	Observed frequencies
Clearcut to clearcut	13.5	.229	11.5	15
Clearcut to outside	11.75			
Clearcut to edge	3.75	.064	3.2	0
Clearcut to buffer	2	.034	1.7	2
Edge to edge	5.5	.093	4.7	8
Edge to outside	3.875			
Edge to clearcut	6.25	.106	5.3	3
Edge to buffer	6.375	.108	5.4	0
Buffer to buffer	15.625	.265	13.3	18
Buffer to outside	5.375			
Buffer to edge	4	.068	3.4	2
Buffer to clearcut	2	.034	1.7	2
Total	80	1.00	50	50

RESULTS

Between June 18 and August 28, 2002, there were 966 lycosid spider captures, 281 captures for *Pterostichus n.sp.*, 168 for *Scaphinotus marginatus*, and 22 for *Scaphinotus angusticollis*. After adjusting for unequal trapping efforts (10 trapping events in early summer, 8 events in mid-summer), the majority of *Pterostichus n.sp.* (91.6%) and lycosids (81.7%) captures were in early summer, while seasonal catches were somewhat more evenly distributed for *S. marginatus* and *S. angusticollis* (43.8% and 63.2% in early summer, respectively; Fig 4.3). Male/female ratios changed most for lycosids, where males made up 81.1% of the catch in early summer, and only 8.8% in late summer (Fig. 4.4).

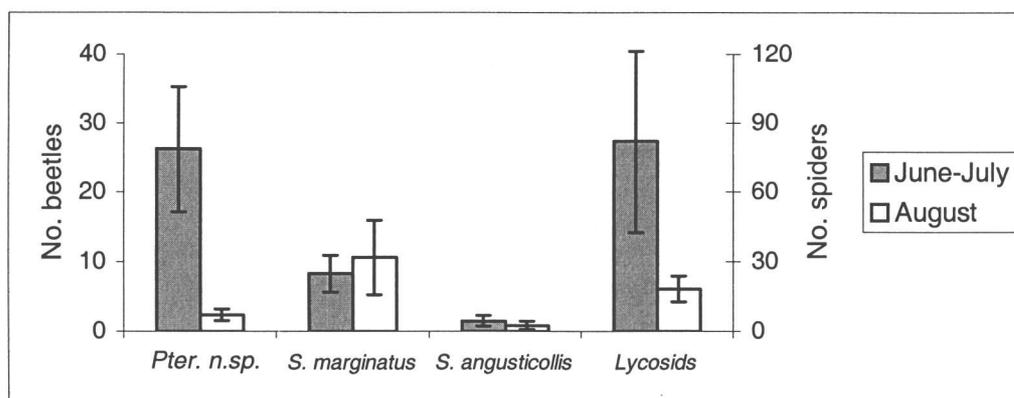


Figure 4.3 Mean number of individuals ($\pm 95\%$ CI) trapped per sample date during two sampling periods: June 18-July 13, 2002 ($n = 10$ sampling dates) and August 8-28, 2002 ($n = 8$). Note separate axis scales for beetles and spiders.

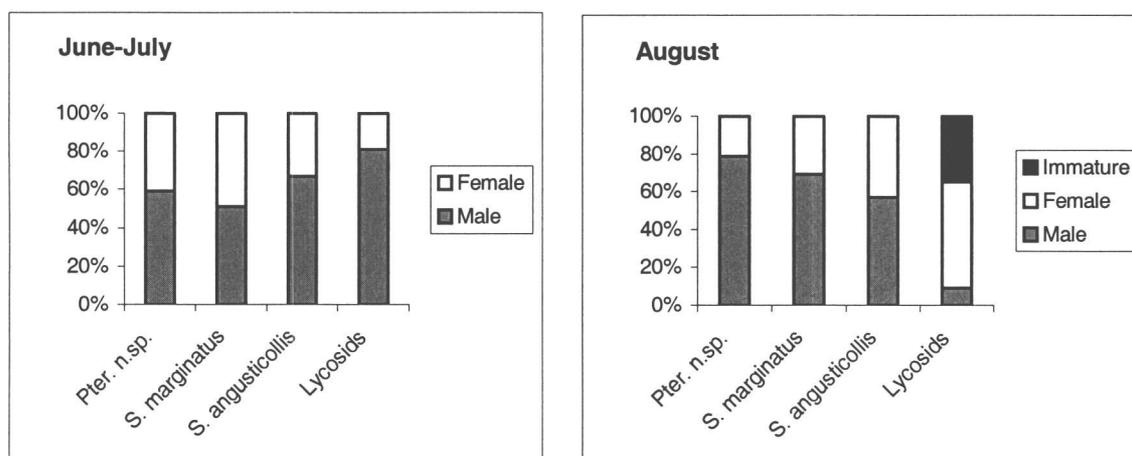


Figure 4.4 Sex ratios of arthropod captures during June 18-July 13, 2002 and August 8-28, 2002.

Spatial pattern and association for arthropods

Analysis with SADIE revealed strong spatial aggregation for two of the four arthropod taxa examined. Table 4.2 provides spatial indices (overall aggregation I_a , mean clustering for patches, V_i , and mean clustering for gaps, V_j) for all four taxa. Where sample numbers permitted, I analyzed males vs. females and/or early vs. late summer separately within a taxon. Both *Pterostichus n.sp.* and *Scaphinotus marginatus* showed essentially random activity-density distributions throughout the sampling grid, whether all individuals were included in the analysis or they were separated by sex or season. *Scaphinotus angusticollis* distributions were strongly aggregated, and clustered into patches and gaps ($p < 0.001$ for all indices; Fig. 4.5a). For all

Table 4.2 Summary of SADIE analyses of arthropod spatial patterns. I_a = overall index of aggregation, V_i = mean clustering index for patches, V_j = mean clustering index for gaps. P-values from randomization tests are in parentheses, those in bold print associated with indicate significant aggregation ($p < 0.050$).

Species	Subset	n	I_a (clustering)	V_i (patches)	V_j (gaps)
<i>Pter. n.sp.</i>	all	281	1.04 (0.327)	1.06 (0.267)	-1.01 (0.396)
<i>Pter. n.sp.</i>	females	118	1.05 (0.316)	0.92 (0.672)	-0.99 (0.460)
<i>Pter. n.sp.</i>	males	152	1.02 (0.383)	1.00 (0.403)	-1.01 (0.400)
<i>S. marginatus</i>	all	168	0.89 (0.742)	0.95 (0.566)	-0.86 (0.830)
<i>S. marginatus</i>	females	63	1.21 (0.105)	1.16 (0.141)	-1.21 (0.113)
<i>S. marginatus</i>	males	98	0.82 (0.898)	0.89 (0.748)	-0.81 (0.920)
<i>S. marginatus</i>	Jun-Jul	83	1.12 (0.203)	1.07 (0.286)	-1.17 (0.150)
<i>S. marginatus</i>	August	85	0.89 (0.723)	0.92 (0.633)	-0.88 (0.764)
<i>S. angusticollis</i>	all	22	1.97 (<0.001)	1.85 (<0.001)	-1.98 (<0.001)
Lycosids	all	966	1.87 (<0.001)	1.77 (<0.001)	-1.75 (<0.001)
Lycosids	females	234	2.34 (<0.001)	2.32 (<0.001)	-2.25 (<0.001)
Lycosids	males	677	1.51 (0.010)	1.35 (0.024)	-1.40 (0.020)
Lycosids	Jun-Jul	819	1.76 (<0.001)	1.63 (0.004)	-1.64 (0.003)
Lycosids	August	147	1.75 (<0.001)	1.72 (<0.001)	-1.62 (0.002)

following grid figures, I refer to “left,” “right,” “upper,” and “lower” portions of the grid as if viewed from the perspective of Figure 4.1. Figure 4.5a indicates a large patch for *S. angusticollis* near the stream in the lower left half of the forested buffer, and a gap throughout the clearcut above. In contrast to these patterns, lycosids, whose distribution also showed strong aggregation ($p < 0.001$ for all indices), had several patches up in the clearcut and edge, and a large gap in the lower left portion of the forested buffer (Fig. 4.5b). High individual clustering indices for several sample units on the right side of the forested buffer, also indicated that lycosid distributions extended down into this portion of the grid. When I analyzed male and female patterns separately (Figs. 4.6a and 4.6b), female distributions included one large patch spread throughout most of the clearcut, while males were aggregated into two smaller patches in the left half of the clearcut. The gap in the forested buffer was also substantially smaller for males than for females.

Figure 4.5 (a-d) Contour maps overlain with classed post maps showing spatial pattern of arthropods and habitat variables. Magnitude of clustering index for patches (v_i) and clustering index for gaps (v_j) for individual sample units indicated by shade and size of circles: $v_i > 1.5 = \bullet$, $1.5 > v_i > 1 = \bullet$, $1 > v_i > 0 = \bullet$, $0 > v_j > -1 = \circ$, $-1 > v_j > -1.5 = \circ$, $-1.5 > v_j > = \circ$. Contour interval cutoffs are at $v_i > 1.5$ (dark shading) and $v_j < -1.5$ (lighter shading), interpolation for contours done by kriging. **(e-f)** Contour and classed post maps showing spatial association between arthropods and habitat variables. Contours interpolate local values of spatial association (χ) and range from -2.1 (black) to 2.1 (white), indicating significant dissociation and association, respectively. Sample units exceeding the upper 95th percentile critical values for χ (significant association) are indicated by open squares.

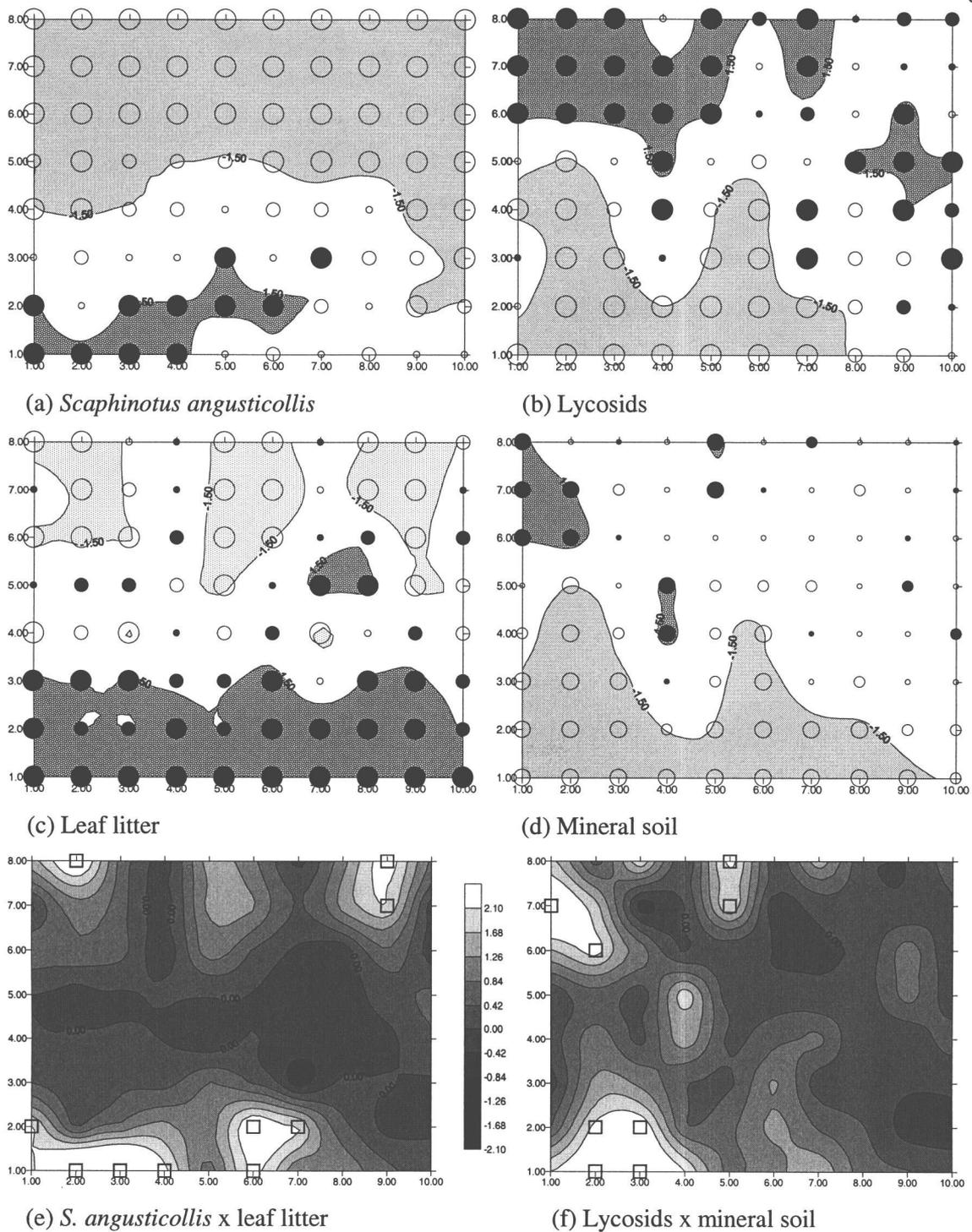


Figure 4.5

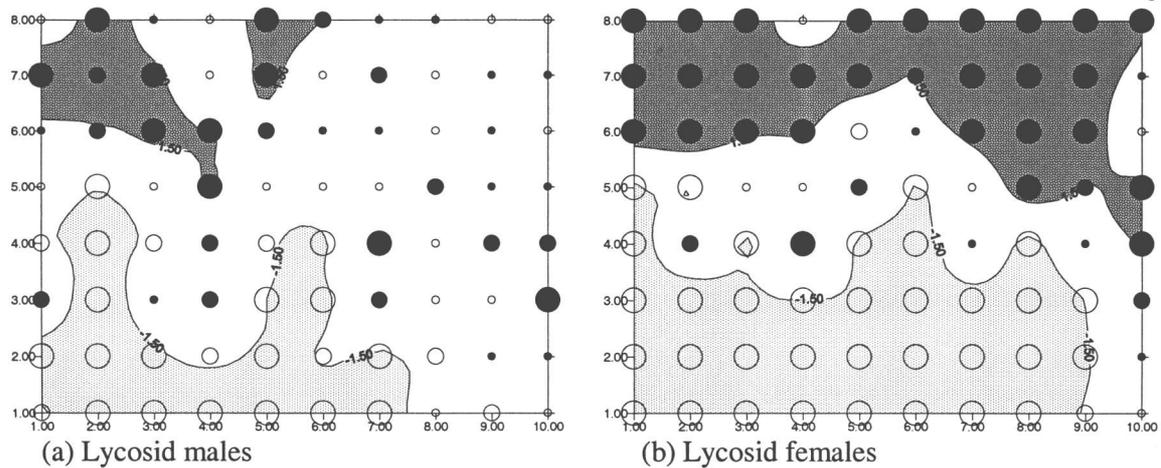


Figure 4.6 Contour maps overlain with classed post maps showing lycosid spatial pattern. Magnitude of clustering index for patches (v_i) and clustering index for gaps (v_j) for individual sample units indicated by shade and size of circles: $v_i > 1.5 = \bullet$, $1.5 > v_i > 1 = \bullet$, $1 > v_i > 0 = \bullet$, $0 > v_j > -1 = \circ$, $-1 > v_j > -1.5 = \circ$, $-1.5 > v_j = \circ$. Contour interval cutoffs are at $v_i > 1.5$ (dark shading) and $v_j < -1.5$ (lighter shading), interpolation for contours done by kriging.

Despite some observable differences in distributions for male and female lycosids, overall, SADIE analysis showed the two sexes to have strongly associated spatial patterns ($X = 0.67$, $p < 0.001$; Table 4.3). SADIE also indicated significant association between males and females of both *S. marginatus* and *Pterostichus n.sp.* (*S. angusticollis* was not included in this analysis because of low total catch numbers). Analysis of seasonal differences in distributions indicated strong association of early and late summer spatial patterns for lycosids ($X = 0.59$, $p < 0.001$; Table 4.3), but weaker seasonal association for *S. marginatus* ($X = 0.22$, $p = 0.040$; Table 4.3).

Table 4.3 Summary of SADIE analysis of arthropod associations. X = overall index of association. P-values from randomization tests are in parentheses, those in bold print associated with X indicate significant association ($p < 0.025$).

Taxon	Comparison	X
<i>Pter. n.sp.</i>	males x females	0.31 (0.003)
<i>S. marginatus</i>	males x females	0.33 (0.003)
<i>S. marginatus</i>	Jun-July x August	0.22 (0.040)
Lycosids	males x females	0.67 (<0.001)
Lycosids	Jun-July x August	0.59 (<0.001)

Spatial pattern and association for habitat variables and potential prey

All habitat variables, with the exception of woody debris (all decay classes combined), showed significant aggregation into patches and/or gaps (Table 4.4). Mineral soil (Fig. 4.5d), herbs, and shrubs had patches in the clearcut and gaps in the forested buffer, while leaf litter (Figure 4.5b), moss, and tree distribution (predictably) showed the reverse pattern of patches in the forested buffer and gaps in the clearcut. Decayed woody debris (class 4-5) showed strong spatial pattern that did not coincide with the forested buffer/clearcut boundary. There were several small patches of woody debris in the lower right quadrant of the grid, and gaps in the other three quadrants. Gastropods (snails and slugs), that may be serving as prey items for snail-feeding *Scaphinotus* species, showed no significant aggregation in their distribution when analyzed as a single taxon.

Table 4.4 Summary of SADIE analyses of habitat variable and gastropod spatial patterns. I_a = overall index of aggregation, V_i = mean clustering index for patches, V_j = mean clustering index for gaps. P-values from randomization tests are in parentheses, those in bold print indicate significant ($p < 0.05$) aggregation.

Habitat variable or prey species	I_a (clustering)	V_i (patches)	V_j (gaps)
Mineral soil (% cover)	1.43 (0.019)	1.38 (0.025)	-1.36 (0.036)
Leaf litter (% cover)	2.06 (<0.001)	1.84 (<0.001)	-2.06 (<0.001)
Moss (% cover)	1.53 (0.008)	1.43 (0.015)	-1.54 (0.007)
Herbs (% cover)	1.47 (0.010)	1.50 (0.029)	-1.35 (0.029)
Shrubs (stem density)	1.42 (0.021)	1.28 (0.048)	-1.26 (0.062)
Trees (basal area) *	1.83 (<0.001)	1.87 (<0.001)	-1.82 (<0.001)
Woody debris (all)	1.26 (0.082)	1.31 (0.051)	-1.30 (0.053)
Woody debris (decay class 4-5)	1.45 (0.016)	1.45 (0.049)	-1.45 (0.016)
Gastropods	1.14 (0.167)	1.04 (0.318)	-1.14 (0.177)

* non-parametric SADIE analysis

Significant associations between spatial patterns of species and habitat variables ($p < 0.025$) were indicated for only two taxa, *S. angusticollis* and lycosids (Table 4.5). Predictably, *S. angusticollis* showed a strong association with the habitat variables that were also patchy in the forested buffer (leaf litter, moss, and tree basal area), and a weaker association with decayed woody debris. Figure 4.5e is a contour map showing significant association between patches of *S. angusticollis* and litter in the lower left corner and center of the forested buffer, and gaps on left and right sides of the clearcut. Likewise, lycosids were strongly associated with habitat

variables that were aggregated into patches in the clearcut, such as mineral soil (Fig. 4.5f) and shrub density. Of the two snail-feeding *Scaphinotus* species, only *S. angusticollis* showed any association with mollusk spatial patterns ($X = 0.21$, $p = 0.033$). To see if *S. angusticollis* spatial pattern might be associated with a finer scale of habitat heterogeneity within the buffer itself, I reran the SADIE analyses on a subset of the species and habitat data restricted to just the buffer. These analyses showed a similar patchy pattern for *S. angusticollis* on the left side of the buffer, and a gap on the right side ($I_a = 1.86$, $p = 0.012$; $V_i = 1.52$, $p = 0.048$; $V_j = -1.96$, $p = 0.008$). The only habitat variable to show some association with the *S. angusticollis* spatial pattern within the buffer was moss cover ($X = 0.37$, $p = 0.039$).

Table 4.5 Summary of SADIE analyses of spatial association between species and habitat variables or gastropods. Values represent X, an overall index of mean spatial association. P-values from randomization tests are in parentheses, those in bold print indicate significant association ($p < 0.025$) or dissociation ($p < 0.975$).

	<i>Pterostichus</i> <i>n.sp.</i>	<i>S. marginatus</i>	<i>S. angusticollis</i>	Lycosids
Mineral soil (% cover)	0.16 (.091)	-0.19 (.924)	-0.65 (>.999)	0.76 (<.001)
Leaf litter (% cover)	-0.21 (.964)	0.18 (.067)	0.66 (<.001)	-0.59 (>.999)
Moss (% cover)	-.14 (.874)	0.22 (.036)	0.52 (<.001)	-.48 (>.999)
Herbs (% cover)	-0.17 (.815)	-0.19 (.927)	-0.42 (>.999)	0.21 (.056)
Shrubs (stem density)	-0.09 (.755)	-0.21 (.938)	-0.53 (>.999)	0.31 (.003)
Trees (basal area)*	-0.05 (.650)	-0.00 (.515)	0.56 (<.001)	-0.40 (.999)
Woody debris (decay class 4-5)	-0.29 (.995)	0.18 (.070)	0.21 (.041)	0.00 (.516)
Gastropods		0.030 (.398)	0.21 (.033)	

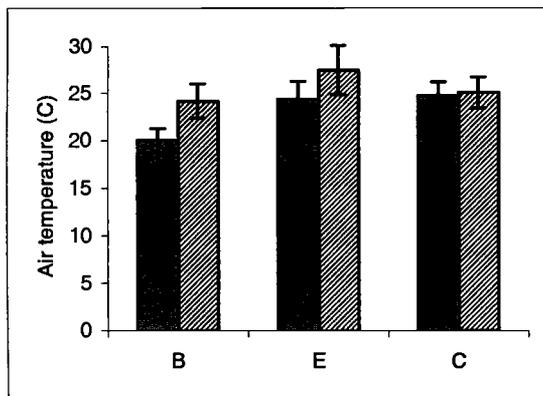
Spatial pattern of microclimate variables and association with arthropods

Overall differences in air temperature, soil temperature, and relative humidity across habitats were compared by averaging individual data logger values within the buffer, edge, and clearcut (Fig. 4.7). In June-July, mean maximum (3PM) air temperature was $\geq 4.3^{\circ}\text{C}$ lower in the buffer than in the edge or the clearcut, soil temperature was $\geq 1.4^{\circ}\text{C}$ lower, and minimum relative humidity was $\geq 14\%$ higher. Microclimate in the edge and clearcut were similar. Between June-July and August, 3PM air and soil temperatures increased in the buffer and the edge, and relative humidity decreased, but these variables showed relatively little seasonal change in the clearcut. In August, differences in microclimate between the buffer and the clearcut were small, while the edge showed the most extreme maximum temperatures and minimum relative humidity ($\geq 2.4^{\circ}\text{C}$ higher air temperature than the buffer or clearcut, $\geq 1.9^{\circ}\text{C}$ higher soil temperature, $\geq 7\%$ lower relative humidity). At midnight, mean temperatures and relative humidity were relatively similar among all habitat types within seasons, but between June-July and August, air temperature increased slightly across habitat types ($1.1\text{-}2.0^{\circ}\text{C}$), and relative humidity decreased (13-16%).

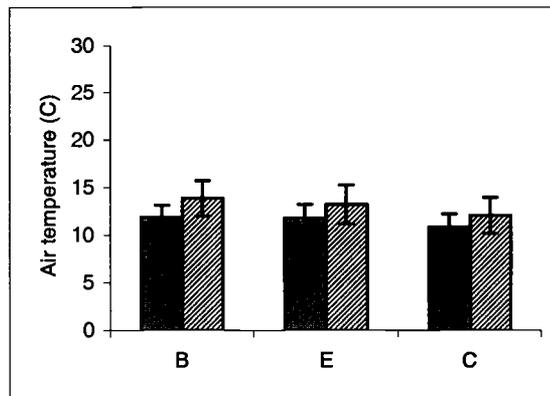
Spatial variability in microclimate within and between habitat types was highest during dry, hot days in mid-afternoon, and decreased considerably on cool, rainy days or at night. Figure 4.8 shows an overlay of mean maximum air and soil temperatures, and mean minimum relative humidity for June-July (a peak activity period for all taxa), on the sampling grid. The left side of the forested buffer, along the stream boundary, remained the coolest and most humid part of the sampling grid. This coincided with the patch where the forest specialist, *S. angusticollis*, was active (Fig. 4.5a). In contrast, the portion of the buffer furthest downstream (to the right), showed higher mean maximum air temperatures. Interestingly, this was the area of the buffer into which lycosid distributions extended (Fig. 4.5b). Soil temperature stayed low all along the stream, but both air and soil temperatures increased, and relative humidity decreased, toward the buffer boundary. Surprisingly, the lowest and highest mean air temperatures occurred only 14 m apart (between the stream edge and the buffer edge) in the far left side of the buffer. Relative humidity and air temperature showed a strong negative association.

In comparison to ranges of microclimate maxima and minima at 3PM in June-July, the ranges at midnight, when all the beetle taxa considered in this study are thought to be active, was much lower (mean air temperature ranged between 10.7 and 12.3°C ; mean soil temperature between 11.5 and 14.7°C ; mean relative humidity between 85 and 92 %). The range of spatial heterogeneity in temperature and humidity across the grid was similar in August, although mean air and soil temperatures were higher, and mean relative humidity was lower, than in June-July.

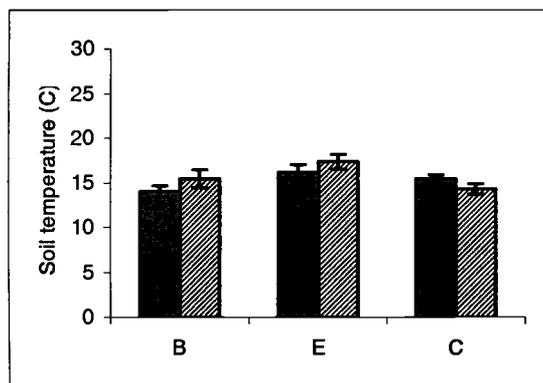
3PM



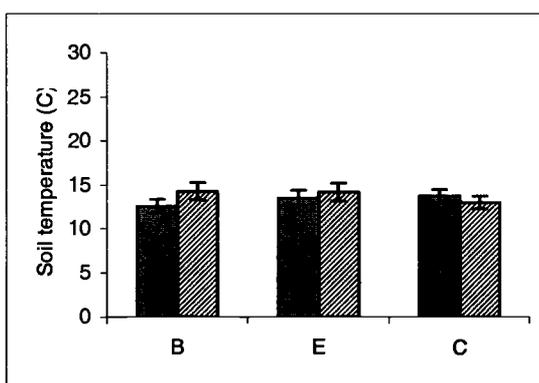
12AM (midnight)



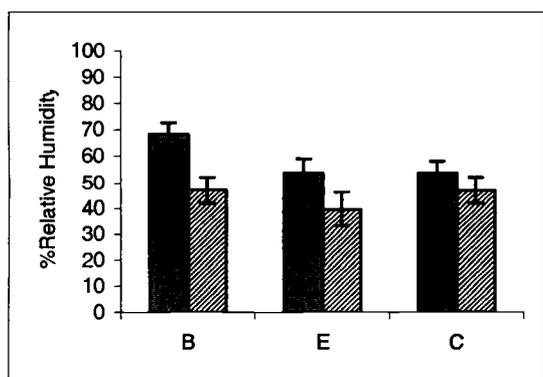
3PM



12AM



3PM



12AM

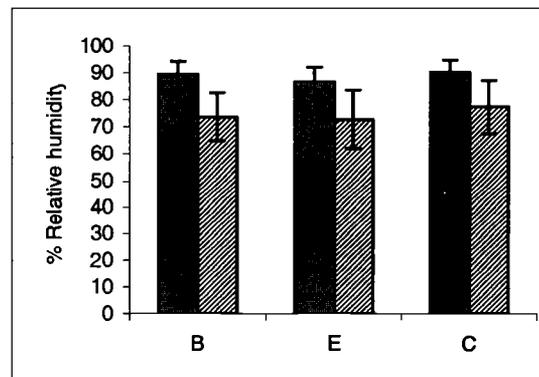


Figure 4.7 Mean air and soil temperatures and % relative humidity (\pm 95% CI) in the buffer (B; $n = 5$), edge (E; $n = 3$), and clearcut (C; $n = 4$) at 3PM and midnight during June-July (gray bars) and August (striped bars), 2002.

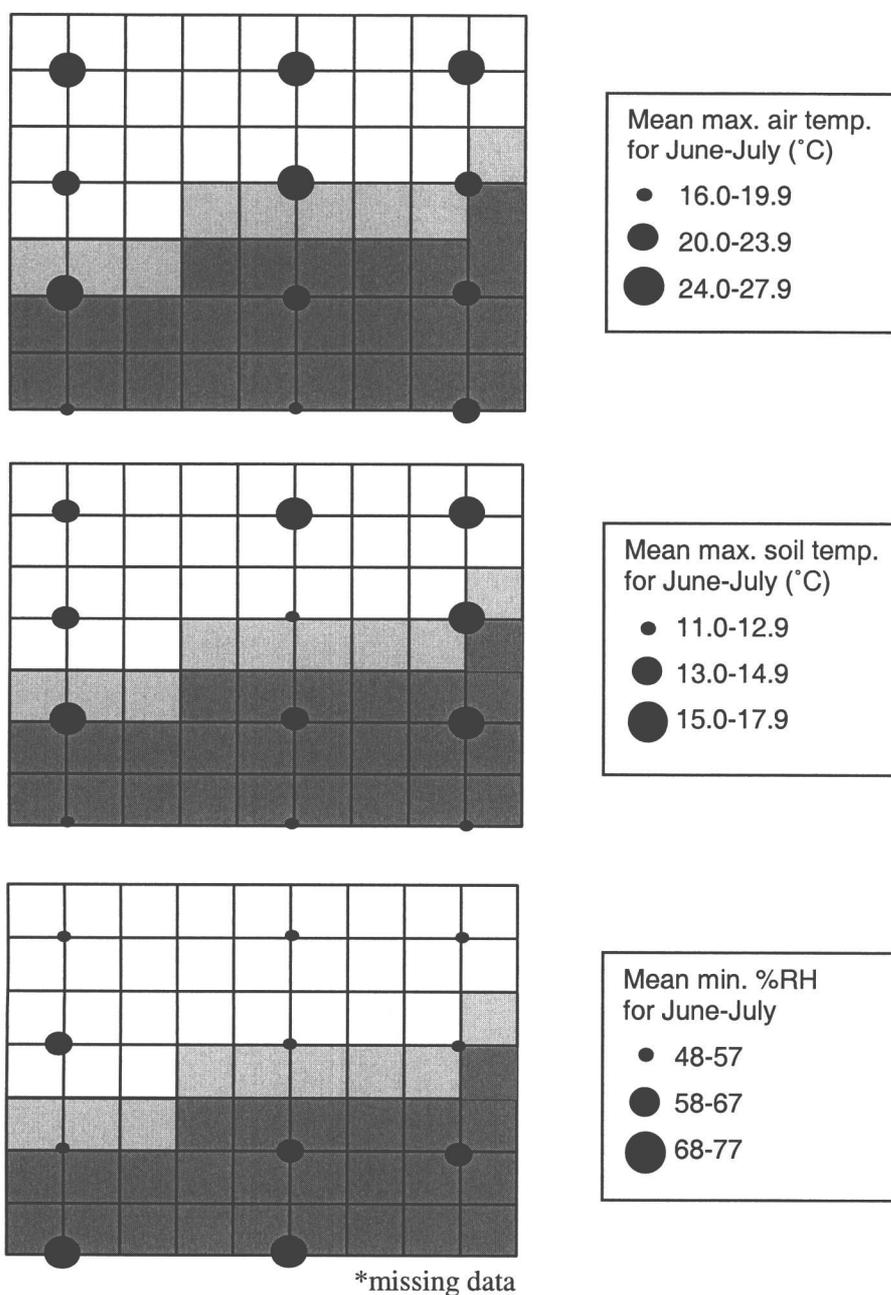


Figure 4.8 Overlay of microclimate variables on sampling grid. Each dot represents the location of a data logger; magnitude of variable indicated by size of dot (see legend). Variables are means of temperature or relative humidity values recorded at 3PM over 26 sampling dates in June-July, 2002.

Effects of microclimate on arthropod activity

Arthropod activity (measured as daily pitfall trap catches) varied with air temperature and relative humidity in early summer, but showed less response to microclimate in late summer (Fig. 4.9). Activity patterns in June-July were very similar for two eurytopic carabid species (*S. marginatus* and *Pterostichus n.sp.*) and the open-habitat associated lycosid spiders. *Scaphinotus angusticollis* was not included on the plot because daily catches were too low. There appeared to be strong positive relationships between the activity of all three taxa with daily air temperature at 3PM, indicating that these arthropods were most active on hot, dry days, and least active on cool, rainy days. Although the two beetle species are presumed to be nocturnal, there was no relationship between midnight air temperature and beetle activity. In late summer, *Pterostichus n. sp.* and the lycosids became much less active, while *S. marginatus* showed another activity peak. However, in August, *S. marginatus* showed little relationship with 3PM (or midnight) air temperatures. Mean soil temperature varied between 10 and 19°C and showed no obvious relationship with the activity of any taxa. Air temperature and relative humidity were clearly negatively correlated.

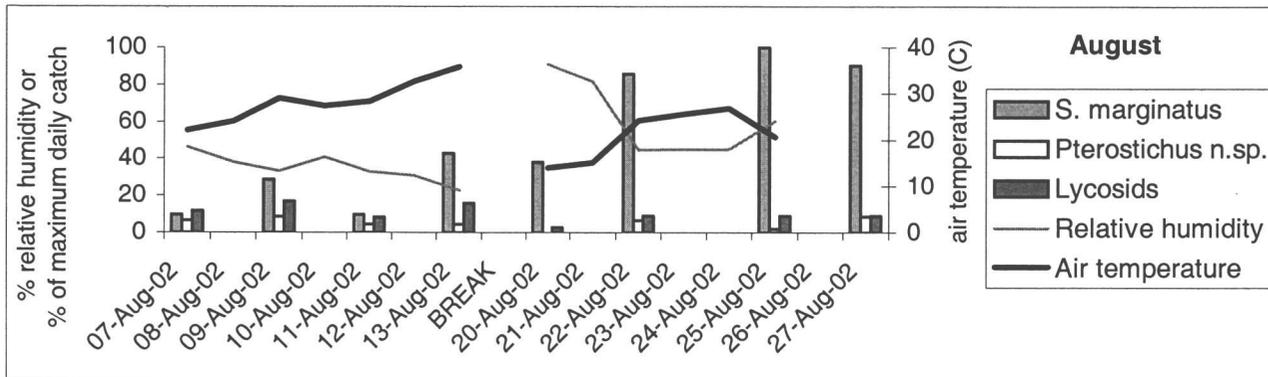
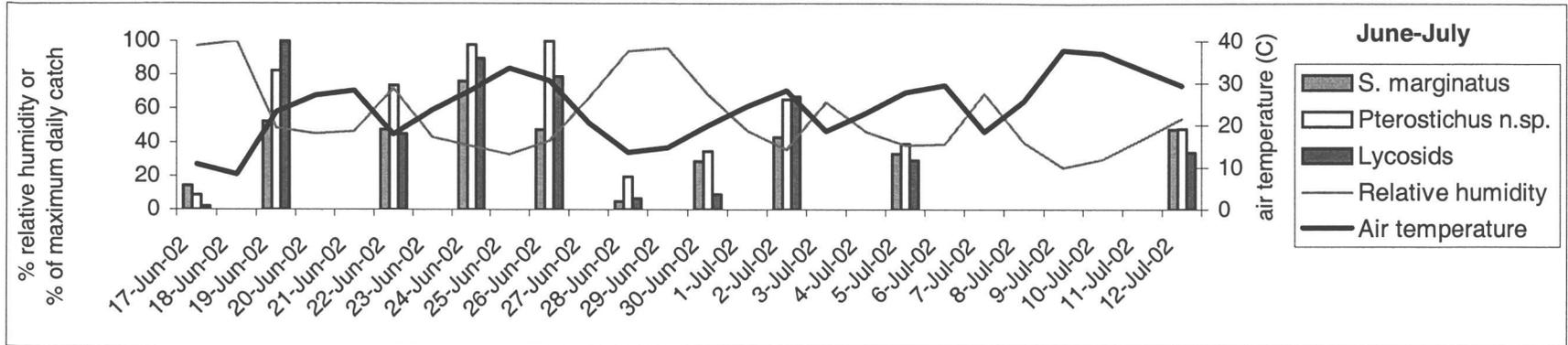


Figure 4.9 Arthropod activity (daily activity standardized for each taxon as a percentage of that taxon's maximum daily pitfall trap catch) and microclimate (mean daily air temperature and relative humidity at 3pm in the clearcut) in June-July (top plot; 10 sampling dates) and in August (bottom plot; 8 sampling dates), 2002. Note break in sampling dates on x-axis, and 3 different scales on y-axis. In August, breaks occur in microclimate plots where no data was recorded.

Arthropod movement analysis: recapture rates

Over four times as many lycosids were marked as any of the three beetle species (Fig 4.10). Among beetles, the number of marked individuals ranged from 161 for *Pterostichus n.sp.* to only 17 for the forest specialist, *S. angusticollis*. The recapture rate (number of individuals captured one or more times divided by the total number marked) was highest for *Pterostichus n.sp.* (33.5%), followed by 17.6% for *S. angusticollis*, 15.6% for *S. marginatus*, and 7.8% for lycosids. The rate for lycosids likely represents an under-estimate because spiders may have lost their marks within a few days, even though they were recaptured later. I was also not able to identify multiple recaptures (or re-markings) of the same lycosid individual. Among the beetles, multiple recaptures of the same individual occurred for only two species. For *Pterostichus n.sp.*, 10 individuals were recaptured twice, 4 individuals were recaptured three times, and one individual was recaptured four times. Seven recaptured beetles of this species (13.0% of those recaptured) had illegible marks on them, and, therefore, could not be used for further analysis. For *S. marginatus*, 3 individuals were recaptured twice, and one individual was recaptured three times. One individual (5.2% of those recaptured) had illegible marks.

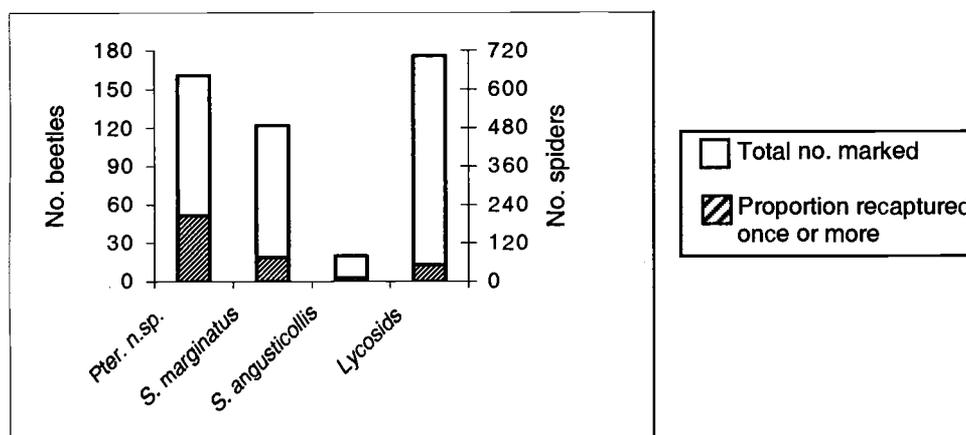


Figure 4.10 Total number of individuals marked between June 18 and August 28, 2002 shown as total column height for each species, number recaptured one or more times is shown as hatched proportion within column (note separate axis scales for beetles and spiders).

For all taxa, substantially more males were marked than females. For *Pterostichus n.sp.*, recapture rates were fairly equal between males (92 marked, 31.5% recaptured) and females (69 marked, 36.2% recaptured), but recapture rates were higher for *S. marginatus* males (73 marked, 17.8% recaptured) than for females (49 marked, 12.2% recaptured), and for *S. angusticollis* females (5 marked, 40.0% recaptured) than for males (12 marked, 8.3% recaptured). Lycosid females had a very low recapture rate of between 1.2% and 3.1% (field determination of

immature males vs. adult females was unreliable in late summer; 161 marked), compared to the adult male recapture rate of 9.9% (466 marked).

Displacement distances and rates

The majority of *Pterostichus n.sp.* recapture events involved beetles with small displacements in a short time (53.2% with a displacement ≤ 7 m in ≤ 6 days while only 1.6% with a displacement > 21 m in ≥ 13 days; Fig. 4.11). The largest displacement recorded for *Pterostichus n.sp.* was 28.9 m, and the mean displacement for the species was 6.5 m (95% CI = 4.5, 8.4). Mean displacements were somewhat higher for females than for males (male = 5.7 m, 95% CI = 3.4, 8.0; female = 8.0 m, 95% CI = 4.4, 11.5). In contrast, *S. marginatus* had a higher proportion of recapture events in which beetles had larger displacements and were recaptured after a longer period of time (28.6% with a displacement > 21 m in ≥ 13 days, compared to 23.8% with a displacement ≤ 7 m in ≤ 6 days). The largest displacement for *S. marginatus* was 66.04 m, and the longest time elapsed between release and recapture was 66 days. The mean displacement for the species was 19.2 m (95% CI = 11.7, 26.8). Males had a larger mean displacement (21.4 m, 95% CI = 11.5, 31.4) than females (13.3 m, 95% CI = 7.1, 19.6). *S. angusticollis* had only three recapture events, the largest displacement was 14 m, the longest time elapsed was 61 days. The mean displacement for this species was 10.3 m (95% CI = 6.3, 14.3). Lycosid mark-release-recapture data consisted of "vertical" (i.e., up-down movement in the sampling grid) distances traveled only, due to the marking method, therefore, mean displacements were not comparable to those of beetles. The mean vertical distance traveled by lycosids was 10.4 m (95% CI = 7.9, 12.8), with a maximum of approximately 38.5 m (this could represent a displacement distance of over 50 m if the horizontal component was included).

As a surrogate for movement rate (distance traveled/time), I calculated a "mean minimum daily displacement" value (Thomas et al. 1998) for each species. For each recapture event, I divided the displacement distance by the days elapsed between mark and recapture, and averaged these values over all events. This mean value represents the minimum distance the beetle had to travel each day to cover the distance between mark/release and recapture, and is likely an underestimate of the actual travel rate. *S. marginatus* showed the highest mean minimum daily displacement of 2.0 m/day (95% CI = 1.3, 2.8), with a lower rate for males (1.8 m/day; 95% CI: 1.0, 2.6) than for females (2.8 m/day; 95% CI = 1.3, 4.3). The mean minimum daily displacement for *Pterostichus n.sp.* was 1.2 m/day (95% CI; 0.8, 1.6); the rate was similar for males (1.3 m; 95% CI: 0.7, 1.9) and females (1.1 m; 95% CI: 0.6, 1.7). *S. angusticollis* had a mean minimum daily displacement of 1.8 m/day (based on only three recaptures; CI: 0, 3.7).

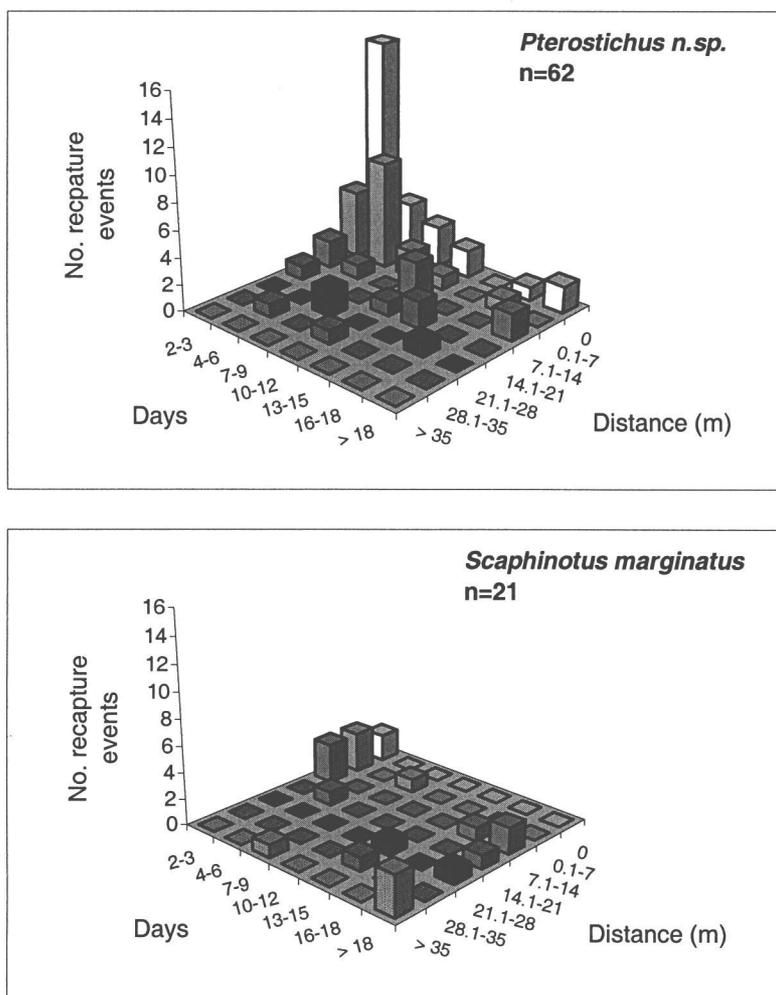


Figure 4.11 Total displacement distance and days elapsed between mark/release and recapture for two species of carabids (across all habitats).

Displacement distances and rates within different habitat types differed for the two eurytopic carabid species (Table 4.6). *Pterostichus n.sp.* had the largest mean displacement and the highest minimum daily displacement rate in the forested buffer and the smallest displacement and lowest movement rate in the edge. Within all habitat types, between 50 and 67% of the recapture events involved 0 m displacement (i.e., a beetle falling into a trap at the same sampling station from which it was released a minimum of 15 hours previously). For *S. marginatus*, the mean displacement distance was also higher in the buffer than in the clearcut. For this species, only 20% of the recapture events in the clearcut involved 0 m displacement, and all recapture events in the buffer involved at least 7 m displacement.

Table 4.6 Mean displacement distance and mean minimum daily displacement rate, compared between habitat types for two carabid species. n = number of recapture events where both mark/release and recapture were in the specified habitat type.

Taxon	Habitat	n	Displacement (m) (\pm 95% CI)	Rate (m/day) (\pm 95% CI)
<i>S. marginatus</i>	Clearcut	10	10.2 (5.1, 15.4)	2.1 (0.9, 3.3)
<i>S. marginatus</i>	Buffer	6	18.7 (3.3, 34.2)	1.7 (0.6, 2.9)
<i>S. marginatus</i>	Edge	0	NA	NA
<i>Pterostichus n.s.</i>	Clearcut	25	4.2 (1.9, 6.4)	1.0 (0.4, 1.6)
<i>Pterostichus n.s.</i>	Buffer	16	6.9 (3.5, 10.4)	1.4 (0.6, 2.3)
<i>Pterostichus n.s.</i>	Edge	12	2.8 (1.8, 6.7)	0.6 (0, 1.2)

Movement within and between habitat types

I built a null model for expected movement patterns between habitat types for each arthropod taxon using: (1) the spatial distribution data from SADIE analysis; and (2) the observed mean displacement distance between release and recapture (see Methods; Table 4.7). As SADIE analysis showed no significant aggregation for the two species, *Pterostichus n.sp.* and *S. marginatus*, they are considered eurytopic (i.e., no habitat specialization) in the model, and are allowed to travel throughout the sampling grid. Because the distribution of *S. angusticollis* was patchy only in the buffer (Fig. 4.5a), it was considered a forest specialist, and displacement distance was therefore irrelevant as it could not cross the buffer boundary into another habitat type. Lycosids were patchy in both the clearcut and the edge, and their distribution extended into a portion of the buffer (Fig. 4.5b). The model thus allowed lycosids to move across all of the clearcut and the edge, and into adjacent portions of the buffer where the clustering index (v_i) for lycosids was high (x,y coordinates (7,3),(10,3),(10,4), see Fig. 4.1 for reference). To allow *Pterostichus n.sp.* to cross habitat boundaries in the model, I increased its displacement distance from the mean observed distance (6.5 m) to 7 m (within the 95% CI, and the minimum distance between traps). For lycosids, as previously mentioned, the observed displacement distance represented only the spiders' vertical movement up and down in the grid. To incorporate horizontal distance into this measure, I doubled the observed mean vertical distance (10.4 m) to arrive at 21.0 m, which I used in the model. The decision to double the vertical distance was based on the beetle movement data, in which a 1:1 ratio of vertical to horizontal movement was approximated over all the observed displacements.

Table 4.7 Summary of spatial distribution, mean displacement, and adjusted displacement distance used in the null model for movement patterns of three beetle species and lycosid spiders across habitat types.

Taxon	Spatial distribution	Mean displacement (m) ($\pm 95\%$ CI)	Distance used in model (m)
<i>Pterostichus n.sp.</i>	eurytopic	6.5 (4.5, 8.4)	7.0
<i>S. marginatus</i>	eurytopic	19.2 (11.7, 26.8)	19.2
<i>S. angusticollis</i>	buffer only	NA	NA
Lycosids	clearcut, edge, portion of buffer	10.4* (7.9, 12.8)	21.0

* vertical distance

Observed and expected frequencies for *Pterostichus n.sp.* were quite similar for all categories (Table 4.8), suggesting that *Pterostichus n.sp.* moved randomly within habitat types and across their boundaries. For the other eurytopic species, *S. marginatus*, the observed frequency was twice as high in the clearcut as expected, and there was less observed movement within or out of the edge than expected. Lycosids (Fig. 4.12) showed far more movement between habitat types (especially into and out of the buffer) than expected. Frequency of movement across habitat type boundaries appeared to increase with increasing mobility (mean displacement distance) of a taxon (Fig. 4.12)

Table 4.8 Observed (in bold) and expected frequencies of four arthropod taxa in nine movement categories within and across habitats. C = clearcut, E = edge, B = forested buffer, (C-C = clearcut to clearcut; E-B = edge to buffer, etc.).

	C-C	C-E	C-B	E-E	E-C	E-B	B-B	B-E	B-C
<i>Pter. n.sp.</i> (expected)	20.3	2.5	0	12.6	2.5	2.5	19.0	2.5	0
(observed)	25	3	0	12	0	1	16	5	0
<i>S. marginatus</i> (expected)	5.0	1.4	0.7	2.0	2.3	2.4	5.8	1.5	0.7
(observed)	10	0	1	0	1	0	6	2	2
<i>S. angusticollis</i> (expected)	3	0	0	0	0	0	0	0	0
(observed)	3	0	0	0	0	0	0	0	0
Lycosids (expected)	14.9	10.5	0.7	12.7	8.1	1.9	1	1.5	0.7
(observed)	19	1	3	4	6	3	7	4	5

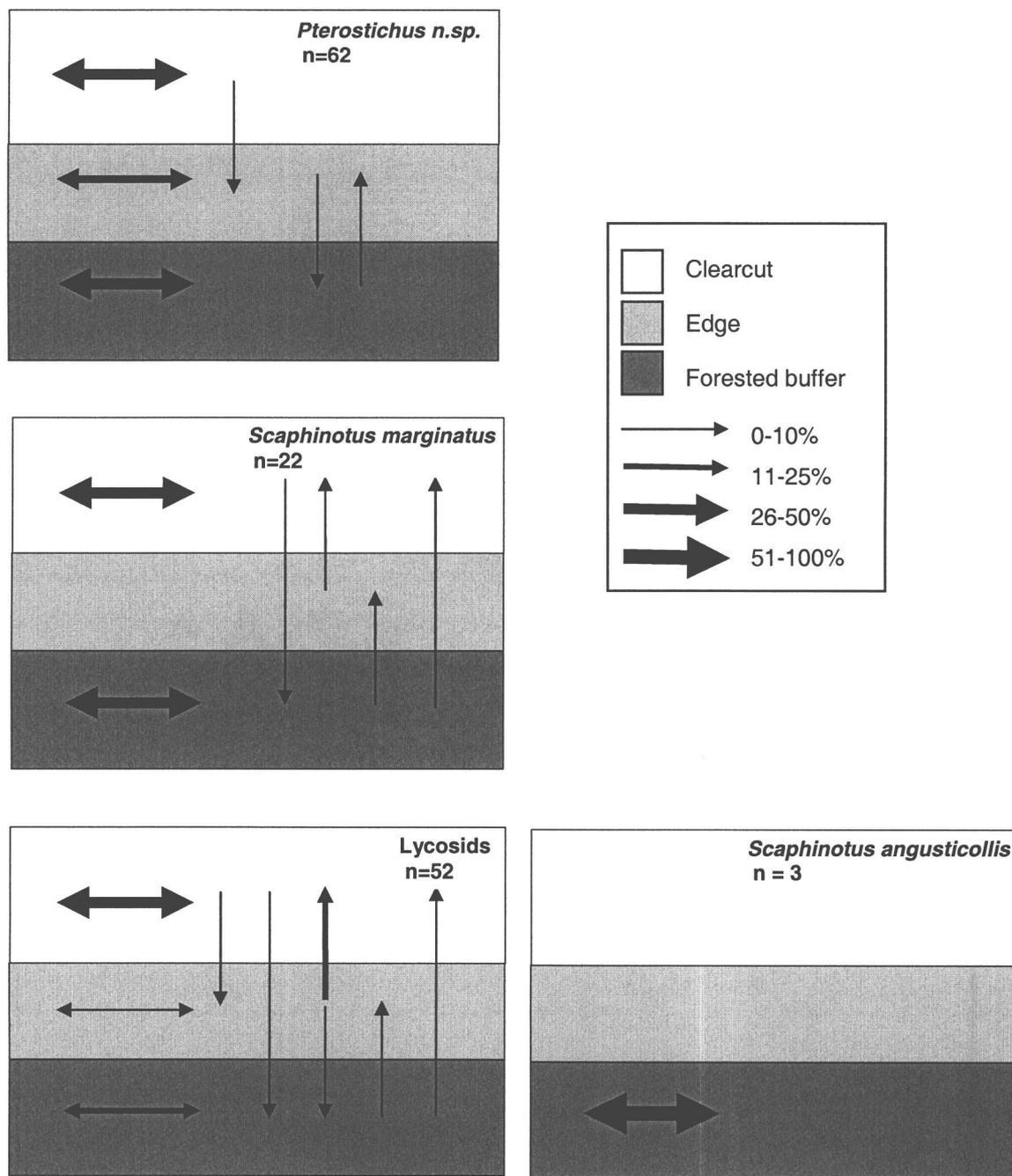


Figure 4.12 Observed movement patterns within and across habitat types for three carabid species and lycosid spiders between June 18 and August 28, 2002. Size of arrow represents the proportion of total recapture events for a taxon within a particular movement category. n = total number of recapture events.

DISCUSSION

Spatial pattern and habitat associations

The distribution of *S. angusticollis*, a forest-associated species, showed strong patchiness in the portion of the forested riparian buffer that was cool and moist; this area was next to the stream and likely insulated from the buffer edge. Topography differed in this portion of the sampling grid. An abrupt, steep slope dropped down to the stream between rows 2 and 1 on the upstream side of the grid (see Fig. 4.1), and therefore this area was more shaded from sunlight than the downstream portion, even though the distance to the edge of the trees was less (in fact, the nearest data logger at the edge of the trees consistently recorded the highest daytime air temperature of any logger on the sampling grid). The association of *S. angusticollis* with moss within the buffer is consistent with their similar requirements for cool, moist areas. The thick leaf/needle litter layer that was patchy throughout most of the forested buffer is typical of mature Douglas-fir forests in the region, and likely contributes to higher soil moisture levels. Carabid beetles vary in their microclimatic tolerances and/or preferences (Thiele 1977, Niemalä et al. 1988, Neve 1994, Atienza et al. 1996). In general, individuals can tolerate a temperature range of approximately 15°C, and they may have the ability to discriminate between differences in relative humidity as small as 5% (Thiele 1977). Because *S. angusticollis* is reported to be nocturnally active, and microclimatic conditions varied little between habitat types at midnight (Fig. 4.7), microclimate alone is likely not directly limiting the activity-density distribution of this species. It may be that the distribution of its gastropod prey is associated with daytime microclimate, or that other life history requirements such as cool, moist oviposition sites, are restricting *S. angusticollis* to stay within the riparian buffer. Given the restricted distribution of this forest species in the sampling grid, its low overall activity-density ($n = 22$) relative to the eurytopic beetles was not surprising.

Both *S. marginatus* and *Pterostichus n.sp.* showed a more random spatial distribution with regard to different habitat types. Twelve teneral (newly emerged) individuals of *S. marginatus* were captured from all parts of the grid between June 27 and August 8, 2002, suggesting that breeding sites were distributed widely, and further confirming this species as a habitat generalist. It is interesting to note that the two species of *Scaphinotus*, both of which are snail-feeding specialists, have quite different habitat requirements. Digweed (1993) reported that *S. marginatus* had distinct size preferences for gastropod prey. As *S. angusticollis* is considerably larger in body size than *S. marginatus*, the two species may be partitioning the gastropod resource based on prey size, mucus production, or other characteristics.

Lycosid activity-density was concentrated primarily in the clearcut. The spiders avoided the cool, moist area of the buffer in which *S. angusticollis* was active, but showed some penetration into the drier, warmer downstream portion of the buffer. Differences in spatial pattern between males and females were most evident in the clearcut, and may be related to the difference in seasonal activity levels between the sexes. In the early summer, lycosid males are actively searching for mates (Moring and Stewart 1994), therefore, they should be easier to catch (males made up over 80% of the June-July lycosid total), and their overall spatial pattern is likely to be more or less random throughout potential mating habitat. Figure 4.6a shows that lycosid males avoided the left side of the buffer, and were only aggregated in the upper left side of the clearcut, where they appeared to be associated with a patch of bare mineral soil (Fig. 4.5d). As lycosids are diurnal, visual hunters, bare substrate provides ideal habitat for catching prey and/or finding mates (Moring and Stewart 1994). During this same time period, female lycosids are relatively less active, as a result, their capture rates were lower (only 20% of the early summer lycosid total), and their distribution was more sharply defined, with one large patch spreading throughout the clearcut, and one large gap extending through much of the buffer and edge habitats. Later in the summer (August), males were no longer active, mated female lycosids were first observed with spiderlings on their backs, and females and immature spiders made up over 90% of the catch. However, only half as many females were caught in August as in June-July, suggesting their activity was still relatively low.

Microclimatic edge effects may have facilitated invasion of the right side of the buffer by open habitat-associated lycosids. When June-July microclimate data were pooled together by habitat, mean air temperature was approximately 4°C lower, and mean relative humidity was over 10% higher, in the forested buffer (at 3PM) than in either the edge or the clearcut. However, within the buffer itself, spatial variation in microclimate was high. Such variation may have been the result of topography, as mentioned above, as well as the "ragged" arrangement of large conifers at the buffer edge, where gaps allowed direct penetration of sunlight into portions of the riparian forest, while large trees shaded other areas for much of the day. Later in the season (when overall temperatures increased and humidity decreased), differences in microclimate between the buffer and the edge/clearcut lessened considerably. As with beetles, spiders are known to have physiological tolerance ranges for air temperature and humidity that influence their activity and habitat preferences (Nentwig 1987), and many lycosids especially, are adapted to warm, dry conditions more typical of open-habitats.

Arthropod activity

The two eurytopic carabid species in this study were presumed to be nocturnal, and as night-time microclimate was relatively consistent throughout the sampling grid, it seems unlikely that their movements across habitat boundaries were directly affected by microclimatic gradients. Activity levels for these two species (as well as the diurnal lycosids) over the June-July season, however, showed a strong association with daytime (3PM) temperatures and humidity levels, and no relationship with nighttime microclimate. When days were dry and warm at 3PM, activity (as measured by pitfall catches) was much higher than when it was cold and wet. Evidence from research on carabid beetles, suggests that diurnal species become more active at higher soil or air temperatures (Baars 1979b, Honek 1988, Kennedy 1994, Neve 1994, Atienza et al. 1996), this also has been observed for lycosids (Nentwig 1987). Honek (1997) found that catch size for day-active carabids in a fallow field increased 6.3% for every 1° increase in mean daily temperature. Baars (Baars 1979b) also found that for day-active beetles, daily maximum temperatures were relevant, but for night-active species, minimum temperatures predicted activity. Neve (1994) and others (Kennedy 1994, Atienza et al. 1996) have reported "critical limits" for night-time temperatures, above which carabids became active, but show no positive or negative relationship with further changes in temperature. It may be that *S. marginatus* and *Pterostichus n.sp.* are not strictly nocturnal in their activity, or that their prey are responding to daytime conditions. There may also be a delayed response to climatic conditions, so that warm, dry days following a wet period provide a flush of prey and stimulate subsequent activity of the nighttime predators.

Seasonal demographic processes also influence changes in arthropod activity over time (Honek 1997). By late summer, the lycosids and *Pterostichus n.sp.* showed decreased levels of activity, despite seemingly favorable climatic conditions. In contrast, *S. marginatus* remained active throughout August. It is likely that much of the August activity represents a new generation of individuals, as this species overwinters as both adult and larva, with teneral emerging in early- to mid-summer (Greene 1975). In August, activity showed no relationship with either nighttime or daytime temperatures or relative humidity. *Scaphinotus angusticollis*, the forest specialist, also remained active in August, although daily catches were too low to discern pattern.

Arthropod movement

Overall recapture rates of 7-35% among arthropod taxa were comparable to those reported in European hedgerows and arable lands for carabids and lycosids (e.g., Mader et al. 1990, Joyce et al. 1999, Kiss and Samu 2000), although recapture rates of over 60% have been

reported for some species (Petit and Burel 1993, Thomas et al. 1998). Given the complex tangle of low vegetation and dead wood on the ground throughout much of the clearcut and edge in this study, recapture rates were higher than might be expected. Higher recapture rates for males than females among lycosids and *S. marginatus* are likely a direct reflection of increased activity among males during the mating season (Moring and Stewart 1994).

Displacement distances and movement rates varied between the taxa, and within a taxon, varied between habitat types. Two basic types of movement have been described for carabids (Baars 1979b, Charrier et al. 1997). Random walking is characterized by short displacements and a high frequency of changes in direction, with the angle of each successive turn being independent of the last. This type of movement is thought to be typical of satiated beetles in favorable habitat (Wallin and Ekbohm 1988). Alternatively, directed movement involves longer displacements, less frequent changes in direction, and more constant turning angles. This type of movement has been associated with beetles in unfavorable habitat, or with beetles actively searching for prey or mates (Kennedy 1994, Charrier et al. 1997). Individuals may display both types of movement depending on their location and physiological state, but without constant observation of the individual (e.g., radio-tracing studies by Charrier et al. 1997, Wallin and Ekbohm 1988, or visual observations by Wiens and Milne 1989) it is difficult to infer the type of movement that has occurred within or across particular habitat types. In the present study, mark-release-recapture data consisted of total displacement and days elapsed between release and recapture events. If these two parameters were positively correlated, it might imply uninterrupted and directed movement between release and recapture points (Petit and Burel 1993). However, no such relationship was evident for *S. marginatus* and *Pterostichus n.sp.* (Fig. 4.11).

Over 45% of *Pterostichus n.sp.* recapture events resulted in 0 m displacement between release and recapture. Some of these beetles may have been attracted by pheromones from previously trapped animals and gone directly back into the trap, however because all traps were closed for 15-24 hours after marking and release of each beetle, it is more likely that many beetles were recaptured while moving randomly in the vicinity of the trap. This phenomenon was observed in the clearcut, edge, and buffer and provides further evidence that this species is eurytopic in its distribution. Mean minimum daily displacement was highest for *Pterostichus n.sp.* within the forested buffer (1.43 m/day), where the open mat of needle litter may have provided a relatively smooth substrate for travel.

Scaphinotus marginatus had a mean displacement distance (19.23 m) between release and recapture almost three times that of *Pterostichus n.sp.* This larger displacement distance may have resulted in part from the longer activity window (the species was active from June to

August), which allowed recaptures after many more days than for the species whose activity peaked in June-July. However, the mean minimum daily displacement was also highest among the beetles (2.03 m/day). Less than 10% of the recapture events resulted in a beetle returning to the same cup from which it was released, further suggesting that this species was more mobile in all parts of the grid. Interestingly, the mean minimum daily displacement for *S. marginatus* was higher in the clearcut than in the buffer. As the substrate throughout much of the clearcut was more complex than in the buffer, this higher displacement rate suggests directed movement, perhaps in pursuit of gastropod prey, which may be more challenging to find in the clearcut than in the buffer. Honek (1988) suggested that differences in speed and activity of beetles in different crop stands were due to differences in temperature rather than physical habitat complexity. However, if nocturnal, minimal differences in night-time temperatures across habitat types would probably not affect the activity of *S. marginatus*.

Movement patterns

Movement patterns within habitat types and across habitat boundaries varied considerably among the four taxa observed in this study. The effects of physical characteristics of fragment edges (e.g., the perimeter-to-area ratio, or the abruptness of structural difference) on animal movement have received much attention in landscape ecology (Forman and Moore 1992, Collinge and Palmer 2002). Relating observed movement patterns to habitat affinity and mobility among arthropods in this study supported the idea that the "permeability" of an edge to animal movement is as much a function of an animal's unique biological tolerances and capabilities, as of any physical edge attributes (Wiens et al. 1985, Stamps et al. 1987, Wiens 1997).

For *S. angusticollis*, a mobile forest specialist, and most likely dependent on the cool, moist conditions of the forest, the buffer edge served as a barrier to movement. Although the recapture data for this species were too few to provide convincing evidence, this conclusion is supported by Duelli (1990), who found that almost all the "hard edge" species in a fragmented landscape were exclusive specialists of natural, undisturbed habitats. Work (2000) described *S. angusticollis* as an "edge-phobic" species, strongly associated with interior forest. The fact that *S. angusticollis* is still active within such a narrow strip of riparian forest seven years after the habitat was altered, suggests either that there is a viable population reproducing within the riparian buffer, or it is using the buffer as a dispersal corridor between larger forest fragments. Sustek (1994b) found that windbreaks in agricultural land 12-25 m wide were adequate for carabid travel, and studies in similar landscapes have found that linear fragments such as hedgerows can provide habitat or dispersal corridors for carabids (Petit and Burel 1993, Charrier

et al. 1997, Joyce et al. 1999). Burel (1989) categorized the carabid fauna of a hedgerow network abutting a forest as “core forest” species that did not venture into hedgerows, “corridor” species that were able to reproduce in the hedgerows, and “peninsula” species whose numbers diminished with distance from the forest. *Scaphinotus angusticollis* may be such a peninsula species, able to survive in suitable portions of the buffer, but not in others, and thus able to use the buffer as a “stepping stone” for dispersal to larger fragments (Gruttke 1994). If dispersal between suitable forest fragments is restricted to forested corridors such as riparian buffers, then these linear fragments will be critical to the long-term survival of metapopulations of *S. angusticollis*. Den Boer (1990) noted that especially for those species adapted to stable habitats, dispersal capabilities were of prime importance for keeping the population viable. If adequate means for dispersal do not exist, then fragmenting the landscape into non-connected island “sinks” will drive the population extinct (Pulliam and Danielson 1991).

The two eurytopic carabid species, *Pterostichus n.sp.* and *S. marginatus*, were expected to move randomly throughout the grid, with no regard for habitat boundaries. *Pterostichus n.sp.* showed essentially random movement, with slightly less movement within the buffer, and slightly more movement out of the buffer than expected. In accordance with the null model, *Pterostichus n.sp.* was not observed to travel between the clearcut and the riparian buffer, due, presumably, to its relatively low mobility. *Scaphinotus marginatus* had a greater mobility range, and so was expected to cross into other habitats more frequently than *Pterostichus n.sp.* Observations of *S. marginatus* movements within the clearcut were twice as frequent as expected, matched expectations within the buffer, and were less frequent within and out of the edge than expected. It may be that the higher mean minimum daily displacement in the clearcut contributed to more frequent captures in this habitat, as “trappability” is a function of activity. These results also suggest that *S. marginatus* was able to cross the edge to get from one habitat type to the other, but avoided staying in the edge itself. One reason for edge avoidance in late summer, especially, may have been in response to extreme maximum air temperature and minimum relative humidity in this zone. Chen et al.(1993) and Williams-Linera (1990) reported microclimate parameters to be more extreme at the forest edge than in either the adjacent cleared land or interior forest because of stable air masses that form at the edge. Because these two eurytopic carabid species appeared capable of moving freely across habitat boundaries, the effects of fragmentation on their long-term population survival will likely be far less severe than for *S. angusticollis*.

Observed movement patterns of lycosids varied substantially from the movements predicted by their habitat association and estimated mobility. Over one-third of the spiders were active within just the clearcut, about as expected. However, over 40% of observed spider

movement was within, into, or out of the buffer, far exceeding expectations of the null model for random movement. These patterns suggest that while lycosids maintained a strong preference for open habitats, they were also able to cross the forest boundary and “invade” a habitat where their overall activity-density distributions were sparse. As mentioned above, this lycosid invasion into the buffer may be facilitated by microclimatic edge effects, although lycosids were recaptured throughout the buffer, even in the cooler, moister portions. This phenomenon of open-habitat species (especially carabids and lycosids) invading the edges of forest fragments has been widely reported by others (Halme and Niemälä 1993, Pajunen et al. 1995, Spence et al. 1996, Koivula 2002). For these species, while the edge represents a boundary to high activity-density distributions (and perhaps breeding sites) associated with open habitat, individuals may still cross the edge to exploit resources within the ameliorated (i.e., warmer, drier) microclimate of the forest fragment. In this study, it may be that breeding males wandering in search of females ended up in both preferred and less-preferred habitats depending on their success. Individuals also may have been visiting the buffer to take advantage of alternative prey resources, but returned to the clearcut when satiated. Increased activity by invading predators may result in intraguild interference (Lang 2003) within the forest predator community, with potential consequences for forest community structure.

In conclusion, the four taxa observed in this study exhibited different responses to the same habitat boundary. Strong associations with habitat and microclimate for *S. angusticollis* likely influenced its perception of the forest boundary as a barrier to movement. The other two carabid species showed no obvious spatial pattern or associations with habitat or microclimate, and consequently, their tendency to cross habitat boundaries was affected mostly by their mobility range. Lastly, while lycosids were largely associated with open and edge habitats and a particular microclimatic regime, they nevertheless perceived the edge as permeable to movement, resulting in their “invasion” of the forested buffer. These observations support the idea held by Stamps et al. (1987), Duelli (1990), Collinge and Palmer (2002) and others, that “edge permeability” in a fragmented landscape is in large part a function of each species’ biology, and therefore cannot be predicted by measuring physical attributes alone. This study further suggests that by collecting detailed spatial distribution and movement data for a variety of taxa we may improve our ability to predict the consequences of fragmentation on forest species and communities.

CHAPTER 5

CONCLUSION

This research sought to assess the ecological significance of headwater stream riparian zones as habitats for forest-floor invertebrates, and to compare the responses of invertebrate communities and species to alternative riparian management treatments. Relationships between invertebrate distributions, activity, microclimate and microhabitat were explored to help explain observed responses. In Chapter 2, community analyses revealed that riparian zones along intact, unmanaged forested headwater streams provided habitat for a distinct "riparian" assemblage within one meter of the stream, where it was cool and humid, although species diversity did not differ from upslope. Patterns upslope of the stream edge were difficult to discern because of strong elevation and block effects on species composition. Riparian buffers of ~30 m width were far more effective at preserving forest invertebrate communities than were clearcuts with minimal or no buffers, and again, microclimate was strongly correlated with community composition, as were some habitat variables such as moss cover and depth of the organic layer. Biological edge effects (i.e., changes in the distributions of invertebrates) in the buffer were not apparent at the community level, however, distributions of individual species appeared to vary in their response to the buffer edge.

Chapter 3 focused exclusively on microclimate, and many of the patterns within and across treatments mirrored community composition patterns observed in Chapter 2. Air temperature and relative humidity at the stream edge in a mature forest (the zone encompassing the "riparian" invertebrate fauna) were significantly lower and higher, respectively, than at 10 m from the stream. A gradient for both variables extended to 20 m upslope before leveling off to upslope forest interior values. This cool, humid "stream effect" on microclimate in the riparian zone was hypothesized to have a modifying influence on potential warm, drying effects from the forest edge, as there was no evidence for microclimatic edge effects in the buffer. Even at the hottest time of the day, on the hottest days of the season, there were no differences in microclimate between the intact forest and buffer treatments. There were clear treatment differences in all microclimate variables, however, when comparing clearcut values to either the buffer or the forest.

In Chapter 4, I assessed biological edge effects associated with the forest/clearcut boundary by examining individual species responses to the riparian buffer edge. Spatial analyses of species distributions, together with movement data from mark-release-recapture experiments,

confirmed ideas put forth by Stamps et al. (1987), Collinge and Palmer (2002), and others that the permeability of an edge is a function of both the biology of an organism, as well as the physical characteristics of the edge. For instance, *Scaphinotus marginatus*, a mobile habitat generalist beetle, was observed to cross the forest edge freely, while *Scaphinotus angusticollis*, a forest specialist beetle, appeared (based on limited data) to perceive the forest edge as a barrier to movement. Altered microclimate within part of the buffer may have facilitated the invasion of mobile, open-habitat associated lycosid spiders. The degree of permeability of the edge for less mobile, forest-associated species, especially, will have consequences for dispersal, population dynamics, and ultimately, survival.

As stream management strategies evolve in the Pacific Northwest, more emphasis is being placed on watershed scale approaches to protecting the ecological integrity of aquatic and riparian resources. Under these plans, managers choose among many options (from no protection to larger, patch reserves) throughout the watershed, based on site-specific information. As we learn more about the significance of small headwater streams and their riparian zones to forest and riparian biota, protection of these landscape features will be of higher concern. Defining appropriate goals for riparian protection, and designing effective management strategies to meet these goals will be the critical challenge. This study examined linear buffers of ~30 m and found they may be sufficient in some places to preserve forest-floor invertebrate communities. The absence of microclimatic edge effects in these buffers was surprising given that the extent of edge effects for parameters such as air temperature and humidity documented in many previous upland forest fragmentation studies ranged between 15 and 240 m (Chen et al. 1995, Murcia 1995). This discrepancy further underscores the fact that riparian ecotones are unique ecological systems, and the application of upland ecological models may sometimes be inappropriate. Another option for riparian protection is to implement larger, isolated patch reserves that may encompass a stream confluence (Cissel et al. 1998), thereby reducing the edge to interior ratio of the forest fragment. If such reserves are large enough to sustain viable populations of organisms, then this design may be an improvement on standard narrow, linear buffers. However, as connectivity with other fragments may be lost, subsequent isolation of forest-associated species for whom a forest edge represents a barrier to dispersal may become an important concern.

BIBLIOGRAPHY

- Adis, J. 1979. Problems of interpreting arthropod sampling with pitfall traps. *Zoologischer Anzeiger* 202:177-184.
- Allegro, G., and R. Sciaky. 2003. Assessing the potential role of ground beetles (Coleoptera, Carabidae) as bioindicators in poplar stands, with a newly proposed ecological index (FAI). *Forest Ecology and Management* 175:275-284.
- Andersen, J. 1985. Humidity responses and water balance of riparian species of Bembidiini (Col., Carabidae). *Ecological Entomology* 10:363-375.
- Andersen, J. 1995. A comparison of pitfall trapping and quadrat sampling of Carabidae (Coleoptera) on river banks. *Entomologica Fennica* 6:65-77.
- Andersen, J. 1997. Habitat distribution of riparian species of Bembidiini (Col., Carabidae) in South and Central Norway. *Fauna Norvegica Series B* 44:11-25.
- Anderson, R. S. 2002. Curculionidae. Pages 722-815 in R. H. Arnett, M. C. Thomas, P. E. Skelley, and J. H. Frank, editors. *American beetles Polyphaga: Scarabaeoidea through Curculionoidea*. CRC Press, Boca Raton, Florida.
- Antvogel, H., and A. Bonn. 2001. Environmental parameters and microspatial distribution of insects: a case study of carabids in an alluvial forest. *Ecography* 24:470-482.
- Atienza, J. C., G. P. Farinos, and J. P. Zaballos. 1996. Role of temperature in habitat selection and activity patterns in the ground beetle *Angoleus nitidus*. *Pedobiologia* 40:240-250.
- Baars, M. A. 1979a. Catches in pitfall traps in relation to mean densities of carabid beetles. *Oecologia* 41:25-46.
- Baars, M. A. 1979b. Patterns of movement of radioactive carabid beetles. *Oecologia* 44:125-140.
- Bedford, S. E., and M. B. Usher. 1994. Distribution of arthropod species across the margins of farm woodlands. *Agriculture, Ecosystems and Environment* 48:295-305.
- Belaoussoff, S., P. G. Kevan, S. Murphy, and C. Swanton. 2003. Assessing tillage disturbance on assemblages of ground beetles (Coleoptera: Carabidae) by using a range of ecological indices. *Biodiversity and Conservation* 12:851-882.
- Bennett, R. G. 1991. The systematics of North American cybaeid spiders (Araneae, Dictynoidea, Cybaeidae). Ph.D. dissertation. University of Guelph, Ontario.
- Biondini, M. E., J. P. W. Mielke, and K. J. Berry. 1988. Data-dependent permutation techniques for the analysis of ecological data. *Vegetatio* 75:161-168.
- Brenner, G. J. 2000. Riparian and upslope beetle communities along a third order stream in the western Cascade Mountain Range, Oregon. Ph.D. dissertation. Oregon State University, Corvallis, Oregon.

- Bright, D. E. 1994. Revision of the genus *Sitona* (Coleoptera: Curculionidae) of North America. *Annals of the Entomological Society of America* 87:277-306.
- Brososke, K. D., J. Chen, R. J. Naiman, and J. F. Franklin. 1997. Harvesting effects on microclimatic gradients from small streams to uplands in western Washington. *Ecological Applications* 7:1188-1200.
- Burel, F. 1989. Landscape structure effects on carabid beetles spatial patterns in western France. *Landscape Ecology* 2:215-226.
- Butterfield, J. 1996. Carabid life-cycle strategies and climate change: a study on an altitude transect. *Ecological Entomology* 21:9-16.
- Camargo, J. L. C., and V. Kapos. 1995. Complex edge effects on soil moisture and microclimate in central Amazonian forest. *Journal of Tropical Ecology* 11:205-221.
- Carvalho, K. S., and H. L. Vasconcelos. 1999. Forest fragmentation in central Amazonia and its effects on litter-dwelling ants. *Biological Conservation* 91:151-157.
- Castelle, A. J., A. W. Johnson, and C. Conolly. 1994. Wetland and stream buffer size requirements--a review. *Journal of Environmental Quality* 23:878-882.
- Chamberlin, R. V., and W. Ivie. 1932. A review of the North American spiders of the genera *Cybaeus* and *Cybaeina*. *Bulletin of the University of Utah* 23:1-43.
- Chamberlin, R. V., and W. Ivie. 1937. New spiders of the family Agelenidae from western North America. *Annals of the Entomological Society of America* 30:211-241.
- Chamberlin, R. V., and W. Ivie. 1940. Agelenid spiders of the genus *Cicurina*. *Bulletin of the University of Utah* 30:1-108.
- Chandler, D. S. 1986. New Pselaphidae from Oregon (Coleoptera). *Pan-Pacific Entomologist* 62:333-339.
- Charrier, S., S. Petit, and F. Burel. 1997. Movements of *Abax parallelepipedus* (Coleoptera, Carabidae) in woody habitats of a hedgerow network landscape: a radio-tracing study. *Agriculture, Ecosystems and Environment* 61:133-144.
- Chen, J., J. F. Franklin, and T. A. Spies. 1993. Contrasting microclimates among clearcut, edge, and interior of old-growth Douglas-fir forest. *Agricultural and Forest Meteorology* 63:219-237.
- Chen, J., J. F. Franklin, and T. A. Spies. 1995. Growing-season microclimatic gradients from clearcut edges into old-growth Douglas-fir forests. *Ecological Applications* 5:74-86.
- Chen, J., S. C. Saunders, T. R. Crow, R. J. Naiman, K. D. Brososke, G. D. Mroz, B. L. Brookshire, and J. F. Franklin. 1999. Microclimate in forest ecosystem and landscape ecology. *Bioscience* 49:288-297.

- Cissel, J. H., F. J. Swanson, G. E. Grant, D. H. Olson, and S. V. Gregory, S. L. Garman, L. R. Ashkenas, M. G. Hunter, J. A. Dertis, J. H. Mayo, M. D. McSwain, S. G. Swetland, K. A. Swindle, and D. O. Wallin. 1998. A landscape plan based on historical fire regimes for a managed forest ecosystem: the Augusta Creek study. General technical report PNW-GTR-422. U.S. Forest Service, Pacific Northwest Research Station, Portland, Oregon.
- Clarke, K. R. 1993. Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* 18:117-143.
- Cockle, K. L., and J. S. Richardson. 2003. Do riparian buffer strips mitigate the impacts of clearcutting on small mammals? *Biological Conservation* 113:133-140.
- Collinge, S. K., M. Holyoak, C. B. Barr, and J. T. Marty. 2001. Riparian habitat fragmentation and population persistence of the threatened valley elderberry longhorn beetle in central California. *Biological Conservation* 100:103-113.
- Collinge, S. K., and T. M. Palmer. 2002. The influences of patch shape and boundary contrast on insect response to fragmentation in California grasslands. *Landscape Ecology* 17:647-656.
- Coulson, J. C., and J. E. L. Butterfield. 1985. The invertebrate communities of peat and upland grasslands in the north of England and some conservation implications. *Biological Conservation* 34:197-225.
- Coyle, F. A. 1971. Systematics and natural history of the mygalomorph spider genus *Antrodiaetus* and related genera (Araneae: Antrodiaetidae). *Bulletin of the Museum of Comparative Zoology* 141:269-402.
- Coyle, F. A. 1981. The mygalomorph spider genus *Microhexura* (Araneae, Dipluridae). *Bulletin of the American Museum of Natural History* 170:64-75.
- Dale, M. R. T., P. Dixon, M.-J. Fortin, P. Legendre, D. E. Myers, and M. S. Rosenberg. 2002. Conceptual and mathematical relationships among methods for spatial analysis. *Ecography* 25:558-577.
- Dangerfield, J. M., A. J. Pik, D. Britton, A. Holmes, M. Gillings, I. Oliver, D. Briscoe, and A. J. Beattie. 2003. Patterns of invertebrate biodiversity across a natural edge. *Austral Ecology* 28:227-236.
- Davies, K. F., and C. R. Margules. 1998. Effects of habitat fragmentation on carabid beetles: experimental evidence. *Journal of Animal Ecology* 67:460-471.
- Davies-Colley, R. J., G. W. Payne, and M. van Elswijk. 2000. Microclimate gradients across a forest edge. *New Zealand Journal of Ecology* 24:111-121.
- de Lima, M. G., and C. Gascon. 1999. The conservation value of linear forest remnants in central Amazonia. *Biological Conservation* 91:241-247.
- Deharveng, L., and S. Lek. 1995. High diversity and community permeability: the riparian Collembola (Insecta) of a Pyrenean massif. *Hydrobiologia* 312:59-74.

- Den Boer, P. J. 1990. The survival value of dispersal in terrestrial arthropods. *Biological Conservation* 54:175-192.
- Didham, R. K. 1997. An overview of invertebrate responses to forest fragmentation. Pages 303-320 in A. D. Watt, N. E. Stork, and M. D. Hunter, editors. *Forests and insects*. Chapman and Hall, London.
- Didham, R. K., P.M. Hammond, J. H. Lawton, P. Eggleton, and N. E. Stork. 1998a. Beetle species responses to tropical forest fragmentation. *Ecological Monographs* 68:295-323.
- Didham, R. K., J. H. Lawton, P. M. Hammond, and P. Eggleton. 1998b. Trophic structure stability and extinction dynamics of beetles (Coleoptera) in tropical forest fragments. *Philosophical Transactions of the Royal Society London B* 353:437-451.
- Digweed, S. C. 1993. Selection of terrestrial gastropod prey by cychrine and pterostichine ground beetles (Coleoptera: Carabidae). *The Canadian Entomologist* 125:463-472.
- Digweed, S. C., C. R. Currie, H. A. Carcamo, and J. R. Spence. 1995. Digging out the "digging-in effect" of pitfall traps: influences of depletion and disturbance on catches of ground beetles (Coleoptera: Carabidae). *Pedobiologia* 39:561-576.
- Dondale, C. D., and J. H. Redner. 1978. The crab spiders of Canada and Alaska (Araneae: Philodromidae and Thomisidae). *The insects and arachnids of Canada*. Part 5. Research Branch Agriculture Canada.
- Dondale, C. D., and J. H. Redner. 1987. The *atrata*, *cubana*, *ferruginea*, *moesta*, *monticola*, *saltuaria*, and *solituda* groups of the spider genus *Pardosa* in North America (Araneae: Lycosidae). *The Canadian Entomologist* 119:1-19.
- Dondale, C. D., and J. H. Redner. 1990. The wolf spiders, nurseryweb spiders, and lynx spiders of Canada and Alaska (Araneae: Lycosidae, Pisauridae, and Oxyopidae). *The insects and arachnids of Canada*. Part 17. Research Branch Agriculture Canada.
- Dong, J., J. Chen, K. D. Brososke, and R. J. Naiman. 1998. Modelling air temperature gradients across managed small streams in western Washington. *Journal of Environmental Management* 53:309-321.
- Doyle, A. T. 1990. Use of riparian and upland habitats by small mammals. *Journal of Mammalogy* 7:14-23.
- Duelli, P. 1990. Population movements of arthropods between natural and cultivated areas. *Biological Conservation* 54:193-207.
- Dufrene, M., and P. Legendre. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs* 67:345-366.
- Dutilleul, P. 1993. Modifying the t-test for assessing the correlation between two spatial processes. *Biometrics* 49:305-314.

- Epstein, M. E., and H. M. Kulman. 1990. Habitat distribution and seasonal occurrence of carabid beetles in East-central Minnesota. *The American Midland Naturalist* 123:209-225.
- Foelix, R. F. 1996. *Biology of spiders*. Oxford University Press and Georg Thieme Verlag, New York.
- Forman, R. T. T., and P. N. Moore. 1992. Theoretical foundations for understanding boundaries in landscape mosaics. Pages 236-258 in A. J. Hansen and F. di Castri, editors. *Landscape boundaries: consequences for biotic diversity and ecological flows*. Vol. 92. Springer-Verlag, New York.
- Franklin, J. F., and C. T. Dyrness. 1988. *Natural vegetation of Oregon and Washington*. Oregon State University Press, Corvallis, Oregon.
- Gardner, M. R., and R. M. Shelley. 1989. New records, species, and genera of caseyid millipeds from the Pacific coast of North America (Diplopoda: Chordeumatida: Caseyidae). *Pan-Pacific Entomologist* 65:177-268.
- Gehlhausen, S. M., M. W. Schwartz, and C.K. Augspurger. 2000. Vegetation and microclimatic edge effects in two mixed-mesophytic forest fragments. *Plant Ecology* 147:21-35.
- Geiger, R., R. H. Aron, and P. Todhunter. 2003. *The climate near the ground*. Rowman and Littlefield Publishers, Inc., Lanham, Maryland.
- Gertsch, W. J., and W. Ivie. 1955. The spider genus *Neon* in North America. *American Museum Novitates* 1743:1-17.
- Greene, A. 1975. Biology of the five species of Cychrini (Coleoptera: Carabidae) in the steppe region of southeastern Washington. *Melanderia* 19:1-43.
- Greenslade, P. J. M. 1964. Pitfall trapping as a method for studying populations of Carabidae (Coleoptera). *Journal of Animal Ecology* 33:301-310.
- Gregory, S. V. 1997. Riparian management in the 21st century. Pages 69-85 in K. A. Kohm and J. F. Franklin, editors. *Creating a forestry for the 21st century*. Island Press, Washington D.C.
- Gregory, S. V., F. J. Swanson, W. A. McKee., and K. W. Cummins. 1991. An ecosystem perspective of riparian zones. *BioScience* 41:540-551.
- Grigarick, A. A., and R. O. Schuster. 1962a. Species of the genus *Batrisodes* from the Pacific slope of western North America. *The Pan-Pacific Entomologist* 38:199-213.
- Grigarick, A. A., and R. O. Schuster, R. O. 1962b. Notes on Tychini from western North America. *The Pan-Pacific Entomologist* 38:169-177.
- Grigarick, A. A., and R. O. Schuster. 1968. A revision of the genus *Cupila* Casey. *The Pan-Pacific Entomologist* 44:38-44.

- Grigarick, A. A., and R. O. Schuster. 1971. A revision of the genus *Actium* Casey and *Actiastes* Casey (Coleoptera: Pselaphidae). University of California Publications in Entomology 67:1-56.
- Grigarick, A. A., and R. O. Schuster. 1980. Discrimination of genera of Euplectini of North and Central America (Coleoptera: Pselaphidae). University of California Publications in Entomology 87:1-56.
- Griswold, C. E. 1987. A revision of the jumping spider genus *Habronattus* F.O.P.-Cambridge (Araneae: Salticidae), with phenetic and cladistic analyses. University of California Publications in Entomology 107:1-344.
- Gruttke, H. 1994. Dispersal of carabid species along a linear sequence of young hedge plantations. Pages 299-303 in K. Desender, M. Dufrene, M. Loreau, M. L. Luff, and J.-P. Maelfait, editors. Carabid beetles: ecology and evolution. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Hagar, J. C. 1999. Influence of riparian buffer width on bird assemblages in western Oregon. *Journal of Wildlife Management* 63:484-496.
- Haila, Y. 1999. Islands and fragments. Pages 234-264 in M. J. Hunter, Jr., editor. *Maintaining diversity in forest ecosystems*. Cambridge University Press, Cambridge, United Kingdom.
- Halme, E., and J. Niemalä. 1993. Carabid beetles in fragments of coniferous forest. *Annales Zoologici Fennici* 30:17-30.
- Halsall, N. B., and S. D. Wratten. 1988. The efficiency of pitfall trapping for polyphagous predatory Carabidae. *Ecological Entomology* 13:293-299.
- Harris, L. D. 1984. *The fragmented forest*. The University of Chicago Press, Chicago, Illinois.
- Hatch, M. H. 1953. *The beetles of the Pacific Northwest. Part I: Introduction and Adephaga*. University of Washington Press, Seattle, Washington.
- Hatch, M. H. 1957. *The beetles of the Pacific Northwest. Part II: Staphyliniformia*. University of Washington Press, Seattle, Washington.
- Hatch, M. H. 1961. *The beetles of the Pacific Northwest. Part III: Pselaphidae and Diversicornia*. University of Washington Press, Seattle, Washington.
- Hatch, M. H. 1971. *The beetles of the Pacific Northwest. Part V: Rhipiceroidea, Sternoxi, Phytophaga, Rhynchophora, and Lamellicornia*. University of Washington Press, Seattle, Washington.
- Heliola, J., M. Koivula, and J. Niemalä. 2001. Distribution of carabid beetles (Coleoptera, Carabidae) across a boreal forest-clearcut ecotone. *Conservation Biology* 15:370-377.
- Hering, D. 1998. Riparian beetles (Coleoptera) along a small stream in the Oregon Coast Range and their interactions with the aquatic environment. *The Coleopterists Bulletin* 52:161-170.

- Hering, D. and H. Plachter. 1997. Riparian ground beetles (Coleoptera, Carabidae) preying on aquatic invertebrates: a feeding strategy in alpine floodplains. *Oecologia* 111:261-270.
- Honek, A. 1988. The effect of crop density and microclimate on pitfall trap catches of Carabidae, Staphylinidae (Coleoptera), and Lycosidae (Araneae) in cereal fields. *Pedobiologia* 32:233-242.
- Honek, A. 1997. The effect of temperature on the activity of Carabidae (Coleoptera) in a fallow field. *European Journal of Entomology* 94:97-104.
- Jennings, D. T., M. W. Houseweart, C. D. Dondale, and J. H. Redner. 1988. Spiders (Araneae) associated with strip-clearcut and dense spruce-fir forests of Maine. *Journal of Arachnology* 16:55-70.
- Joyce, K. A., J. M. Holland, and C. P. Doncaster. 1999. Influences of hedgerow intersections and gaps on the movement of carabid beetles. *Bulletin of Entomological Research* 89:523-531.
- Kauffman, J. B., M. Mahrt, L. Mahrt, and W. D. Edge. 2001. Wildlife of riparian habitats. Pages 361-388 in D. H. Johnson and T. A. O'Neil, editors. *Wildlife-habitat relationships in Oregon and Washington*. Oregon State University Press, Corvallis, Oregon.
- Kawaguchi, Y., and S. Nakano. 2001. Contribution of terrestrial invertebrates to the annual resource budget for salmonids in forest and grassland reaches of a headwater stream. *Freshwater Biology* 46:303-316.
- Kelsey, K. A., and S. D. West. 1998. Riparian wildlife. Pages 235-252 in R. J. Naiman, and R. E. Bilby, editors. *River ecology and management*. Springer-Verlag, New York.
- Kennedy, P. J. 1994. The distribution and movement of ground beetles in relation to set-aside arable land. Pages 439-444 in K. Desender, M. Dufrene, M. Loreau, M. L. Luff, and J.-P. Maelfait, editors. *Carabid beetles: ecology and evolution*. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Kevan, D. K. M., and G. G. E. Scudder. 1989. Illustrated keys to the families of terrestrial arthropods of Canada 1. Myriapods (millipedes, centipedes, etc.). *Biological Survey of Canada Taxonomic Series No. 1*:1-88.
- Kiss, B., and F. Samu. 2000. Evaluation of population densities of the common wolf spider *Pardosa agrestis* (Araneae: Lycosidae) in Hungarian alfalfa fields using mark-recapture. *European Journal of Entomology* 97:191-195.
- Klein, B. C. 1989. Effects of forest fragmentation on dung and carrion beetle communities in Central Amazonia. *Ecology* 70:1715-1725.
- Koivula, M. 2002. Alternative harvesting methods and boreal carabid beetles (Coleoptera, Carabidae). *Forest Ecology and Management* 167:103-121.
- Kremen, C. 1992. Assessing the indicator properties of species assemblages for natural areas monitoring. *Ecological Applications* 2:203-217.

- Kremen, C., R. K. Colwell, T. L. Erwin, D. D. Murphy, R. F. Noss, and M. A. Sanjayan. 1993. Terrestrial arthropod assemblages: their use in conservation planning. *Conservation Biology* 7:796-808.
- Kruskal, J. B. 1964. Nonmetric multidimensional scaling: a numerical method. *Psychometrika* 29:115-129.
- LaBonte, J. R. 2002. Habitat associations of riparian beetles (Coleoptera) at Big Beaver Creek Research Natural Area, North Cascades National Park, Washington. M.S. thesis. Oregon State University, Corvallis, Oregon.
- Lang, A. 2003. Intraguild interference and biocontrol effects of generalist predators in a winter wheat field. *Oecologia* 134:144-153.
- Larochelle, A., and M.-C. Lariviere. 2003. A natural history of the ground-beetles (Colopetera: Carabidae) of America north of Mexico. Pensoft, Sofia, Bulgaria.
- Lattin, J. D. 1993. Arthropod diversity and conservation in old-growth Northwest forests. *American Zoologist* 33:578-587.
- Laurance, W. F., and E. Yensen. 1991. Predicting the impacts of edge effects in fragmented habitats. *Biological Conservation* 55:77-92.
- Lindroth, C. H. 1961-1969. The ground-beetles (Carabidae, excl. Cicindelinae) of Canada and Alaska. Parts 1-6. *Opuscula Entomologica Supplementa* 20,24,29,33,34,35:1-1192.
- Lock, P. A., and R. J. Naiman. 1998. Effects of stream size on bird community structure in coastal temperate forests of the Pacific Northwest, U.S.A. *Journal of Biogeography* 25:773-782.
- Lowrie, D. C. 1973. The microhabitats of western wolf spiders of the genus *Pardosa*. *Entomological News* 84:103-116.
- Lowrie, D. C., and C. D. Dondale. 1981. A revision of the *nigra* group of the genus *Pardosa* in North America (Araneae, Lycosidae). *Bulletin of the American Museum of Natural History* 170:125-139.
- Machtans, C. S., M.-A. Villard, and S. J. Hannon. 1996. Use of riparian buffer strips as movement corridors by forest birds. *Conservation Biology* 10:1366-1379.
- Mader, H. J., C. Schell, and P. Kornacker. 1990. Linear barriers to arthropod movements in the landscape. *Biological Conservation* 54:209-222.
- Madson, S. L. 1998. Correlation between structural heterogeneity and arthropod biodiversity : implications for management of Pacific Northwest forests. M.S. thesis. Oregon State University, Corvallis, Oregon.
- Magura, T., B. Tothmeresz, and T. Molnar. 2001. Forest edge and diversity: carabids along forest-grassland transects. *Biodiversity and Conservation* 10:287-300.

- Marsh, G. A., and R. O. Schuster. 1962. A revision of the genus *Sonoma* Casey (Coleoptera: Pselaphidae). *The Coleopterist's Bulletin* 16:33-56.
- Martin, M., F. Bastardie, D. Richard, and F. Burel. 2001. Studying boundary effects on animal movement in heterogeneous landscapes: the case of *Abax ater* (Coleoptera: Carabidae) in hedgerow network landscapes. *Comptes Rendus de L'Academie des Sciences - Serie Iii, Sciences de la Vie* 324:1029-1035.
- Maser, C., and J. M. Trappe. 1984. The seen and unseen world of the fallen tree. General technical report PNW-164. U.S. Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, Oregon.
- Mather, P. M. 1976. Computational methods of multivariate analysis in physical geography. J. Wiley and Sons, London, United Kingdom.
- Matlack, G. R. 1993. Microenvironment variation within and among forest edge sites in the eastern United States. *Biological Conservation* 66:185-194.
- Matlack, G. R., and J. A. Litvaitis. 1999. Forest edges. Pages 210-233 in M. J. Hunter, Jr., editor. *Maintaining biodiversity in forest ecosystems*. Cambridge University Press, Cambridge, United Kingdom.
- Mauremooto, J. R., S. D. Wratten, S. P. Worner, and G. L. A. Fry. 1995. Permeability of hedgerows to predatory carabid beetles. *Agriculture, Ecosystems and Environment* 52:141-148.
- McComb, W. C., K. McGarigal, and R. G. Anthony. 1993. Small mammal and amphibian abundance in streamside and upslope habitats of mature Douglas-fir stands, western Oregon. *Northwest Science* 67:7-15.
- McCune, B., and J. B. Grace. 2002. *Analysis of ecological communities*. MJM Software Design, Gleneden Beach, Oregon.
- McCune, B., and M. J. Mefford. 1999. MJM Software Design, Gleneden Beach, Oregon, USA.
- McIver, J. D., A. R. Moldenke, and G. L. Parsons. 1990. Litter spiders as bio-indicators of recovery after clearcutting in a western coniferous forest. *Northwest Environmental Journal* 6:410-412.
- Meiners, S. J., and S. T. Pickett. 1999. Changes in community and population responses across a forest-field gradient. *Ecography* 22:261-267.
- Meyer, J. L., and J. B. Wallace. 2001. Lost linkages and lotic ecology: rediscovering small streams. Pages 295-317 in M. C. Press, N. J. Huntly, and S. A. Levin, editors. *Ecology: achievement and challenge*. Blackwell Science, Oxford, United Kingdom.
- Moring, J. B., and K. W. Stewart. 1994. Habitat partitioning by the wolf spider (Araneae, Lycosidae) guild in streamside and riparian vegetation zones of the Conejos River, Colorado. *The Journal of Arachnology* 22:205-217.

- Murcia, C. 1995. Edge effects in fragmented forests: implications for conservation. *Trends in Ecology and Evolution* 10:58-62.
- Naiman, R. J., and H. Decamps. 1997. The ecology of interfaces: riparian zones. *Annual Review of Ecology and Systematics* 28:621-658.
- Naiman, R. J., H. Decamps, and M. Pollock. 1993. The role of riparian corridors in maintaining regional biodiversity. *Ecological Applications* 3:209-212.
- Naiman, R. J., K. L. Fetherston, J. McKay, and J. Chen. 1998. Riparian forests. Pages 289-323 in R. J. Naiman and R. E. Bilby. *River ecology and management: lessons from the Pacific coastal ecoregion*. Springer-Verlag, New York.
- Nakano, S., and M. Murakami. 2001. Reciprocal subsidies: dynamic interdependence between terrestrial and aquatic food webs. *Proceedings of the National Academy of Sciences* 98:166-170.
- Nentwig, W. 1987. *Ecophysiology of spiders*. Springer-Verlag, Berlin.
- Neve, G. 1994. Influence of temperature and humidity on the activity of three *Carabus* species. Pages 189-192 in K. Desender, M. Dufrene, M. Loreau, M. L. Luff, and J.-P. Maelfait, editors. *Carabid beetles: ecology and evolution*. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Newmark, W. D. 2001. Tanzanian forest edge microclimatic gradients: dynamic patterns. *Biotropica* 33:2-11.
- Niemalä, J. 1997. Invertebrates and boreal forest management. *Conservation Biology* 11:601-610.
- Niemalä, J., Y. Haila, E. Halme, T. Lahti, T. Pajunen, and P. Punttila. 1988. The distribution of carabid beetles in fragments of old coniferous taiga and adjacent managed forests. *Zoologica Fennici* 25:107-119.
- Niemalä, J., D. Langor, and J. R. Spence. 1993a. Effects of clear-cut harvesting on boreal ground-beetle assemblages (Coleoptera: Carabidae) in western Canada. *Conservation Biology* 7:551-561.
- Niemalä, J., J. R. Spence, D. Langor, Y. Haila, and H. Tukia. 1993b. Logging and boreal ground-beetle assemblages on two continents: implications for conservation. Pages 29-50 in K. J. Gaston, T. R. New, and M. J. Samways, editors. *Perspectives on insect conservation*. Intercept, Ltd., Andover, United Kingdom.
- Nilsson, C., G. Grelsson, M. Johansson, and U. Sperens. 1989. Patterns of plant species richness along riverbanks. *Ecology* 70:77-84.
- O'Keefe, S. T. 1996. Revision of the nearctic genus *Lophoderus* Casey (Coleoptera: Scydmaenidae). Entomological Society of America, Lanham, Maryland.
- O'Laughlin, J., and G. H. Belt. 1995. Functional approaches to riparian buffer strip design. *Journal of Forestry* 93:29-32.

- Oliver, I., and A. J. Beattie. 1996a. Designing a cost-effective invertebrate survey: a test of methods for rapid assessment of biodiversity. *Ecological Applications* 6:594-607.
- Oliver, I., and A. J. Beattie. 1996b. Invertebrate morphospecies as surrogates for species: a case study. *Conservation Biology* 10:99-109.
- Olson, D. H., S. S. Chan, and C. R. Thompson. 2002. Riparian buffers and thinning designs in western Oregon headwaters accomplish multiple resource objectives. Pages 81-91 in A. C. Johnson, R. W. Haynes, and R. A. Monserud, editors. *Congruent management of multiple resources: proceedings from the wood compatibility initiative workshop*. General technical report PNW-GTR-563. U.S. Forest Service, Pacific Northwest Research Station, Portland, Oregon.
- Olson, D. H., B. Hansen, S. Chan, and P. Cunningham. 1999. A synthesis of forested headwater habitats and species: a case study of the compatibility of resource production and protection. U.S. Forest Service Progress Report: Compatibility Initiative Study.
- Olson, D. M. 1994. The distribution of leaf litter invertebrates along a neotropical altitudinal gradient. *Journal of Tropical Ecology* 10:129-150.
- Olson, D. H., S. S. Chan, G. Weaver, P. Cunningham, A. Moldenke, R. Progar, P. S. Muir, B. McCune, A. Rosso, and E. B. Peterson. 2000. Characterizing stream, riparian, upslope habitats and species in Oregon managed headwater forests. Pages 83-88 in J. Wiggington and R. Beschta, editors. *Riparian ecology and management in multi-land use watersheds*. International conference of the American Water Resources Association, Portland, OR. TPS-00-2. AWRA Publication, Middleburg, Virginia.
- Omland, K. 2002. Larval habitat and reintroduction site selection for *Cicindela puritana* in Connecticut. *Northeastern Naturalist* 9:433-450.
- Pabst, R. J., and T. A. Spies. 1998. Distribution of herbs and shrubs in relation to landform and canopy cover in riparian forests of coastal Oregon. *Canadian Journal of Botany* 76:298-311.
- Pajunen, T., Y. Haila, E. Halme, J. Niemälä, and P. Punttila. 1995. Ground-dwelling spiders (Arachnida, Araneae) in fragmented old forests and surrounding managed forests in southern Finland. *Ecography* 18:62-72.
- Pearson, D. L. 1994. Selecting indicator taxa for the quantitative assessment of biodiversity. *Philosophical Transactions of the Royal Society London B*. 345:75-79.
- Pearson, S. F., and D. A. Manuwal. 2001. Breeding bird response to riparian buffer width in managed Pacific Northwest Douglas-Fir forests. *Ecological Applications* 11:840-853.
- Peckham, G. W., and E. G. Peckham. 1909. Revision of the Attidae of North America. *Transactions of the Wisconsin Academy of Sciences* 16:355-646.
- Perry, J. 1995. Spatial analysis by distance indices. *The Journal of Animal Ecology* 64:303-314.
- Perry, J. N. 1998. Measures of spatial pattern for counts. *Ecology* 79:1008-1017.

- Perry, J. N., and P. M. Dixon. 2002. A new method to measure spatial association for ecological count data. *Ecoscience* 9:133-141.
- Perry, J. N., A. M. Liebhold, M. S. Rosenberg, J. Dungan, M. Miriti, A. Jakomulska, and S. Citron-Pousty. 2002. Illustrations and guidelines for selecting statistical methods for quantifying spatial pattern in ecological data. *Ecography* 25:578-600.
- Perry, J. N., L. Winder, J. M. Holland, and R. D. Alston. 1999. Red-blue plots for detecting clusters in count data. *Ecology Letters* 2:106-113.
- Petit, S., and F. Burel. 1998. Effects of landscape dynamics on the metapopulation of a ground beetle (Coleoptera, Carabidae) in a hedgerow network. *Agriculture, Ecosystems and Environment* 69:243-252.
- Petit, S., and S. Burel. 1993. Movement of *Abax ater* (Col. Carabidae): do forest species survive in hedgerow networks? *Vie Milieu* 43:119-124.
- Pilsbry, H. A. 1940. Land Mollusca of North America (north of Mexico). The Academy of Natural Sciences of Philadelphia Monographs. Number 3. Volume 1, part 2.
- Pilsbry, H. A. 1946. Land Mollusca of North America (north of Mexico). The Academy of Natural Sciences of Philadelphia Monographs. Number 3. Volume 2, part 1.
- Pilsbry, H. A. 1948. Land Mollusca of North America (north of Mexico). The Academy of Natural Sciences of Philadelphia Monographs. Number 3. Volume 2, part 2.
- Platnick, N. I., and C. D. Dondale. 1992. The ground spiders of Canada and Alaska (Araneae: Gnaphosidae). The insects and arachnids of Canada. Part 19. Research Branch Agriculture Canada.
- Pollock, M. M. 1998. Biodiversity. Pages 430-452 in R. J. Naiman and R. E. Bilby, editors. *River ecology and management: lessons from the Pacific coastal ecoregion*. Springer, New York.
- Pollock, M. M., R. J. Naiman, and T. A. Hanley. 1998. Plant species richness in forested and emergent wetlands--a test of biodiversity theory. *Ecology* 79:94-105.
- Pulliam, H. R., and B. J. Danielson. 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. *The American Naturalist* 137, Supplement:S50-S66.
- Raedeke, K. J. 1988. Introduction. Pages xiii-xv in K. J. Raedeke, editor. *Riparian wildlife and forestry interactions*. Institute of Forest Resources Contribution Number 59, University of Washington, Seattle, Washington.
- Reynolds, B.C., and D. A. Crossley Jr. 1997. Spatial variation in herbivory by forest canopy arthropods along an elevation gradient. *Environmental Entomology* 26:1232-1239.
- Risser, P. G. 1995. The status of the science examining ecotones. *Bioscience* 45:318-325.
- Rosenberg, D. M., H. V. Danks, and D. M. Lehmkuhl. 1986. Importance of insects in environmental impact assessment. *Environmental Management* 10:773-783.

- Roth, V. D. 1952a. The genus *Cybaeus* in Oregon. *Annals of the Entomological Society of America* 45:205-219.
- Roth, V. D. 1952b. Notes and a new species in *Cybaeina*. *The Pan-Pacific Entomologist* 28:195-201.
- Roth, V. D. 1993. Spider genera of North America. University of Florida, Gainesville, Florida.
- Roth, V. D., and P. L. Brame. 1972. Nearctic genera of the spider family Agelenidae (Arachnida: Araneida). *American Museum Novitates* 2505:1-52.
- Rykken, J. J., D. E. Capen, and S. P. Mahabir. 1997. Ground beetles as indicators of land type diversity in the Green Mountains of Vermont. *Conservation Biology* 11:522-530.
- Saunders, D. A., R. J. Hobbs, and C. R. Margules. 1991. Biological consequences of ecosystem fragmentation: a review. *Conservation Biology* 5:18-32.
- Schowalter, T. D., Y. L. Zhang, and J. J. Rykken. 2003. Litter invertebrate responses to variable density thinning in western Washington forest. *Ecological Applications* 13:1204-1211.
- Schuster, R. O., and A. A. Grigarick. 1960. A revision of the genus *Oropus* Casey (Coleoptera: Pselaphidae). *Pacific Insects* 2:269-299.
- Schuster, R. O., and Marsh, G. A. 1956. A revision of the genus *Pselaptrichus* Brendel (Coleoptera: Pselaphidae). *University of California Publications in Entomology* 11:117-158.
- Schuster, R. O., and G. A. Marsh. 1958. A study of the North American genus *Megarafonus* Casey (Coleoptera: Pselaphidae). *Pan-Pacific Entomologist* 34:187-194.
- Sedell, J. R., G. H. Reeves, and K. M. Burnett. 1994. Development and evaluation of aquatic conservation strategies. *Journal of Forestry* 92:28-31.
- Shannon, C. E., and W. Weaver. 1949. *The mathematical theory of communication*. The University of Illinois Press, Urbana, Illinois.
- Shear, W. A. 1971. The milliped family Conotylidae in North America, with a description of the new family Adritylidae (Diplopoda: Chordeumida). *Bulletin of the Museum of Comparative Zoology* 141:55-98.
- Shear, W. A. 1973. The milliped family Rhiscosomididae (Diplipoda: Chordeumida: Striarioidea). *Psyche* 80:189-203.
- Shelley, R. M. 1990. A new milliped of the genus *Metaxycheir* from the Pacific coast of Canada (Polydesmida: Xystodesmidae), with remarks on the tribe Chonaphini and western Canadian and Alaskan diplopod fauna. *Canadian Journal of Zoology* 68:2310-2322.
- Shelley, R. M. 1993. Revision of the milliped genus *Scytonotus* Koch (Polydesmida: Polydesmidae). *Brimleyana* 19:1-60.

- Shelley, R. M. 1994a. Revision of the milliped family Paeromopodidae, and elevation of the Aprosphylosomatinae to family status (Julida: Paeromopodoidea). *Entomologica Scandinavica* 25:169-214.
- Shelley, R. M. 1994b. The milliped family Nearctodesmidae in northwestern North America, with accounts of *Sakophallus* and *S. simplex* Chamberlin (Polydesmida). *Canadian Journal of Zoology* 72:470-495.
- Shelley, R. M. 1995. The milliped family Hirudisomatidae in the new world (Polyzoniida). *Brimleyana* 23:103-143.
- Sheridan, C. D., and D. H. Olson. 2003. Amphibian assemblages in zero-order basins in the Oregon Coast Range. *Canadian Journal of Forest Research* 33:1452-1477.
- Spence, J. R. 1979. Riparian carabid guilds--a spontaneous question generator. Pages 525-537 in T. L. Erwin, G. E. Ball, and D. W. Whitehead. *Carabid beetles: their evolution, natural history, and classification*. W. Junk Publishers, The Hague, The Netherlands.
- Spence, J. R., D. W. Langor, J. Niemalä, H. A. Carcamo, and C. R. Currie. 1996. Northern forestry and carabids: the case for concern about old-growth species. *Annales Zoologici Fennici* 33:173-184.
- Spence, J. R., and J. K. Niemalä. 1994. Sampling carabid assemblages with pitfall traps: the madness and the method. *The Canadian Entomologist* 126:881-894.
- Stamps, J. A., M. Buechner, and V. V. Krishnan. 1987. The effects of edge permeability and habitat geometry on emigration from patches of habitat. *The American Naturalist* 129:533-552.
- Sustek, Z. 1994a. Classification of the carabid assemblages in the floodplain forests in Moravia and Slovakia. Pages 371-376 in K. Desender, M. Dufrene, M. Loreau, M. L. Luff, and J.-P. Maelfait, editors. *Carabid beetles: ecology and evolution*. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Sustek, Z. 1994b. Windbreaks as migration corridors for carabids in an agricultural landscape. Pages 377-382 in K. Desender, M. Dufrene, M. Loreau, M. L. Luff, and J.-P. Maelfait, editors. *Carabid beetles: ecology and evolution*. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Thiele, H.-U. 1977. *Carabid beetles in their environments*. Springer-Verlag, Berlin, Germany.
- Thomas, C. F. G. 1995. A rapid method for handling and marking carabids in the field. Pages 57-59 in S. Toft and W. Riedel, editors. *Arthropod natural enemies in arable land I*. Volume 70. Aarhus University Press, Aarhus, Denmark.
- Thomas, C. F. G., L. Parkinson, and E. J. P. Marshall. 1998. Isolating the components of activity-density for the carabid beetle *Pterostichus melanarius* in farmland. *Oecologia* 116:103-112.

- Topping, C. J., and K. D. Sunderland. 1992. Limitations to the use of pitfall traps in ecological studies exemplified by a study of spiders in a field of winter wheat. *Journal of Applied Ecology* 29:485-491.
- Touyama, Y., and T. Yamamoto. 1997. Ecological study of the myrmecofauna in pine forests with different altitudes and physiognomies. *Japanese Journal of Ecology* 47:145-150.
- Tuchman, E. T., K. P. Connaughton, L. E. Freedman, and C. B. Moriwaki. 1996. The Northwest Forest Plan: a report to the president and congress. U.S. Department of Agriculture, Office of Forestry and Economic Assistance.
- Uetz, G. W. 1976. Gradient analysis of spider communities in a streamside forest. *Oecologia* 22:373-385.
- USDA and USDI. 1994. Record of decision for amendments to Forest Service and Bureau of Land Management planning documents within the range of the northern spotted owl: standards and guidelines for management of habitat for late successional and old-growth forest related species within the range of the northern spotted owl. USDA Forest Service and USDI Bureau of Land Management, Washington, D.C.
- van Wilgenburg, L., D. F. Mazerolle, and K. A. Hobson. 2001. Patterns of arthropod abundance, vegetation, and microclimate at boreal forest edge and interior in two landscapes: implications for forest birds. *Ecoscience* 8:454-461.
- Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* 37:130-137.
- Vesely, D. G., and W. C. McComb. 2002. Salamander abundance and amphibian species richness in riparian buffer strips in the Oregon coast range. *Forest Science* 48:291-297.
- Wallin, H., and B. S. Ekbom. 1988. Movements of carabid beetles (Coleoptera: Carabidae) inhabiting cereal fields: a field tracing study. *Oecologia* 77:39-43.
- Wenninger, E. J. and W. F. Fagan. 2000. Effect of river flow manipulation on wolf spider assemblages at three desert riparian sites. *The Journal of Arachnology* 28:115-122.
- Wiens, J. A., C. S. Crawford, and J. R. Gosz. 1985. Boundary dynamics: a conceptual framework for studying landscape ecosystems. *Oikos* 45:421-427.
- Wiens, J. A., and B. T. Milne. 1989. Scaling of 'landscapes' in landscape ecology, or, landscape ecology from a beetle's perspective. *Landscape Ecology* 3:87-96.
- Wiens, J.A., R. L. Schooley, and R. D. Weeks, Jr. 1997. Patchy landscapes and animal movements: do beetles percolate? *Oikos* 78:257-264.
- Williams-Linera, G. 1990. Vegetation structure and environmental conditions of forest edges in Panama. *Journal of Ecology* 78:356-373.

- Work, T. T. 2000. Edge effects of clearcut harvesting on ground arthropod species composition and predator community structure in old-growth Douglas-fir forests. Ph.D. dissertation. Oregon State University, Corvallis, Oregon.
- Young, A., and N. Mitchell. 1994. Microclimate and vegetation edge effects in a fragmented podocarp-broadleaf forest in New Zealand. *Biological Conservation* 67:63-72.
- Young, K. A. 2000. Riparian zone management in the Pacific Northwest: who's cutting what? *Environmental Management* 26:131-144.
- Zulka, K. P. 1994. Carabids in a Central European floodplain: species distribution and survival during inundations. Pages 399-405 K. Desender, M. Dufrene, M. Loreau, M. L. Luff, and J.-P. Maelfait, editors. *Carabid beetles: ecology and evolution*. Kluwer Academic Publishers, Dordrecht, The Netherlands.

APPENDICES

Appendix 1 References used for invertebrate taxonomy.

Taxon	References
Antrodiaetidae	Coyle 1971
Dipluridae	Coyle 1981
Mecicobothriidae	Roth 1993
Agelenidae	Chamberlin and Ivie 1932, Chamberlin and Ivie 1937, Chamberlin and Ivie 1940, Roth 1952a, Roth 1952b, Roth and Brame 1972, Bennett 1991
Gnaphosidae	Platnick and Dondale 1992
Lycosidae	Lowrie and Dondale 1981, Dondale and Redner 1987, Dondale and Redner 1990
Thomisidae	Dondale and Redner 1978
Salticidae	Peckham and Peckham 1909, Gertsch and Ivie 1955, Griswold 1987
Carabidae	Hatch 1953, Lindroth 1961-1969
Scydmaenidae	Hatch 1957, O'Keefe 1996
Pselaphinae	Schuster and Marsh 1956, Schuster and Marsh 1958, Schuster and Grigarick 1960, Hatch 1961, Grigarick and Schuster 1962a, Grigarick and Schuster 1962b, Marsh and Schuster 1962, Grigarick and Schuster 1968, Grigarick and Schuster 1971, Grigarick and Schuster 1980, Chandler 1986
Curculionidae	Hatch 1971, Bright 1994, Anderson 2002
Gastropoda	Pilsbry 1940, Pilsbry 1946, Pilsbry 1948
Caseyidae	Gardner and Shelley 1989
Paeromopodidae	Shelley 1994a
Nearctodesmidae	Shelley 1994b
Polyxenidae	Kevan and Scudder 1989
Xystodesmidae	Shelley 1990, Shelley 1993
Rhiscosomididae	Shear 1973
Conotylidae	Shear 1971
Hirudisomatidae	Shelley 1995
Polydesmidae	Shelley 1993

Appendix 2 Functional role (P = predator, D = detritivore, H = herbivore), overall abundance, frequency (out of 15 possible sites), and mean abundance between 1 and 20 m from the stream in buffer, clearcut, and forest treatments, for 203 identified taxa. In Taxon column, *n.sp.* = undescribed species; *sp.* = unidentified species.

Family	Taxon name and author	Functional group	Total abundance	Site frequency	Forest (n=5)		Buffer (n=5)		Clearcut (n=5)	
					Mean	SE	Mean	SE	Mean	SE
Lycosidae	<i>Pardosa dorsalis</i> Banks	P	2227	12	7.8	6.6	73.6	42.2	248.2	129.3
Carabidae	<i>Scaphinotus angusticollis</i> (Fischer von Waldheim)	P	1124	6	156.4	127.3	41.0	38.3	10.4	10.2
Xystodesmidae	<i>Harpaphe haydeniana haydeniana</i> (Wood)	D	1032	15	31.4	9.8	89.6	56.5	40.6	16.8
Carabidae	<i>Scaphinotus marginatus</i> (Fischer von Waldheim)	P	885	15	28.8	10.7	69.4	39.3	33.8	23.8
Curculionidae	<i>Steremnius carinatus</i> (Boheman)	H	742	15	25.8	5.9	56.2	21.9	24.4	13.6
Agelenidae	<i>Cybaeus eutypus</i> Chamberlin & Ivie	P	718	13	32.0	12.7	56.4	18.2	22.2	12.5
Haplotrematidae	<i>Ancotrema sportella</i> (Gould)	P	479	13	35.2	16.5	33.8	16.2	16.2	7.4
Carabidae	<i>Trachypachus holmbergi</i> Mannerheim	P	369	5	0.0	0.0	2.4	2.4	35.4	35.2
Agelenidae	<i>Cybaeus cascadius</i> Roth	P	363	11	27.4	11.0	17.2	7.8	14.2	8.5
Carabidae	<i>Pterostichus n.sp.</i> LaBonte	P	349	9	4.6	3.1	41.2	41.0	15.0	12.6
Polygyridae	<i>Vespericola columbianus</i> (Lea)	H	334	15	22.2	8.8	21.8	5.5	11.6	1.8
Gnaphosidae	<i>Zelotes fratris</i> Chamberlin	P	334	12	1.0	0.8	5.0	3.8	38.4	13.6
Haplotrematidae	<i>Haplotrema vancouverense</i> (Lea)	P	321	15	22.8	11.5	12.0	2.6	14.6	4.4
Carabidae	<i>Pterostichus lama</i> Menetries	P	289	12	10.4	7.1	4.8	2.4	22.6	7.4
Lycosidae	<i>Alopecosa kochii</i> (Keyserling)	P	248	11	0.2	0.2	0.4	0.4	32.8	25.7
Nearctodesmidae	<i>Kepolydesmus anderisus</i> (Chamberlin)	D	233	10	10.8	7.2	11.2	6.8	16.4	8.7
Carabidae	<i>Pterostichus herculeanus</i> Mannerheim	P	226	14	8.0	4.2	10.2	7.2	8.0	5.8
Carabidae	<i>Pterostichus crenicollis</i> LeConte	P	224	14	21.4	5.9	12.4	6.2	10.6	5.7
Pselaphinae	<i>Batrisodes albionicus</i> (Aube)	P	215	14	6.4	2.3	20.2	11.6	13.2	4.1
Agelenidae	<i>Cybaeus multnoma</i> Chamberlin & Ivie	P	201	12	9.6	6.5	12.6	5.9	13.0	5.4
Agelenidae	<i>Cybaeus reticulatus</i> Simon	P	186	14	9.2	4.4	15.6	9.7	6.6	3.9
Agelenidae	<i>Calymmaria n.sp.</i>	P	185	14	7.6	3.4	13.4	5.9	10.0	4.6
Carabidae	<i>Scaphinotus angulatus</i> (Harris)	P	173	14	8.6	3.0	10.8	3.6	3.2	1.3
Pselaphinae	<i>Oropus striatus</i> (LeConte)	P	162	14	10.4	5.5	6.4	1.6	9.6	3.9
Carabidae	<i>Harpalus spp.</i>	H	146	13	0.0	0.0	0.0	0.0	9.0	6.9

Appendix 2 (Continued)

Family	Taxon name and author	Functional group	Total abundance	Site frequency	Forest (n=5)		Buffer (n=5)		Clearcut (n=5)	
					Mean	SE	Mean	SE	Mean	SE
Carabidae	<i>Promecognathus crassus</i> Leconte	P	146	7	10.8	6.7	7.8	5.6	2.2	1.4
Lycosidae	<i>Pardosa californica</i> Keyserling	P	143	7	0.0	0.0	1.6	0.7	19.0	11.4
Agelenidae	<i>Cybaeus simplex</i> Roth	P	130	7	2.4	2.4	6.2	4.5	10.8	5.5
Xystodesmidae	<i>Chonaphe armata</i> (Harger)	D	129	13	2.4	1.1	4.8	2.8	8.6	6.0
Cicindelidae	<i>Omus dejeani</i> Reiche	P	126	11	0.6	0.4	2.8	2.6	12.8	7.4
Scydmaenidae	<i>Lophioderus arcifer</i> Casey	P	119	13	7.0	3.5	5.2	2.9	7.6	5.7
Gnaphosidae	<i>Callilepis pluto</i> Banks	P	112	9	0.0	0.0	0.0	0.0	15.0	5.1
Pselaphinae	<i>Sonoma hespera</i> Park & Wagner	P	107	9	7.2	3.4	7.6	3.7	3.6	2.1
Lycosidae	<i>Pardosa dorsuncata</i> Lowrie & Dondale	P	106	10	0.0	0.0	3.4	2.7	5.0	2.3
Caseyidae	<i>Caseya dendrogona</i> Buckett & Shelley	D	104	10	4.2	2.4	7.0	3.2	3.0	1.9
Carabidae	<i>Pterostichus neobrunneus</i> Lindroth	P	94	5	1.0	0.8	0.2	0.2	6.0	6.0
Pselaphinae	<i>Cupila excavata</i> Park & Wagner	P	93	12	3.0	1.2	10.0	7.3	2.6	1.2
Antrodiaetidae	<i>Antrodiaetus pacificus</i> (Simon)	P	88	15	3.8	1.5	5.0	1.7	5.0	1.1
Carabidae	<i>Pterostichus inopinus</i> (Casey)	P	84	13	5.4	2.4	3.4	0.9	2.2	0.9
Pselaphinae	<i>Actium barri</i> Park & Wagner	P	83	7	4.6	2.8	3.6	3.6	5.0	3.0
Thomisidae	<i>Xysticus montanensis</i> Keyserling	P	80	10	0.2	0.2	0.2	0.2	8.8	3.8
Carabidae	<i>Pterostichus castaneus</i> (Dejean)	P	78	10	5.0	2.3	4.0	2.4	3.2	2.7
Pselaphinae	<i>Pselaptrichus intimus</i> Schuster & Marsh	P	75	9	3.0	2.5	4.6	2.5	5.4	3.6
Pselaphinae	<i>Lucifotychus impellus</i> Park & Wagner	P	68	12	4.0	1.2	4.8	2.9	2.4	1.5
Thomisidae	<i>Xysticus pretiosus</i> Gertsch	P	68	14	1.0	0.5	9.0	3.7	1.8	0.5
Gnaphosidae	<i>Zelotes puritanus</i> Chamberlin	P	68	9	0.0	0.0	0.0	0.0	8.4	2.8
Arionidae	<i>Hemphillia dromedarius</i> Branson	H	67	8	6.6	4.7	4.8	4.1	0.6	0.4
Agelenidae	<i>Cryphoeca exlinae</i> Roth	P	63	12	3.2	1.7	6.8	5.6	0.8	0.4
Pselaphinae	<i>Pselaptrichus perfidus</i> Schuster & Marsh	P	62	9	3.8	3.3	2.2	1.2	2.0	1.8
Pselaphinae	<i>Sonoma olycalida</i> Park & Wagner	P	62	10	2.6	1.4	3.6	2.2	2.6	1.5
Scydmaenidae	<i>Lophioderus septemlatus</i> O'Keefe	P	61	8	3.8	2.5	1.0	0.5	4.6	4.4
Nearctodesmidae	<i>Nearctodesmus insulanus</i> (Chamberlin)	D	60	9	2.2	1.3	6.4	3.4	3.4	2.9

Appendix 2 (Continued)

Family	Taxon name and author	Functional group	Total abundance	Site frequency	Forest (n=5)		Buffer (n=5)		Clearcut (n=5)	
					Mean	SE	Mean	SE	Mean	SE
Curculionidae	<i>Panscopus torpidus</i> LeConte	H	56	3	0.0	0.0	0.8	0.6	1.6	1.6
Arionidae	<i>Prophyaon andersoni</i> (Cooper)	H	56	11	5.2	2.4	1.8	0.8	3.2	1.9
Paeromopodidae	<i>Californiulus euphanus</i> (Chamberlin)	D	55	9	1.8	1.8	3.4	2.7	1.0	1.0
Carabidae	<i>Pterostichus pumilis pumilis</i> Casey	P	55	4	2.8	1.5	0.0	0.0	7.8	7.8
Agelenidae	<i>Blabomma n.sp.</i>	P	52	7	1.6	1.0	2.8	2.3	2.6	2.1
Curculionidae	<i>Nemocestes incomptus</i> Horn	H	52	10	1.6	1.2	3.0	1.8	3.6	2.2
Hirudisomatidae	<i>Octoglena anura</i> (Cook)	D	52	11	4.4	2.2	0.6	0.2	3.2	2.0
Carabidae	<i>Cychnus tuberculatus</i> Harris	P	50	6	4.2	2.7	3.2	2.7	1.4	0.9
Carabidae	<i>Notiophilus sylvaticus</i> Eschscholtz	P	47	8	2.0	0.9	3.2	1.8	2.2	2.0
Antrodiaetidae	<i>Antrodiaetus pugnax</i> (Chamberlin)	P	45	6	0.8	0.8	3.4	2.1	1.8	1.2
Curculionidae	<i>Dyslobus lecontei</i> Casey	H	45	8	1.4	0.7	2.8	2.6	2.8	1.7
Antrodiaetidae	<i>Antrodiaetus occultus</i> Coyle	P	43	6	0.8	0.5	4.2	3.3	1.2	1.0
Pselaphinae	<i>Sonoma conifera</i> Chandler	P	43	7	4.6	2.8	2.2	1.6	1.2	0.8
Carabidae	<i>Zacotus matthewsii</i> LeConte	P	43	9	2.2	1.1	3.8	1.9	0.8	0.6
Scydmaenidae	<i>Lophioderus similis</i> Marsh	P	40	9	2.6	1.5	1.2	1.0	3.0	1.3
Curculionidae	<i>Otiorynchus rugostriatus</i> (Goeze)	H	39	6	0.2	0.2	0.4	0.4	3.2	1.8
Pselaphinae	<i>Sonoma margemina</i> Park & Wagner	P	39	7	4.0	3.5	1.6	0.7	0.6	0.6
Punctidae	<i>Punctum randolphi</i> (Dall)	H	38	11	2.2	0.9	3.4	1.3	1.2	0.5
Dipluridae	<i>Microhexura idahoana</i> Chamberlin & Ivie	P	37	7	0.8	0.4	3.0	1.8	2.6	2.6
Scydmaenidae	<i>Scydmaenus pacificus</i> Casey	P	36	12	1.0	0.6	3.2	2.3	2.0	0.8
Carabidae	<i>Pterostichus inanis</i> Horn	P	36	4	0.0	0.0	0.2	0.2	5.4	5.4
Carabidae	<i>Pterostichus campbelli</i> Bousquet	P	33	4	1.6	1.2	2.8	2.8	2.2	2.2
Polydesmidae	<i>Scytonotus insulanus</i> Attems	D	31	8	1.0	1.0	1.4	0.7	2.8	1.7
Curculionidae	<i>Agasphaerops niger</i> Horn	H	30	4	0.6	0.4	0.0	0.0	3.2	3.2
Agelenidae	<i>Cybaeina confusa</i> Chamberlin & Ivie	P	30	12	1.2	0.5	1.0	0.5	3.0	0.7
Curculionidae	<i>Sthereus horridus</i> (Mannerheim)	H	30	7	2.2	1.0	0.8	0.6	1.4	0.9
Carabidae	<i>Microlestes nigrinus</i> (Mannerheim)	P	28	8	0.0	0.0	0.2	0.2	3.6	1.7

Appendix 2 (Continued)

Family	Taxon name and author	Functional group	Total abundance	Site frequency	Forest (n=5)		Buffer (n=5)		Clearcut (n=5)	
					Mean	SE	Mean	SE	Mean	SE
Carychiidae	<i>Carychium occidentale</i> Pilsbry	H	27	5	1.0	0.8	2.6	2.6	1.8	1.6
Scydmaenidae	<i>Catalinus n.sp.1</i>	P	27	8	0.8	0.4	1.8	1.1	2.0	1.5
Agelenidae	<i>Cybaeus scopulatus</i> Chamberlin & Ivie	P	24	3	1.2	1.2	1.0	1.0	0.8	0.8
Curculionidae	<i>Geodercodes latipennis</i> Casey	H	23	4	0.2	0.2	1.2	1.2	2.8	1.7
Curculionidae	<i>Rhyncolus brunneus</i> Mannerheim	H	22	6	0.8	0.8	0.2	0.2	2.4	1.5
Cicindelidae	<i>Cicindela longilabris</i> Say	P	21	1	0.0	0.0	0.0	0.0	4.2	4.2
Carabidae	<i>Carabus taedatus taedatus</i> Fabricius	P	20	1	0.0	0.0	0.0	0.0	0.6	0.6
Zonitidae	<i>Pristiloma lansingi</i> (Bland)	H	19	8	1.2	0.7	1.8	0.6	0.6	0.4
Scydmaenidae	<i>Veraphis sp.1</i>	P	19	3	0.0	0.0	2.8	2.8	0.0	0.0
Gnaphosidae	<i>Zelotes josephine</i> Platnick & Shadab	P	19	4	0.0	0.0	0.0	0.0	3.0	1.8
Pselaphinae	<i>Actium retractum</i> Casey	P	18	6	1.2	0.8	1.0	0.6	1.0	0.6
Polygyridae	<i>Cryptomastix germana</i> (Gould)	H	18	3	1.4	1.4	1.2	1.2	0.8	0.8
Agelenidae	<i>Cicurina idahoana</i> Chamberlin	P	17	5	0.2	0.2	0.2	0.2	1.8	1.1
Curculionidae	<i>Otiorhynchus sulcatus</i> (Fabricius)	H	17	3	0.0	0.0	1.0	1.0	1.4	1.4
Caseyidae	<i>Ochrogramma n.sp.</i>	D	16	8	1.4	0.6	0.8	0.4	0.6	0.4
Thomisidae	<i>Ozyptila pacifica</i> Banks	P	16	3	0.0	0.0	0.0	0.0	2.0	1.5
Pselaphinae	<i>Sonoma parviceps</i> (Maklin)	P	16	8	1.4	0.7	1.2	0.6	0.4	0.2
Lycosidae	<i>Pardosa vancouveri</i> Emerton	P	15	3	0.0	0.0	0.0	0.0	0.4	0.2
Pselaphinae	<i>Pselaptrichus rothi</i> Park	P	15	7	0.8	0.6	1.2	0.7	0.6	0.4
Carabidae	<i>Pterostichus amethystinus</i> Mannerheim	P	15	7	0.6	0.4	1.4	0.4	0.6	0.6
Lycosidae	<i>Pardosa wyuta</i> Gertsch	P	14	4	0.0	0.0	0.0	0.0	1.8	1.6
Carabidae	<i>Amara spp.</i>	H	13	2	0.0	0.0	0.0	0.0	1.0	1.0
Agelenidae	<i>Cybaeus n.sp.</i>	P	13	5	1.4	0.7	0.8	0.8	0.4	0.4
Salticidae	<i>Evarcha prozysinskii</i> Marusik & Logunov	P	13	7	0.2	0.2	0.4	0.4	1.4	0.2
Conotylidae	<i>Taiyutyla corvallis</i> Chamberlin	D	13	8	1.0	0.4	0.4	0.2	0.0	0.0
Carabidae	<i>Amara sp.3</i>	H	12	6	0.0	0.0	0.0	0.0	1.0	0.5
Arionidae	<i>Gliabates oregonius</i> Webb	H	12	6	1.0	0.4	0.6	0.6	0.4	0.2

Appendix 2 (Continued)

Family	Taxon name and author	Functional group	Total abundance	Site frequency	Forest (n=5)		Buffer (n=5)		Clearcut (n=5)	
					Mean	SE	Mean	SE	Mean	SE
Salticidae	<i>Habronattus jucundus</i> (G. & E. Peckham)	P	11	5	0.0	0.0	0.0	0.0	1.2	1.0
Arionidae	<i>Prophyaon vanattae</i> Pilsbry	H	11	5	0.2	0.2	1.0	0.6	0.8	0.6
Zonitidae	<i>Striatura pugetensis</i> (Dall)	H	11	5	1.2	0.6	0.2	0.2	0.8	0.8
Gnaphosidae	<i>Micaria pulicaria</i> (Sundevall)	P	10	5	0.0	0.0	0.0	0.0	1.8	0.4
Curculionidae	<i>Rhinoncus castor</i> (Fabricius)	H	10	1	0.0	0.0	0.0	0.0	2.0	2.0
Lycosidae	<i>Schizocosa mccooki</i> (Montgomery)	P	10	2	0.0	0.0	0.0	0.0	1.6	1.6
Carabidae	<i>Bembidion iridescens</i> (LeConte)	P	9	5	0.2	0.2	0.2	0.2	1.0	0.6
Carabidae	<i>Elaphropus parvulus</i> (Dejean)	P	9	1	0.0	0.0	0.0	0.0	1.8	1.8
Pselaphinae	<i>Megarafonus lentus</i> Schuster & Marsh	P	9	4	0.8	0.5	0.0	0.0	0.2	0.2
Curculionidae	<i>Sitona lineellus</i> (Bonsdorff)	H	9	1	0.0	0.0	0.0	0.0	0.0	0.0
Parajulidae	<i>Uroblaniulini n.sp.</i>	D	9	2	1.2	1.2	0.4	0.4	0.0	0.0
Arionidae	<i>Ariolimax columbianus</i> (Gould)	H	8	7	0.2	0.2	0.8	0.4	0.2	0.2
Polyxenidae	<i>Polyxenus lagurus</i> (Linnaeus)	D	8	3	0.2	0.2	0.0	0.0	0.6	0.6
Curculionidae	<i>Sthereus quadrituberculatus</i> Motschulsky	H	8	4	0.8	0.6	0.0	0.0	0.6	0.6
Pselaphinae	<i>Abdiunguis fenderi</i> Park & Wagner	P	7	5	0.6	0.4	0.6	0.4	0.2	0.2
Scydmaenidae	<i>Scydmaenus fuchsi</i> Brendel	P	7	4	0.0	0.0	0.0	0.0	0.6	0.4
Carabidae	<i>Bradycellus conformis</i> (Fall)	P	7	1	0.0	0.0	0.0	0.0	1.4	1.4
Curculionidae	<i>Dyslobus productus</i> Hatch	H	7	1	0.0	0.0	0.0	0.0	1.2	1.2
Carabidae	<i>Scaphinotus rugiceps rugiceps</i> (Horn)	P	7	1	0.0	0.0	0.0	0.0	0.6	0.6
Gnaphosidae	<i>Sergiolus montanus</i> (Emerton)	P	7	5	0.6	0.4	0.8	0.4	0.0	0.0
Caseyidae	<i>Vasingtona irritans</i> (Chamberlin)	D	7	4	0.4	0.4	0.2	0.2	0.2	0.2
Salticidae	<i>Habronattus oregonensis</i> (G. & E. Peckham)	P	6	6	0.0	0.0	0.0	0.0	0.8	0.2
Carabidae	<i>Leistus ferruginosus</i> Mannerheim	P	6	3	0.4	0.4	0.0	0.0	0.8	0.6
Scydmaenidae	<i>Lophoderus insignis</i> Marsh	P	6	4	0.4	0.2	0.6	0.6	0.2	0.2
Pselaphinae	<i>Oropus n.sp.</i>	P	6	3	0.8	0.8	0.0	0.0	0.2	0.2
Carabidae	<i>Pterostichus johnsoni</i> Ulke	P	6	2	0.2	0.2	0.0	0.0	1.0	1.0
Curculionidae	<i>Sitona californius</i> Fahraeus	H	6	3	0.0	0.0	0.0	0.0	0.4	0.2

Appendix 2 (Continued)

Family	Taxon name and author	Functional group	Total abundance	Site frequency	Forest (n=5)		Buffer (n=5)		Clearcut (n=5)	
					Mean	SE	Mean	SE	Mean	SE
Parajulidae	<i>Bollmaniulus ?furcifer</i> (Harger)	D	5	3	0.4	0.4	0.0	0.0	0.6	0.4
Carabidae	<i>Platynus ovipennis</i> (Mannerheim)	P	5	1	1.0	1.0	0.0	0.0	0.0	0.0
Arionidae	<i>Prophysaon dubium</i> Cockerell	H	5	3	0.0	0.0	0.2	0.2	0.0	0.0
Curculionidae	<i>Steremnius tuberosus</i> Gyllenhal	H	5	4	0.2	0.2	0.4	0.2	0.4	0.4
Striariidae	<i>Striaria n.sp.1</i>	D	5	4	0.2	0.2	0.4	0.2	0.2	0.2
Striariidae	<i>Striariidae n.sp.</i>	D	5	4	0.2	0.2	0.4	0.2	0.2	0.2
Curculionidae	<i>Cnemogonus lecontei</i> Dietz	H	4	1	0.0	0.0	0.0	0.0	0.6	0.6
Pupillidae	<i>Columella edentula</i> (Draparnaud)	H	4	2	0.6	0.6	0.2	0.2	0.0	0.0
Agelenidae	<i>Cybaeus signifer</i> Simon	P	4	3	0.2	0.2	0.6	0.4	0.0	0.0
Helicarionidae	<i>Euconulus fulvus</i> (Muller)	H	4	2	0.2	0.2	0.0	0.0	0.4	0.4
Pselaphinae	<i>Lucifotychus cognatus</i> Leconte	P	4	2	0.0	0.0	0.6	0.6	0.2	0.2
Gnaphosidae	<i>Micaria coloradensis</i> Banks	P	4	2	0.0	0.0	0.0	0.0	0.4	0.4
Caseyidae	<i>Opiona n.sp.</i>	D	4	2	0.0	0.0	0.4	0.4	0.2	0.2
Curculionidae	<i>Panscopus gemmatus</i> LeConte	H	4	4	0.0	0.0	0.0	0.0	0.0	0.0
Valloniidae	<i>Planogyra clappi</i> (Pilsbry)	H	4	3	0.0	0.0	0.6	0.4	0.2	0.2
Curculionidae	<i>Rhynchaenus rufipes</i> (LeConte)	H	4	2	0.6	0.6	0.2	0.2	0.0	0.0
Pupillidae	<i>Vertigo columbiana</i> (Pilsbry & Vanatta)	H	4	4	0.0	0.0	0.6	0.2	0.2	0.2
Parajulidae	<i>Bollmaniulini n.sp.</i>	D	3	1	0.0	0.0	0.0	0.0	0.6	0.6
Curculionidae	<i>Nemocestes puncticollis</i> Casey	H	3	2	0.2	0.2	0.0	0.0	0.0	0.0
Curculionidae	<i>Otiorhynchus ovatus</i> (Linnaeus)	H	3	2	0.0	0.0	0.0	0.0	0.4	0.2
Pselaphinae	<i>Reichenbachia sp.1</i>	P	3	1	0.0	0.0	0.6	0.6	0.0	0.0
Pselaphinae	<i>Sonoma cascadia</i> Chandler	P	3	2	0.2	0.2	0.4	0.4	0.0	0.0
Pselaphinae	<i>Tetrascapha n.sp.</i>	P	3	2	0.0	0.0	0.6	0.4	0.0	0.0
Carabidae	<i>Amara sp.1</i>	H	2	1	0.0	0.0	0.0	0.0	0.2	0.2
Carabidae	<i>Amara sp.2</i>	H	2	1	0.0	0.0	0.0	0.0	0.0	0.0
Carabidae	<i>Anchomenus aeneolus</i> (LeConte)	P	2	1	0.0	0.0	0.0	0.0	0.4	0.4
Carabidae	<i>Bembidion castum</i> Casey	P	2	2	0.0	0.0	0.2	0.2	0.2	0.2

Appendix 2 (Continued)

Family	Taxon name and author	Functional group	Total abundance	Site frequency	Forest (n=5)		Buffer (n=5)		Clearcut (n=5)	
					Mean	SE	Mean	SE	Mean	SE
Gnaphosidae	<i>Callilepis eremella</i> Chamberlin	P	2	1	0.0	0.0	0.0	0.0	0.4	0.4
Scydmaenidae	<i>Catalinus n.sp.2</i>	P	2	2	0.0	0.0	0.2	0.2	0.2	0.2
Cicindelidae	<i>Cicindela oregona</i> Leconte	P	2	1	0.0	0.0	0.0	0.0	0.4	0.4
Agelenidae	<i>Cicurina pusilla</i> (Simon)	P	2	1	0.0	0.0	0.0	0.0	0.4	0.4
Curculionidae	<i>Cryptorhyncus lapathi</i> (Linnaeus)	H	2	1	0.0	0.0	0.0	0.0	0.4	0.4
Curculionidae	<i>Dioprophorus repens</i> (Casey)	H	2	1	0.0	0.0	0.0	0.0	0.4	0.4
Salticidae	<i>Habronattus hirsutus</i> (Peckham)	P	2	2	0.0	0.0	0.0	0.0	0.2	0.2
Carabidae	<i>Harpalus sp.1</i>	H	2	2	0.0	0.0	0.0	0.0	0.2	0.2
Mecicobothriidae	<i>Hexura rothi</i> Gertsch & Platnick	P	2	1	0.0	0.0	0.0	0.0	0.0	0.0
Thomisidae	<i>Misumena vatia</i> (Clerck)	P	2	2	0.0	0.0	0.0	0.0	0.0	0.0
Salticidae	<i>Neon reticulatus</i> Blackwall	P	2	1	0.0	0.0	0.0	0.0	0.4	0.4
Pselaphinae	<i>Pselaptrichus n.sp.</i>	P	2	1	0.0	0.0	0.4	0.4	0.0	0.0
Striariidae	<i>Striaria n.sp.2</i>	D	2	2	0.0	0.0	0.0	0.0	0.2	0.2
Thomisidae	<i>Xysticus locuples</i> Keyserling	P	2	2	0.0	0.0	0.0	0.0	0.2	0.2
Pselaphinae	<i>Actium fastosum</i> Grigarick & Schuster	P	1	1	0.0	0.0	0.0	0.0	0.0	0.0
Carabidae	<i>Amara sp.4</i>	H	1	1	0.0	0.0	0.0	0.0	0.0	0.0
Carabidae	<i>Anisodactylus binotatus</i> (Fabricius)	P	1	1	0.0	0.0	0.0	0.0	0.0	0.0
Curculionidae	<i>Baris sparsus</i> LeConte	H	1	1	0.0	0.0	0.0	0.0	0.2	0.2
Pselaphinae	<i>Batrisodes cicatricosis</i> Brendel	P	1	1	0.0	0.0	0.0	0.0	0.2	0.2
Carabidae	<i>Bembidion platynoides</i> Hayward	P	1	1	0.0	0.0	0.0	0.0	0.2	0.2
Carabidae	<i>Bembidion sp.1</i>	P	1	1	0.0	0.0	0.2	0.2	0.0	0.0
Carabidae	<i>Bembidion spectabile</i> (Mannerheim)	P	1	1	0.0	0.0	0.0	0.0	0.2	0.2
Thomisidae	<i>Coriarachne brunneipes</i> Banks	P	1	1	0.0	0.0	0.0	0.0	0.0	0.0
Curculionidae	<i>Dietzella zimmermanni</i> (Gyllenhal)	H	1	1	0.0	0.0	0.0	0.0	0.2	0.2
Gnaphosidae	<i>Drasyllus depressus</i> (Emerton)	P	1	1	0.0	0.0	0.0	0.0	0.2	0.2
Pselaphinae	<i>Foveoscapha terracola</i> Park & Wagner	P	1	1	0.0	0.0	0.2	0.2	0.0	0.0
Salticidae	<i>Habronattus americanus</i> (Keyserling)	P	1	1	0.0	0.0	0.0	0.0	0.2	0.2

Appendix 2 (Continued)

Family	Taxon name and author	Functional group	Total abundance	Site frequency	Forest (n=5)		Buffer (n=5)		Clearcut (n=5)	
					Mean	SE	Mean	SE	Mean	SE
Pselaphinae	<i>Lucifotychus n.sp.</i>	P	1	1	0.0	0.0	0.0	0.0	0.2	0.2
Bradybaenidae	<i>Monadenia fidelis</i> (Gray)	H	1	1	0.2	0.2	0.0	0.0	0.0	0.0
Pupillidae	<i>Nearctula rowellii</i> (Newcomb)	H	1	1	0.0	0.0	0.0	0.0	0.2	0.2
Pselaphinae	<i>Oropus magnidens</i> Schuster & Grigarick	P	1	1	0.2	0.2	0.0	0.0	0.0	0.0
Curculionidae	<i>Pachyrhinus elegans</i> (Couper)	H	1	1	0.0	0.0	0.0	0.0	0.0	0.0
Curculionidae	<i>Pissodes fasciatus</i> LeConte	H	1	1	0.2	0.2	0.0	0.0	0.0	0.0
Curculionidae	<i>Pissodes piperi</i> Hopkins	H	1	1	0.2	0.2	0.0	0.0	0.0	0.0
Zonitidae	<i>Pristiloma johnsoni</i> (Dall)	H	1	1	0.0	0.0	0.2	0.2	0.0	0.0
Carabidae	<i>Pterostichus testaceus</i> (Van Dyke)	P	1	1	0.0	0.0	0.0	0.0	0.2	0.2
Rhiscosomididae	<i>Rhiscosomides sp.1</i>	D	1	1	0.0	0.0	0.0	0.0	0.0	0.0
Gnaphosidae	<i>Sergiolus columbianus</i> (Emerton)	P	1	1	0.0	0.0	0.0	0.0	0.2	0.2
Pselaphinae	<i>Sonoma n.sp.1</i>	P	1	1	0.2	0.2	0.0	0.0	0.0	0.0
Pselaphinae	<i>Sonoma n.sp.2</i>	P	1	1	0.0	0.0	0.2	0.2	0.0	0.0
Carabidae	<i>Trechus obtusus</i> Erichson	P	1	1	0.2	0.2	0.0	0.0	0.0	0.0
Pselaphinae	<i>Tyrus corticinus</i> (Casey)	P	1	1	0.0	0.0	0.0	0.0	0.2	0.2
Thomisidae	<i>Xysticus benefactor</i> Keyserling	P	1	1	0.0	0.0	0.0	0.0	0.0	0.0