AN ABSTRACT OF THE THESIS OF

Chris D. Sheridan for the degree of Master of Science in Forest Science presented on June 3, 2002.

Title: Plant and Amphibian Assemblages in Zero-Order Basins in the Oregon Coast Range.

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Abstract approved: ______________________________

Thomas A. Spies

We have a poor understanding of the biotic communities in zero-order basins, drainages extending from ridgelines to the initiation of first-order streams. This study describes baseline plant and amphibian composition in unmanaged zero-order basins in the Oregon Coast Range. Specifically, I studied: *i*) the spatial distribution and diversity of species, including riparian-associates; and *ii*) the dominant environmental, spatial and geomorphic gradients in species composition. The results of this research have implications for riparian management in steep, forested landscapes in the Pacific Northwest.

The composition of tree and shrub layers in zero-order basins was more similar to upland areas than to larger-order riparian areas. Douglas-fir, western hemlock, and western red cedar had highest basal areas; bigleaf maple had highest hardwood density. Convergent areas (areas collecting surface flow) had significantly lower relative densities than surrounding slopes.

I identified 138 forest floor herb, shrub, and seedling tree species in zero-order basins. Gradient analysis and empirical modeling suggested that the composition of forest floor plant assemblages was associated with environmental parameters related to geomorphic position and overstory characteristics, such as distance from basin center, basin aspect and overstory relative density. Vegetation types, developed using classification, followed similar environmental patterns. Vegetation types were useful in clarifying environmental gradients acting on groups of plant species, and in delineating the lateral extent of geomorphic and fluvial influences. Riparian-associated vegetation types were mostly restricted to valley floors and lower slope areas.

Geomorphic and lateral surfaces were drivers of environmental gradients in zero-order basins; plant species composition followed these geomorphic gradients. Surfaces close to basin center ("inner gorges"), including valley centers, splash zones, and lower slope areas, supported the highest plant species diversity and most distinct plant assemblages.

The spatial distribution patterns of amphibian species and assemblages were characterized along longitudinal and lateral gradients, and relative to three geomorphic surfaces (valleys, headmost areas and slopes), and empirical species-habitat models were developed. I identified eight amphibian species in zero-order basins (865 total captures), and analyzed data for six. Headmost areas supported a distinctive upland amphibian assemblage, while valley floors had the highest riparian amphibian diversity. Captures of three riparian species were higher in valley surfaces, within 5 m of the center of zero-order basins, while captures of three upland species were highest in areas 2-5 m from center. Upland-associated species were captured two times farther from basin centers than riparian-associated species. The best predictors of amphibian captures in empirical models were geomorphic, stability/ disturbance, moisture and overstory parameters. Ordination and indicator species analysis facilitated characterization of amphibian species assemblages within geomorphic surface zones, and suggested spatial compression of habitats and species in zero-order basins, in comparison to broader spatial extents in larger basins.

Plant and amphibian assemblages in unmanaged zero-order basins were most similar to each other in their lateral and geomorphic spatial patterning, including the importance of inner gorge areas for support of diverse communities. Plant species were strongly associated with geomorphic position parameters, while amphibians

had stronger ties to discrete microhabitat elements such as moisture levels and large substrate. Amphibians appeared to have a more distinctive assemblage in headmost areas than plant species.

Results suggest that assemblages of plants and amphibians in these basins are distinct from both larger-order riparian assemblages and from vegetation in surrounding hillslopes. Riparian management designs could take these spatial patterns and habitat associations into account to maintain the ecological integrity of headwater communities. The longitudinal and lateral extents of landscape areas managed to minimize risk to persistence of zero-order basin plant and amphibian assemblages would need to incorporate both fluvial and hillslope disturbance regimes, and microhabitat features associated with them.

Plant and Amphibian Assemblages in Zero-Order Basins in the Oregon Coast Range

by

Chris D. Sheridan

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Dean of Graduate School

I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

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Chris D. Sheridan, Author

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PLANT AND AMPHIBIAN ASSEMBLAGES IN ZERO-ORDER BASINS IN THE OREGON COAST RANGE

CHAPTER 1. INTRODUCTION

In western North America, headwater drainages make up a large proportion of the forested landscape (Hack and Goodlett 1960, Benda 1990, Appendix V-G in USDA and USDI 1994). Because of their distinctive environments, frequency and aerial extent in mountainous forest landscapes, their role in transport of materials down-gradient to higher-order systems (Benda 1990, May, 2001), and influence on downstream water quality (FEMAT 1993, Beschta et al. 1987), it is probable that small headwater drainages are important in the maintenance of species diversity and ecosystem integrity in forested landscapes in the Pacific Northwest.

Management of ecosystems to meet requirements of biodiversity policies requires maintenance and restoration of habitat to support well-distributed populations of native species within geophysical landscape units such as riparian areas (FEMAT 1993). A significant component of ecosystem management in drainage basins in the Pacific Northwest has focused on riparian areas lower in drainages to mitigate the effects of disturbance from forest management. Buffer widths have traditionally been established based on stream size and fish usage (Belt and O'Laughlin 1994), extending some pre-determined distance laterally from fluvial center. Headwater areas, particularly basins supporting ephemeral streams, receive minimal protection in current management guidelines, across land ownerships in the Pacific Northwest (Gregory 1997, Young 2000). Recently, biotic resources and ecological values in headwater areas have received increased scrutiny (Headwaters Research Cooperative Workshop, Oregon State University, October, 2001; Small streams and riparian zone management symposium and workshop, March 2002, University of British Columbia, B.C.), resulting in reassessment of ecological values warranting protection in watersheds in the Pacific Northwest.

Ephemeral systems, also called zero-order basins, dominate the drainage area of most soil-mantled hillslopes (Hack and Goodlett 1960, Benda 1990, Kikuchi and Miura 1993). Zero-order basins are hillslope units where flow lines converge on a hollow (Tsukamoto, Ohta and Noguchi 1982), including catchment areas above sustained scour and deposition as well as intermittent scour areas, extending from ridgelines down to the initiation of first-order streams. No studies have been conducted to characterize biotic communities in unmanaged zero-order basins, and the upper limits of riparian species in the headwaters of drainage basins have not been well defined. If riparian species are present in zero-order basins, these basins may be important in maintenance of ecosystem integrity in forested landscapes, and may provide connectivity to adjacent basins.

At the landscape scale, studies have been conducted characterizing overstory gradients for the entire State of Oregon (Ohmann and Spies 1998), as well as vegetation patterns in geophysical landforms present in the Oregon Coast Range Province (Kovalchick and Chitwood 1990, Minore and Weatherly 1994, Pabst and

Spies 1998, Pabst and Spies 1999). The Coastal Landscape Analysis and Modeling Study (CLAMS) involves landscape-level mapping of the composition and dynamics of overstory, plant, and faunal characteristics in upland and riparian zones in the Coast Range of Oregon (Spies et al. 2002). CLAMS vegetation and faunal habitat suitability models incorporate results from smaller scale studies of geophysical landscape units (e.g., riparian areas) and processes (e.g., debris flow). However, although modeling efforts have incorporated physical processes associated with zero-order basins including disturbance frequency, downed wood and sediment transport, and hydrology, biotic patterns in zero-order basins have not been incorporated in models.

My overall goal was to characterize biotic communities utilizing unmanaged zero-order basins in the central Coast Range of Oregon, to provide reference conditions useful for a variety of future analyses and management decisions. Study goals were to *i*) provide baseline information for future research on effects of disturbance or management activities on biotic communities in zero-order basins; *ii*) determine to what extent zero-order basins provide habitat for riparian-adapted flora and fauna; and *iii*) provide information to assist forest managers in discerning whether zero-order basin systems represent distinct landscape features. To characterize communities in zero-order basins, I chose to describe plant and amphibian assemblages.

In the second chapter of this thesis, I characterize plant assemblages in unmanaged zero-order basins. There is a lack of information regarding herb, shrub and tree distributions and their relationship to environmental gradients in zero-order basins. In chapter two I examine the spatial distribution of herb, shrub and tree species and changes in plant composition along lateral and geomorphic gradients, and I identify the important environmental parameters associated with the distribution of plant species. Additionally, zero-order basin vegetation types are developed, to simplify vegetation complexity and provide forest managers with a set of vegetation types to rapidly characterize zero-order basin vegetation.

The third chapter of the thesis characterizes amphibian assemblages in unmanaged zero-order basins. Where conditions are favorable, forest-dwelling amphibians can exceed mammals and birds in biomass and density (e.g., Burton and Likens 1975, Bury 1988). Additionally, amphibians are considered indicator species for environmental stress, due to their life histories and sensitivities to environmental change (e.g., Blaustein et al. 1995, Houlahan et al. 2000). Because of their importance in riparian food webs and their role as biological indicators, several amphibians have been included as Survey and Manage species under the Pacific Northwest Federal Northwest Forest Plan, and they and other riparian fauna represent one of the Aquatic Conservation Strategy values to be restored and maintained (USDA USDI 1994). Although it is clear that amphibians play a key role in riparian systems, there is a lack of information regarding amphibian usage of zero-order basins. Chapter three analyzes amphibian spatial distribution patterns along longitudinal and lateral gradients, and develops empirical models to quantify amphibian associations with environmental parameters, including microhabitat, forest structure and geomorphic parameters.

The fourth chapter synthesizes information from analyses of plants, amphibians and geomorphology in unmanaged zero-order basins. Chapter four characterizes similarities between the taxa, mechanisms for their co-occurrence, and similar environmental characteristics associated with species in each taxon. Finally, I develop implications of the information for management of floral and faunal communities in zero-order basins.

CHAPTER 2. PLANT ASSEMBLAGES IN ZERO-ORDER BASINS IN THE OREGON COAST RANGE

INTRODUCTION

In mountainous areas of western North America, headwater drainages make up a significant proportion of the forested landscape (Hack and Goodlett 1960, Benda 1990, Appendix V-G in USDA and USDI 1994). For example, in the central Coast Range of Oregon, stream drainage density is 2.9 km of stream per km^2 (USDI 2000), and 76% of these are first- and second-order (Strahler 1964) stream systems (USDI 2000). Headwater systems play an important role in transport of materials down-gradient to higher-order systems (Benda 1990, May, 2001), and influence downstream water quality (Beschta et al. 1987, USDA USDI 1993). Because of their frequency, position within drainage networks, and unique fluvial and hillslope processes, headwater drainages may play a role in the maintenance of species diversity in the Pacific Northwest, however these landscape elements have received relatively little scientific attention.

Management of biotic resources in headwater areas has also been minimal. Riparian forest buffers, where disturbance from forest management is reduced or eliminated, have traditionally been established based on stream size and fish usage (Belt and O'Laughlin 1994), with limited protection of smaller basins. As a result of federal review of ecosystem management in the Pacific Northwest (FEMAT 1993), more attention has focused on conservation efforts in first- and second-order basins

(Table 2.1). However, protection of native communities in zero-order basins is negligible under current management guidelines. Without a better understanding of the ecological characteristics of these basins, it is impossible to know how best to maintain their functions in managed landscapes.

Several studies have described the geomorphology of headwater areas (Hack and Goodlett 1960, Tsukamoto et al. 1982, Benda 1990, Kikuchi and Miura 1993). Within headwater areas, zero-order basins are hillslope units where flow lines converge on a hollow (Tsukamoto et al. 1982), including intermittent scour areas, extending from ridgelines down to the initiation of first-order streams (Figure 2.1). Zero-order basins may include areas defined as hollows (Montgomery and Dietrich 1989, Benda 1990), ephemeral or intermittent streams or the uppermost portions of first-order streams (USDA USDI 1994). Zero-order basins can be further divided into geomorphic surfaces including valleys, slopes, headmost areas and ridges (Figure 2.1). Zero-order basins have been studied for their unique physical characteristics, including their disturbance regime (Benda 1988, Reneau and Dietrich 1990, May 2001) and moisture relations (Dietrich et al. 1997, Montgomery and Dietrich 1989).

Table 2.1. Comparison of management practices for perennial and intermittent basins in forested mountain streams of the Pacific Northwest (adapted from Young 2000). Intermittent systems include both 1st and 2nd-order streams, and zero-order basins (described in text).

	Basin type		
	Perennial	**Intermittent**	
Provincial/ State government	**> 2nd order**	**1st - 2nd order**	**Zero-order**
British Columbia	20-m buffer; 20-m management zone	No buffer; 20-m management zone	None
US Federal lands (NFP Lands)	1-2 site-potential tree heights	1 site-potential tree height	Variable by slope/ geology
Washington State/Private	No buffer; 7.5-m - 30-m management zone	None	None
Oregon State/Private	6-m buffer; 30-m management zone	6-m buffer; 15-m management zone	None
California State/Private	45-m management zone	15-m management zone	None

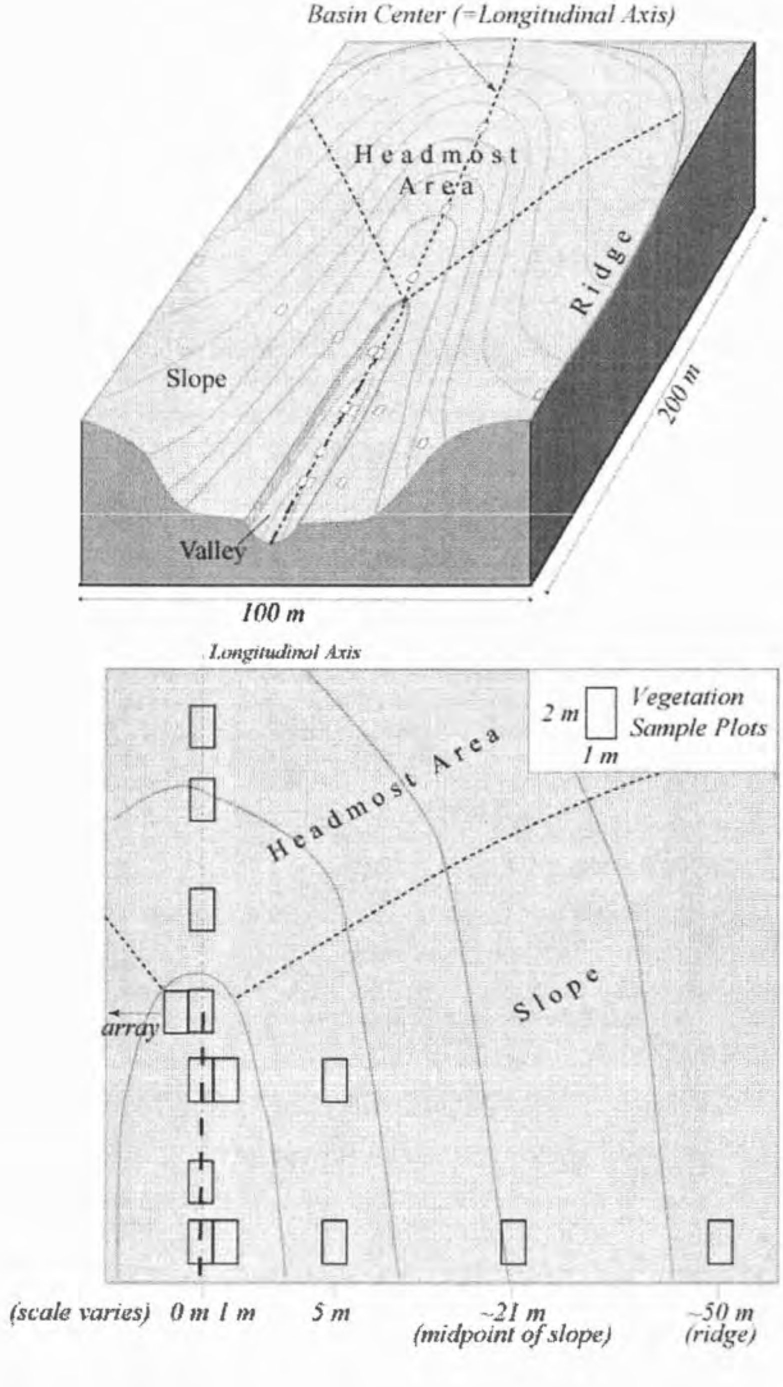

Figure 2.1. Schematic of geomorphic surfaces and plant sampling plots within zero-order basins.

Riparian plant assemblages in the Pacific Northwest have been described (Henderson 1978, Swanson and Lienkaemper 1982, Hemstrom and Logan 1986, Minore and Weatherly 1994, Hibbs and Giordano 1996), and several studies (Pabst and Spies 1998, 1999, Nierenberg and Hibbs 2000) have focused on vegetation in smaller unmanaged basins. However, no studies have specifically characterized herb and shrub assemblages in unmanaged zero-order basins, and it is unclear if zero-order basins support vegetation patterns distinct from surrounding hillslopes and larger-order riparian systems downstream. The upstream limits of riparian-associated plant species and plant assemblages in drainage basins have not been established, either.

Geomorphology plays a dominant role in structuring plant communities in headwater basins (Kovalchik and Chitwood 1990, Gregory et al. 1991, Pabst and Spies 1998). In zero-order basins in Japan, Kikuchi and Miura (1993) found a distinct change in overstory tree composition and structure moving from planar slopes, dominated by coniferous forest, to convergent valleys (Figure 2.1), supporting open deciduous broadleaf forest. The effects of geomorphic gradients on herbaceous and shrub assemblages in unmanaged zero-order basins have not been studied.

There is a lack of information regarding the composition of plant assemblages in zero-order basins, their support of riparian species, and their associations with physical characteristics. I characterized zero-order basin plant assemblages in unmanaged forests to provide baseline information on their composition and associations with geomorphic and environmental parameters. Specifically, I sought to:

(i) Characterize the geomorphology, trees, herbs, shrubs, and plant species diversity of zero-order basins, including riparian-associated species.

(ii) Identify and explain the dominant gradients in plant species composition in terms of physical environment.

(iii) Classify vegetation types in zero-order basins, including riparian-associated types, and characterize environmental conditions associated with these types.

(iv) Identify plant species associated with different geomorphic surfaces, and with different lateral zones nested hierarchically within these surfaces, to clarify the effects of geomorphic and lateral gradients on plant species composition.

METHODS

Study area

The study area was chosen for the presence of large unmanaged areas, for the relatively high density of first-order systems (Table 2.2), and to control landscape attributes including plant association, geology, elevation and marine influence. Work was conducted on United States federal lands administered by the Coos Bay District of the Bureau of Land Management (BLM) in the central Oregon Coast Range

(Figure 2.2). The area encompassed approximately 850 km^2 of the headwaters of the Coquille River Basin (4767N to 4798N UTM, 418E to 445E UTM).

Table 2.2. Zero-order basin characteristics measured in the study area (n = 63).

Parameter	Mean (range)
Landscape characteristics	
Number of first-order systems per km^2*	11.5 (8, 17)
Number of zero-order basins per 1st- order	1.56 (1, 4)
Zero-order basin characteristics	
Distance from ocean (km)	43.3 (35.9, 55.3)
Ridge elevation (m)	599.4 (227.1, 807.9)
Basin gradient (°)	20.2 (3.5, 41.2)
Basin area (ha) **	1.1 (0.1, 7.2)
Basin total length (m)	274.4 (85.5, 783)
Distance to initiation of scour/ deposition (m)	165.5 (64, 630)
Distance to start of channelization (m)	193.5 (48, 637)
Distance to start of flow (m)	182.7 (152.8, 652.0)
Channel width [where present] (m)	0.9 (0, 3.5)
Valley width (m)	4.5 (1.2, 10.0)
Slope length (m)	51.1 (7, 194)

* Initiation points of first-order systems, determined using GIS analysis.

** Measured using flow accumulation algorithms; initiation of scour as "pour point".

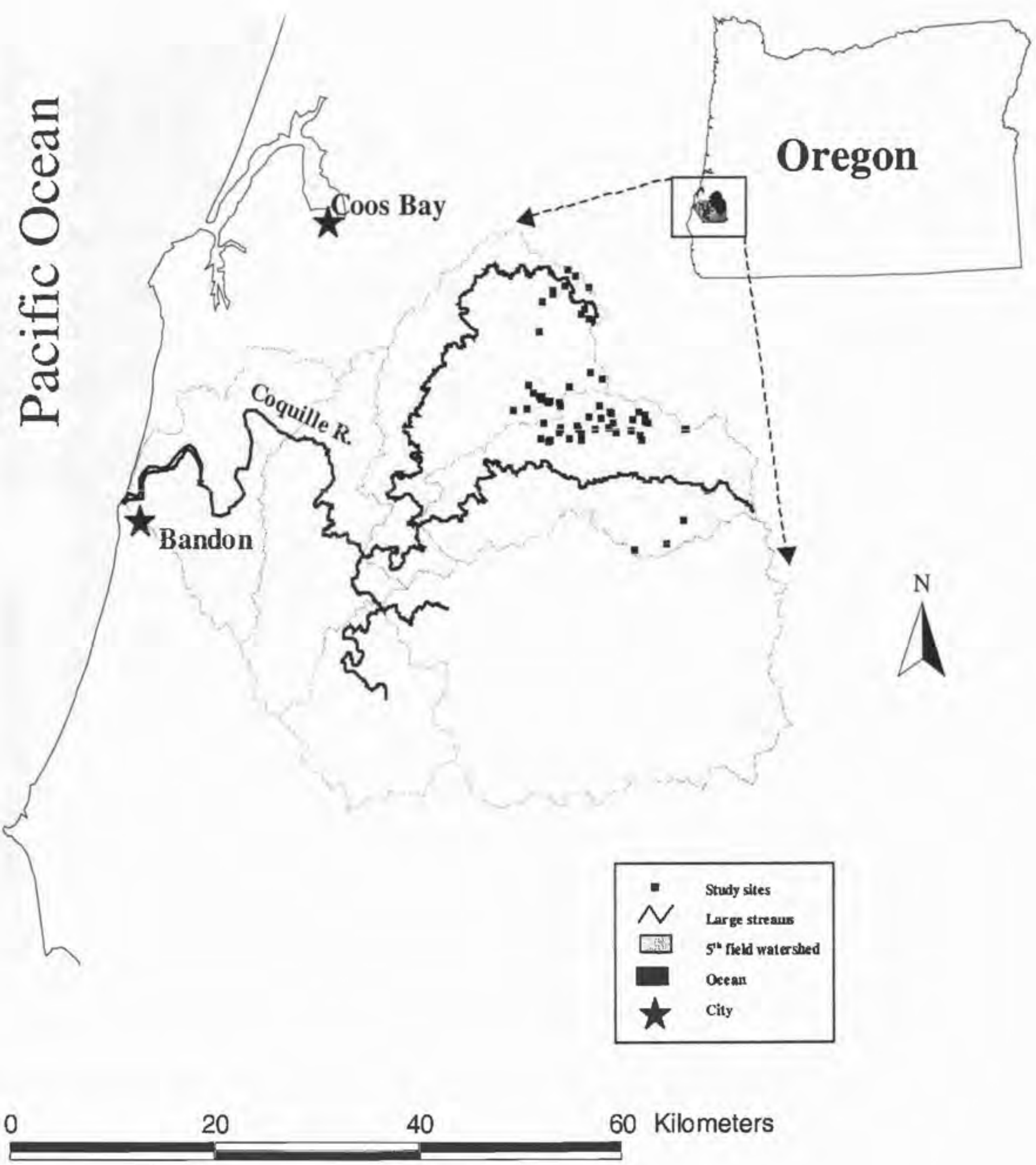

Figure 2.2. Location of 63 study sites within the study area.

This region is underlain by uplifted sea floor sediment and basalt, with geologic formations composed of sandstone and sandy siltstone (USDI 2000). Soils in study sites included principally series in the Preacher-Bohannon and Umpcoos-Rock Outcrop units. The area is deeply dissected by stream networks, including many steep headwater channels. The study area supported approximately 18 zero-order basins per km^2, each averaging just over 1 ha in size above the initiation point of scour and thus encompassing less than 1% of the landscape (Table 2.2). Within the Coast Range physiographic province, maximum air temperatures seldom exceed 30° C, and minimum air temperatures rarely fall below freezing (USDI 2000). Most precipitation occurs as rainfall, ranging from 1397 mm to over 3810-mm annually (OSU 1982).

The study area falls within the western hemlock (*Tsuga heterophylla*) zone (Franklin and Dyrness 1969). Stands in the study area are dominated by Douglas-fir (*Pseudotsuga menziesii*), and include western hemlock, western red cedar (*Thuja plicata*) and grand fir (*Abies grandis*). Hardwoods occupy less than 10% of stands, and include bigleaf maple (*Acer macrophyllum*), chinquapin (*Castanopsis chrysophylla*) and California bay (*Umbellularia californica*). Common shrub species include evergreen huckleberry (*Vaccinium ovatum*) and salal (*Gaultheria shallon*). Herbaceous species include sword fern (*Polystichum munitum*) and oxalis (*Oxalis oregana*). Riparian areas support hardwoods including red alder (*Alnus rubra*) and mesic conifers like western red cedar. Common riparian shrub species include salmonberry (*Rubus spectabilis*) and stinking black currant (*Ribes bracteosum*). Common riparian herbs include maidenhair fern (*Adiantum pedatum*), lady fern (*Athyrium filix-femina*), and deer fern (*Blechnum spicant*).

Historically, fire was the most important disturbance process affecting vegetation patterns in the study area (USDI 2000). Unmanaged portions of the study area include stands 250 and 450 years old, originating after stand-replacing fires in the periods from 1534 to1590 or from 1735 to1798 (USDI 2000). At least nine major fire events have been identified in the study area through fire scar analysis (USDI 2000), and numerous smaller underburns probably influenced understory development in forest stands. Zero-order basin geomorphology including ridges, occasional treeless areas and moister microclimates would be expected to further modify fire effects.

Zero-order basins are the principal initiation points for landslides in the steep, deeply-dissected mountainous landscapes of the Pacific Northwest (Dietrich et al. 1986). The process of landsliding is cyclic, involving failure followed by periods of recharge. In the Coast Range of Oregon, one cycle may be close to 100 years for in-channel failures (USDI 2000). Landslides often follow large fire episodes. Disturbance regimes in unmanaged zero-order basins can lead to high levels of downed wood in comparison to unmanaged upslope areas (Spies et al. 1988). Study site selection was not stratified by fire or landslide disturbance history, and the sample thus has a range of times since natural disturbance.

In the Pacific Northwest, human activities including the use of fire, overstory removal, and road installation have affected the historic frequency of landslides (Robison et al. 1999), the fire return interval (USDI 2000), and, at smaller spatial scales, substrate characteristics and fluvial processes. Native Americans managed forested landscapes in the Coquille Basin prior to1900, using fire. This landscape modification occurred principally in lower valleys, removed from the study area. The General Land Office (GLO) sold timber on lands in the study area starting in 1924, beginning with the areas close to river valleys. The Bureau of Land Management has continued timber harvest and road installation since receiving lands from the GLO, including lands adjacent to many study sites. Anthropogenic influences on disturbance regimes in study sites were minimized, by selecting zero-order basins in stands regenerated after fires and aged over 200 years, with negligible evidence of overstory cutting or road effects ("unmanaged", hereafter). Zero-order basins in the sample were probably not logged historically due to difficult access (sites are relatively far from developed commerce centers) and due to the inherently steep and unstable nature of zero-order basins in general.

Study sites

Within the study area, 222 zero-order basins within unmanaged stands were identified from geographic information system (GIS) maps of land ownership, stand ages, roads, contour crenulations (produced by 10-m digital elevation models), and first-order systems. A set of selection criteria was applied *a priori* to all zero-order basins within the study area to identify suitable sites. Sites disturbed by management activities, sites > 0.8 km from a transportation corridor, and zero-order basins that did not terminate at the tip of a first-order channel (Dietrich et al. 1987) were eliminated. Preliminary observations suggested that zero-order basin environmental parameters varied with differences in slope and aspect. I therefore stratified basins into high (> 39°) and low (< 39°) slope classes, and into south and west-facing (120°-300°) and north and east-facing (301°-119°) aspect classes. All 222 systems were numbered, and a random number generator was used to determine order of sites visited, alternating by slope/aspect class. The sample population analyzed in this study includes the first 63 randomly selected zero-order basins from the inference population of 222 zero-order basins.

Survey plot establishment

In the field, I delineated the extent of each zero-order basin as areas extending downslope from ridgeline to the point where fluvial scour became clearly more continuous than discontinuous (estimated visually over a channel length of 15 m), often at the junction with another zero-order drainage. A longitudinal axis was established within delineated zero-order basins, along and parallel to the most fluvially active portion of the basin (Figure 2.1). This longitudinal axis was considered the center of the basin. Measurements of distance-from-ridge to sampling plot were measured along this axis. Lateral distances were measured perpendicular to this axis (Figure 2.1, detail area).

Several authors (Hack and Goodlet 1960, Gregory et al. 1991, Pabst and Spies 1998) have suggested that community patterns and biological diversity in headwater riparian drainage basins are organized by landforms shaped by geomorphic processes. I therefore delineated four geomorphic surfaces within zero-order basins: valleys, headmost areas, slopes, and ridges (Figure 2.1), and stratified plant and environmental sampling by them. Valley geomorphic surfaces were defined as convergent areas (collecting surface flow), downstream of the first evidence of scour and deposition, but above sustained scour. Headmost geomorphic surfaces were defined as convergent areas above the first evidence of scour and deposition, extending to a topographic break. Headmost zones were inclusive of both hollows and source areas, as defined by Montgomery and Dietrich (1989). Slope geomorphic surfaces were defined as the planar surfaces (where surface flow lines would be parallel), extending laterally between valley margins and ridges. Ridges were defined as the convex surfaces connecting slope surfaces in one zero-order basin to slope surfaces in adjoining basins. I further stratified zero-order basins into lateral distance zones, to characterize changes in plant composition and environmental parameters at finer spatial scales within geomorphic surfaces. Lateral zones were a refinement of geomorphic surface zones, hierarchically-nested within the geomorphic surface typology, eliminating the valley zone and adding 1-m wide zones centered on points 0 m, 1 m and 5 m from basin center.

I established 17 plots for sampling plant cover and environmental parameters within the four geomorphic surfaces and six lateral zones in each zero-order basin in the sample (Figure 2.1). I established seven plots randomly along the longitudinal axis, four in the valley zone and three in the headmost zone, each a minimum of 10 m apart. I established lateral plots 1 m and 5 m from basin center, perpendicular to three of the valley (0 m) plots (Figure 2.1). I established additional sampling points perpendicular to the uppermost and lowermost valley plots, exactly halfway between basin center and ridgelines in the slope zone, and in ridge geomorphic zones at the slope break between basins.

Individual plots were 1 m in width, to approximate the mean channel width for zero-order basins (Figure 2.1). I used flexible rubber tubing for my sampling frame, staked to an approximate 1-m x 2-m rectangle, but deformable to allow it to fit within constraints of the geomorphic surface. The sampling area for an individual plot was therefore always 2 m^2, although sampling shape was slightly variable.

Plant data collection

I collected data on plant cover during the months of July, August and September of three years (1999, 2000, 2001). Using established plots, I measured herbaceous and shrub cover, overstory cover and density, and plot-scale environmental parameters. I measured additional environmental parameters at larger spatial scales. I visually estimated percent plant cover for each plant species in a plot. Cover values less than 1% were assigned a 1% value. I defined cover as the percentage of ground surface obscured by any portion of the plant under 2 m in height, rooted in the same geomorphic surface and elevation as the plot frame. Herbaceous plants (forbs and graminoids), shrubs and seedling trees that fit these definitions were included in cover estimates. Canopy cover and density of overstory trees and shrubs over 2 m tall were estimated separately (below). Plant nomenclature followed Hitchcock and Cronquist (1973) and Jepson (1993).

Environmental variables

I measured 33 environmental variables which I hypothesized might be important in structuring plant assemblages in zero-order basins (Daubenmire 1947), as descriptors of environmental conditions, and for use in empirical models describing plant composition (Table 2.3). Environmental data were collected at both the plot and zero-order basin spatial scales. At the plot scale, data were collected for three parameters describing plot position, five parameters for surface moisture and stability, four parameters for substrate composition, and eight parameters for overstory conditions. Binary parameters for the presence/absence of saturation,

Table 2.3. Description of habitat parameters collected at the plot or zero-order basin scale, and covariates.

Parameter	Units	Description
Plot scale		
Ridge distance	m	Ridgeline to plot slope distance, divided by distance from ridgeline to initiation of scour.
Distance from basin center	m	Perpendicular slope distance from center of the basin to plot location.
Plot height	m	Difference in elevation between a plot and valley floor (basin center).
Substrate/fluvial		
Surface moisture	1-7	Integer index of plot moisture, modeled on categories developed by Crisafulli (Olson et al. 1999). Values range from 1 ('dry') to 7 ('flowing').
Saturation	0, 1	Presence/absence of field-estimated 'saturated' conditions in plot (Surface moisture ≥ 5).
Scour	0, 1	Presence/absence of scour (removal of above-ground vegetation and litter).
Deposition	0, 1	Presence/absence of deposition (material mobilized into the plot by fluvial or hillslope disturbance).
Stability	0, 1	Presence/absence of stable conditions (no scour or deposition) in plot.
Large substrate	%	Visual estimate of percent of plot surface obscured by gravel, cobble, boulders, or bedrock (substrates > 5 mm).
Organic substrate	%	Visual estimate of percent of plot surface obscured by litter, organic material, bark, or downed wood.
Organic depth	cm	Organic matter depth averaged from five points/plot.
Litter depth	cm	Litter depth averaged from five points/plot.
Overstory		
Canopy cover	%	Percent of view screen obscured in a canopy viewer (Mueller-Dombois and Ellenburg 1974) stationed at plot center.
Conifer canopy cover	%	Canopy cover of conifers; assessed with a canopy viewer.
Hardwood canopy cover	%	Canopy cover of hardwood species; assessed with a canopy viewer.
Large overstory	m^2/ha	Basal area of trees over 70 cm in diameter.
Relative density	0-100	Tree density metric calculated from basal area and quadratic mean diameters (Curtis 1982), using basal area from variable-radius overstory plots and visually estimated diameters.
Relative density within geomorphic surface	0-100	Relative density (similar to Curtis 1982), calculated using only trees rooted in the same geomorphic surface as the variable-radius plot.

Table 2.3. (continued)

Parameter	Units	Description
Plot scale (continued)		
Relative density of hemlock	0-100	Relative density (similar to Curtis (1982)), calculated using only western hemlock trees in variable-radius overstory plots.
Relative density of hardwood	0-100	Relative density (similar to Curtis (1982)), calculated using only hardwood species in variable-radius overstory plots.
Zero-order basin scale		
Geomorphic surface	Cat.	Three categories: valley, headmost area and slope.
Basin gradient	°	Slope of zero-order basin, calculated as the difference in elevation along the basin length.
Basin depth	m	Difference in elevation between the midpoint of the geomorphic surface and the surrounding ridgeline.
Heat load index	0-1	A measure of the solar exposure of a site, calculated using the formula: 1-cos(aspect-45)/2 (Beers et al. 1966), where aspect is the aspect of the basin. 0 represents cool (45°) aspects, 1.0 represents warm (225°) aspects.
Basin area	ha	Area potentially contributing surface flow to the point of initiation of scour and deposition in a zero-order basin. Generated in ARC/INFO, using flow direction and accumulation algorithms and a 10 m digital elevation model. Point of initiation of scour and deposition in the field used as "pour point".
Covariates		
Year of survey	Cat.	Categorical variable for year of survey (1999, 2000, 2001).
Elevation	m	Height above sea level of the highest point (ridgeline) in a zero-order basin (measured using an altimeter).
Stand age	years	Time since last stand-replacing event for forested areas in the zero-order basin, derived from ARC/INFO GIS coverages of the study area.
Ocean distance	km	Distance from the basin to the ocean, derived from ARC/INFO GIS coverages of the study area.
Geology class	Cat.	Three classes: Flournoy, Tyee, Flournoy/Tyee boundary.
Soil class	Cat.	Three classes, based on soil map units, defined in the Soil Survey of Coos County, OR (USDA 1989): A (38F, 58F, 44E), B (46D 46E 46F), C (44D, 44E).
Disturbance due to roads	0-4	Four categories: 0 (no disturbance) through 3 (roads potentially affecting drainage and stability).
Disturbance due to harvest	0-4	Four categories: 0 (no discernible human influence) - 3(removal affecting basal area measurement).

scour, deposition, and stability in individual plots became proportions when averaged for lateral or geomorphic zones. Overstory densities were measured using variable-radius sampling in one plot per geomorphic surface. Basal area collected on sloped ground was corrected to horizontal by multiplying it by the secant of plot slope angle in 1999, using a relascope in 2000, and by tilting the wedge prism to approximate hillslope gradient in 2001 (Pabst, pers. comm.). I calculated relative density similarly to Curtis (1982), using visual estimates of tree diameter corrected using measured diameters (1 out of 50 trees measured). Due to errors associated with visual estimates of diameters and irregular plot spacing, estimates of basal area and relative density had relatively high coefficients of variation and moderate bias, and were thus used principally for comparison between geomorphic surfaces.

At the zero-order basin scale, I collected data on five geomorphic variables including basin gradient, basin depth, heat load index (a cosine transformation of basin aspect (Beers et al. 1966)), and basin area. Data collected on covariates included year of survey, elevation of ridgeline, stand age and distance from ocean, as well as categorical covariates for geological formation, soil class, disturbance due to roads, and disturbance due to harvest.

Data analysis

A number of analyses were performed to characterize plant assemblages in zero-order basins, including gradient analysis and classification. Plot data was averaged for each geomorphic surface to address questions about basin geomorphology, overstory and shrub characteristics (Figure 2.3). Plot data was averaged for each lateral zone to investigate plant species composition, develop vegetation types and quantify diversity in zero-order basins (Figure 2.3).

To provide a geomorphic context for analysis of overstory and forest floor plant species composition in zero-order basins, I calculated means and confidence intervals for basin gradient, frequency of fluvial disturbance, and downed wood volumes within the four geomorphic surfaces. I estimated means and confidence intervals for the basal area of each overstory tree species, and overstory metrics for all tallied trees, for each geomorphic surface. I quantified differences in overstory relative density between different geomorphic surfaces using a mixed linear model (PROC MIXED, SAS 1999), using an "unstructured" correlation structure to model spatial autocorrelation between geomorphic surfaces within a zero-order basin.

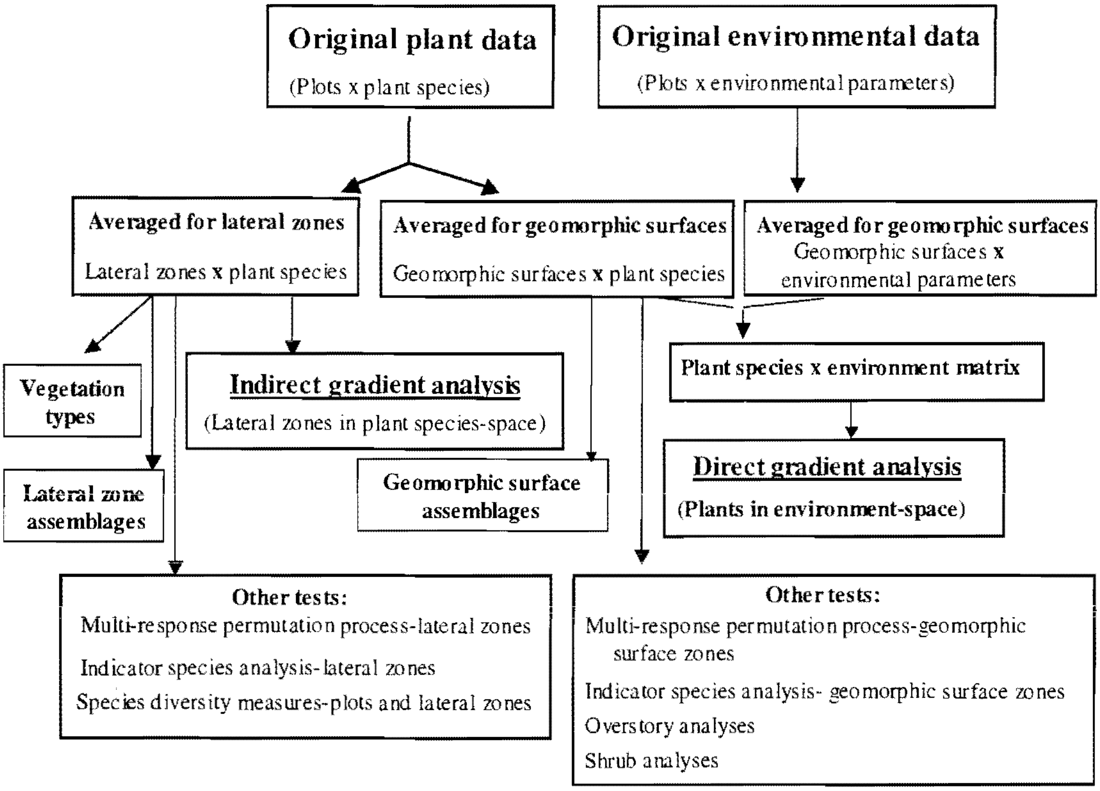

Figure 2.3. General flow diagram for analyses, showing strata used in analyses, types of multivariate analyses, and other analyses.

Gradient analyses

Indirect gradient analysis

I used indirect gradient analysis as the primary tool for characterizing gradients in herb, shrub and seedling tree composition, and for determining the environmental parameters important in structuring plant assemblages in zero-order basins. For this analysis, I averaged species cover for each of six geomorphic/ lateral zones: 0 m, 1 m, and 5 m from basin center, as well as headmost, slope and ridge zones. I eliminated rare species and log-transformed data, to reduce skew. I used nonmetric multidimensional scaling (NMS) (Mather 1976) with PC-ORD software (McCune and Mefford 1997) as the ordination method. NMS uses ranked distance metrics, and is thus resistant to skewed community data sets with large numbers of zeros (Clarke 1993). A Sorenson distance measure was employed, and detrended correspondence analysis (Hill 1979) was used to establish starting coordinates for the ordination, to ensure a global minimum solution. I selected the smallest number of dimensions that maintained interpretable levels of "stress": stress is a measure of dissimilarity between the original space and the reduced ordination space. Stress levels for NMS iterations were compared to randomized data in a Monte Carlo test, using 30 runs of randomized data, to quantify the fit of the ordination. The final ordination was rotated to maximize correlations between the first axis and the single most highly-correlated environmental variable, and to maximize the interpretable portion of the ordination in the smallest number of axes.

Interpretation of ordination axes was facilitated by overlay of lateral zone membership on ordination points, and by calculation of correlations between axis scores and both plant species covers and environmental parameter values (averaged for each lateral zone). Spearman's rank correlations were calculated between environmental variables and each axis in the ordination solution, to assess the relative importance of each variable in each axis. Joint plots (Jongman et al. 1987) were developed to show the relationship between important environmental parameters and ordination axes, and between species' covers and axis scores. Joint plots represented vectors formed from the hypotenuse of a right triangle, with the two other sides being r-values between the environmental parameter or species cover and the two axes.

Models for environmental effects on plant species composition

For each axis in the ordination of lateral zones in plant species-space, I developed and evaluated sets of uni- and multivariate empirical models describing plant ordination axis score as a function of landscape, geomorphic, fluvial, substrate and overstory parameters. I used an information-theoretic approach to model development and selection, including careful *a priori* development of ecological models from literature describing plant-environment relationships (Appendix A). I used mixed linear models (PROC MIXED, SAS Institute 1999) to model relationships between variables, with an "unstructured" correlation structure to address spatial autocorrelation between lateral zones within a zero-order basin. Values for environmental parameters were averaged for each lateral zone. The response for all models was NMS axis score, in standard deviates from axis centroids, an index of an experimental unit's (i.e. lateral zone's) position in plant assemblage-space. The *a priori* model set used for the three ordination axes included 17 ecological models and two covariate models (Appendix B). Because ecological models were not hierarchically nested (Burnham and Anderson 2001), I developed a single global model containing the majority of the uncorrelated parameters used in each model set, to assess model fit and overdispersion for the model set. A null model, a model with only an intercept and no explanatory variables, was included to determine if any of the collected variables gave better fit to the response (axis score) than consideration of the response mean alone.

Since no prior studies of plant composition in zero-order basins had been performed from which to draw inference, I had only moderate confidence in my *a priori* ecological models. Therefore, after completing *a priori* model selection and ranking, I performed *a posteriori* analysis on the data set to place *a priori* results in context, and to develop hypotheses for future research. *A posteriori* models used the top 10 parameters correlated with axis scores for each axis, plus any additional terms appearing in models within 2 AIC units of the best models in analysis of the *a priori* model set. Final *a posteriori* models included all one-parameter models, as well as the top 50 two-parameter models, the top 50 three-parameter models and the top 50 four-parameter models, as judged by model R^2 values. For *a posteriori* analysis for each axis, *a posteriori* sets were combined with *a priori* sets to form a final combined (full) model set. Final full model sets included 164 models for Axis 1, and 163 models for Axis 2 and Axis 3.

Ranking of empirical models and model inference

For each model set, I used Akaike's Information Criterion (AIC), an estimate of Kullback-Liebler distance (the loss of information when a model is used to approximate truth), for model selection and ranking (Burnham and Anderson 1998). I used the second-order version of AIC, AICc, to address the moderately small sample size (N = 375). The model with the smallest AICc value was judged the best approximation for the information in the data, relative to the models considered. The statistic ΔAICc measured the difference between the AICc value for a given model and the model with the lowest AICc value in the set. Models within 2 AICc units of the best approximating model (ΔAICc ≤ 2) were considered reasonable competitors with the best model, and were interpreted. Models with ΔAICc > 2 were considered unlikely to be the best fit to the data in the model set. Additionally, ΔAICc values were used to compute Akaike weights (*w*), estimates of the relative likelihood of each model, given the likelihood of the full set of candidate models (Burnham and

Anderson 2001). Models with ΔAICc ≤ 2 were investigated for model fit by evaluating their generalized coefficients of determination (Nagelkerke 1991), and by comparison of best models to the rank of the null model.

I compared the relative importance of model parameters in predicting ordination scores by comparing coefficient ranges (inclusive 95% confidence intervals) and coefficient directions of effect in models with ΔAICc ≤ 2, and by computing parameter predictor weights (Burnham and Anderson 2001), indicators of the importance of individual parameters in predicting response considering the entire model set. Predictor weights were calculated by summing the Akaike weights of all models in which a parameter occurred, adjusted to account for unbalanced model sets (Stoddard 2001) and normalized to sum to 1.0. I used the full model sets for calculation of parameter predictor weights, for all parameters within the set of models whose cumulative (summed) model weights (*w*) were ≤ 0.995 ("0.995 cumulative model weight", hereafter) for each model set.

Direct gradient analysis: plant species in environment-space

I performed a direct gradient analysis (Brazner and Beals 1997) of plant species in environment-space to compare to results of the indirect gradient analysis of lateral zones in species-space. This allowed me to determine how key environmental parameters observed in indirect analysis acted on species cover and composition. Direct gradient analysis allows direct exploration of species-environment relationships, but it requires the assumption that all environmental parameters used in the analysis are important in determining species composition. For this analysis, I averaged species cover and environmental variables for each geomorphic surface zone in each zero-order basin (Figure 2.3). The plant species matrix included covers of 104 species in 252 experimental units (geomorphic surfaces within zero-order basins). The environmental matrix used variables that were important in indirect gradient analysis. A general relativization was applied to environmental parameters to address different units between parameters. Following matrix multiplication, I relativized species values to reduce the coefficient of variation. I used nonmetric multidimensional scaling (NMS) as the ordination technique, using software in PC-ORD (McCune and Mefford 1997), similarly to indirect gradient analysis. The final ordination was rotated to maximize correlations between the first axis and the single most highly correlated environmental variable. Correlations between ordination scores and environmental parameters were used to define the strongest gradients in plant-species relationships.

Plant species classifications

I developed three classifications of plant species in zero-order basins: vegetation types, geomorphic surface zone assemblages and lateral zone assemblages

(Figure 2.3). Vegetation types, groups of plots with similar species composition, were developed to analyze environmental conditions associated with groups of species and to identify groups useful for rapid assessment and management of plant assemblages in zero-order basins. Species assemblages associated with both geomorphic and lateral zones were identified to quantify the effects of geomorphic and lateral gradients on plant species occurrence in geomorphic and lateral zones in basins, and to contrast the utility of geomorphic and lateral typologies in describing plant composition.

Vegetation types

Vegetation types, based on similarities in plant species composition, were developed to simplify the complex and continuous variation in plant composition. Hierarchical cluster analysis with relative Euclidian distance and Ward's linkage method in PC-ORD (McCune and Mefford 1997) was used to group experimental units (lateral zones in basins) into seven vegetation types. The total number of types was restricted to seven, because it was a parsimonious compromise between group number and group distinction, and appeared to best represent the number of assemblages observed in the field.

I used indicator species analysis (Dufrene and Legendre 1997) to assign individual species to vegetation types and to quantify the strength of association between individual species and the seven vegetation types. Indicator species analysis combines information on the abundance of a species in a group with consistency of occurrence of the species in that group to provide indicator values, the percent of perfect indication of a species for each class in a typology, ranging from 0 (no indication) to 100 (perfect indication). Maximum indicator values are the indicator value for the class the species was most strongly associated with in a typology. I evaluated the statistical significance of the maximum indicator value of each species with its associated vegetation type, using a Monte Carlo method with 2000 iterations (PCORD, McCune and Mefford 1997). For representation, I assigned each plant species to the vegetation type for which it was the best indicator. However, vegetation types were not mutually exclusive in the field; not all species in a vegetation type would be expected to occur in a plot assigned to that type. In addition, a given species might occur in plots typed to several different vegetation types.

For each species, I estimated its average cover in each lateral zone across basins, as well as the average cover for the study area. I calculated the percent of experimental units in each lateral zone assigned to each vegetation type, as well as the percent of all experimental units assigned to each type. I named vegetation types using the genus name of the species with the highest maximum indicator value for that type. Means for key environmental parameters were calculated for experimental units in each of the seven vegetation types, to characterize environmental conditions associated with each vegetation type.

Geomorphic and lateral zone species assemblages

I identified plant species assemblages in geomorphic surface zones and finer-resolution lateral distance zones, to compare the effects of geomorphic and lateral gradients in zero-order basins on plant species composition. I compared plant assemblages associated with geomorphic surface zones (valley, headmost, slope and ridge) with assemblages associated with lateral zones (0 m, 1 m, and 5 m from basin center, in addition to headmost, slope and ridge zones), using indicator species analysis (Dufrene and Legendre 1997). Indicator species values were calculated for each species, for each zone in each typology. The statistical significance of maximum indicator values were evaluated using a Monte Carlo method with 2000 iterations. Mutually exclusive plant species assemblages were created for each zone in each typology, by considering only species whose maximum indicator values were significantly higher than values from Monte Carlo simulations at the 0.05 level, similarly to Warnke (1998).

I compared the effectiveness of geomorphic surface and lateral zone typologies at describing plant-environment relationships, both to each other and to vegetation type classifications. I compared the sum of indicator values for all species for each class, the number of species associated with each zone or type, and the number of species in each stratum whose maximum indicator values were significantly higher than random expectation ($p \leq 0.05$). For the geomorphic surface and lateral zone typologies, I compared the results from a multi-response permutation procedure (MRPP) (Mielke 1984). MRPP is a non-parametric technique to test the hypothesis of no significant difference between groups. I used MRPP in PC-ORD (McCune and Mefford 1997) with Sorenson distance and a rank transformation. Size of the effect of geomorphic and lateral zones on species composition was estimated using the chance-corrected within-group agreement (*A*), an estimate of within-group homogeneity compared to random expectation. When all items in a group are identical, *A* has its highest value (1.0). Results of MRPP for geomorphic surface and lateral zone typologies were compared to each other, to the effect of zero-order basins (pseudoreplication effect), and to several covariates. MRPP could not be applied to vegetation type classifications, because the species matrix to be tested was used to generate the vegetation type classifications.

Plant diversity in zero-order basins

I estimated plant species richness and diversity using three indices (N0, N1, N2) proposed by Hill (1973). N0 was calculated as species richness, N1 was calculated as exp(-Shannon's Index) and N2 was calculated as the reciprocal of Simpson's Index. For these analyses, 35 samples not identified to species were removed, leaving 138 plant species. The number of plots in each lateral zone was standardized for each lateral zone in each basin by randomly deleting plots, to provide exactly two plots per lateral zone per zero-order basin. Plant cover was averaged for each lateral zone in each basin.

Shrubs in zero-order basins

Several researchers (Hibbs and Giordano 1996, Pabst and Spies 1998) have documented the dominance of shrubs in Oregon Coast Range headwater riparian forests, suggesting that tall shrubs in Coast Range riparian areas represent an important biotic control over both herb composition and tree regeneration. I hypothesized that shrubs might play an important role in structuring plant assemblages in zero-order basins as well. I therefore analyzed shrub species independently, in addition to their inclusion in the previous forest floor analyses. For the independent analysis of shrub characteristics, I averaged shrub cover for each geomorphic surface zone in each zero-order basin, considering only species defined as shrubs by Garrison and Skovlin (1976). I estimated cover means and confidence intervals for each shrub species, by geomorphic surface. I also subjectively assigned shrub species to one of three moisture classes (wet, mesic, dry), based on their assignments to vegetation types with average surface moistures of > 2 (wet), 1.5-2 (mesic) or < 1.5 (dry), then estimated means and confidence intervals for these shrub moisture classes.

RESULTS

Geomorphic and overstory characteristics in zero-order basins

There were an average of 11.5 initiation points of first-order streams per kilometer, and each first-order system contained one to two zero-order basins (Table 2.2), suggesting a density of 18 zero-order basins per km^2 in the study area. Areas contributing to the initiation point of scour and deposition in zero-order basins were about one ha in size, and entire zero-order basins made up less than one percent of the landscape in the study area. Basins in the study area were steeper and narrower than larger riparian drainages observed downstream. Headmost and slope surfaces dominated basins: valley floor widths were < 5 m wide, accounting for 2% of the total surface area (Table 2.2). Slope surfaces averaged over 50 m in length, with slope plots established an average of 24 m (95% CI: 21.8, 26.6) from basin center. Convergent surfaces (valleys and headmost areas) were the most fluvially active. Fluvial disturbance, defined as > 25% cover by large substrates, and $\geq$ 25% of plot surfaces showing some scour, occurred primarily in valley surfaces and occasionally in headmost areas (Table 2.4).

Table 2.4. Selected environmental characteristics for zero-order basins (n=63). Values were calculated from plot data, averaged for each geomorphic surface (with 95% confidence intervals (CI)). "Fluvially disturbed" was defined as > 25% cover by large substrates, and $\geq$ 25% of surfaces showing some scour.

Parameter	**Valley**	**Headmost**	**Slope**	**Ridge**
Gradient (°)	25.9 (24.7, 27.2)	32.5 (30.8, 34.2)	33.2 (32.1, 34.3)	27.6 (25.3, 29.8)
Litter depth (cm)	0.33 (0.27, 0.38)	1.19 (1.05, 1.33)	1.34 (1.22, 1.46)	1.7 (1.5, 1.9)
Fluvially disturbed (%)	71.4	11.1	0	0
Downed wood volume (m^3/ha)	1010.0 (540.7, 1479.3)	449.0 (258.7, 639.3)	501.7 (316.8, 686.6)	135.4 (64.7, 206.2)

Coniferous tree species had the highest densities and basal areas in all geomorphic surfaces (Table 2.5). Douglas-fir and western hemlock had the highest overall basal areas, followed by western red cedar. Douglas-fir and western hemlock achieved their highest basal areas in ridge geomorphic surfaces, followed by slope areas. Western red cedar was the only conifer that had highest basal area in valley surfaces.

Densities of hardwood species were low (Table 2.5), with the most common being big-leaf maple in slope and headmost areas. Upper slopes and ridges also supported hardwoods, principally California bay and big-leaf maple.

Table 2.5. Mean overstory tree basal area (m^2/ha) (with 95% CI) for geomorphic surfaces in zero-order basins (n=63). Results are ordered by decreasing basal area.

Tree species	Valley	Headmost	Slope	Nose	Basin means
Douglas fir	26.0 (22.6, 29.4)	37.9 (33.7, 42.2)	42.5 (37.4, 47.6)	56.7 (51.1, 62.3)	40.0 (37.6, 42.5)
Western hemlock	13.2 (10.3, 16.0)	19.3 (15.8, 22.8)	21.0 (17.2, 24.8)	24.1 (19.8, 28.4)	19.2 (17.3, 21.0)
Western red-cedar	6.2 (4.6, 7.9)	4.8 (2.7, 6.8)	5.1 (3.2, 7.0)	3.0 (1.7, 4.3)	4.8 (3.9, 5.7)
Big-leaf maple	3.1 (1.7, 4.5)	3.5 (2.0, 5.0)	4.2 (2.5, 5.8)	1.6 (0.7, 2.6)	3.1 (2.4, 3.8)
California bay	1.1 (0.4, 1.8)	2.3 (1.2, 3.4)	3 (1.6, 4.4)	2.9 (1.6, 4.3)	2.3 (1.7, 2.8)
Red alder	1.6 (0.7, 2.4)	1.6 (0.7, 2.5)	1.4 (0.4, 2.5)	1.4 (0.4, 2.4)	1.5 (1.1, 2.0)
Chinkapin	0.2 (-0.1, 0.6)	0.4 (0, 0.9)	0.7 (0.1, 1.3)	0.9 (0.2, 1.5)	0.5 (0.3, 0.8)
Incense cedar	0.1 (-0.1, 0.2)	0	0.5 (-0.3, 1.3)	0.7 (-0.3, 1.8)	0.3 (0, 0.6)
Yew	0.2 (-0.1, 0.6)	0.1 (-0.1, 0.2)	0.3 (-0.1, 0.1)	0.2 (-0.2, 0.5)	0.2 (0.0, 0.3)
Vine-maple	0	0.1 (-0.1, 0.2)	0.2 (-0.1, 0.4)	0.1 (-0.1, 0.3)	0.1 (-0.1, 0.2)
Madrone	0	0	0	0.1 (-0.1, 0.3)	0.0 (-0.0, 0.1)
Scouler's willow	0	0	0	0.1 (-0.1, 0.3)	0.0 (-0.0, 0.1)
Tanoak	0	0	0	0.1 (-0.1, 0.2)	0.0 (-0.0, 0.1)

Red alder, a common riparian species in larger-order riparian corridors, was a minor component of zero-order basins. Red alder had similar basal area coverage across the four geomorphic surfaces.

There were significant differences in tree densities between geomorphic surfaces, and they appeared to follow a gradient of decreasing fluvial/hillslope disturbance, from valleys upslope through ridge surfaces (Table 2.6). Overstory relative density was significantly different between geomorphic surfaces ($F_{3/62} = 35.2$; $p < .0001$), and between surfaces considering only trees rooted in the geomorphic surface being measured ($F_{3/62} = 116.4$; $p < .0001$). The relative density of trees within valley areas was approximately 12 relative density units lower than headmost areas (Table 2.7). Headmost areas and slope areas did not differ ($p > 0.05$) in their relative densities, although headmost areas had fewer trees per hectare. Considering only trees rooted in the geomorphic surface being measured, headmost areas had relative densities 11 units lower than slope areas. The relative density of slope areas was approximately 10 units lower than ridge areas, however slope surfaces had similar densities to ridge surfaces considering only trees rooted in the geomorphic surface being measured.

Table 2.6. Metrics of overstory density (95% CI) for four geomorphic surfaces (n = 63) and entire zero-order basins (n = 252). BA = basal area (m^2/ha), RD = relative density.

Overstory metric	**Valley**	**Headmost**	**Slope**	**Ridge**	**Basin means**
Total BA (m^2/ha)	55.2 (48.8, 61.6)	72.1 (65.9, 78.2)	79.8 (72.7, 86.9)	93.3 (86.2, 100.3)	75.1 (71.4, 78.8)
BA of trees > 70 cm (m^2/ha)	36.1 (30.9, 41.2)	47.8 (41.5, 54.0)	51.3 (45.1, 57.4)	59.6 (51.7, 67.4)	48.7 (45.4, 52.0)
Relative density (RD)	38.7 (33.9, 43.4)	50.8 (46.5, 55.1)	55.4 (50.6, 60.2)	66.1 (61.2, 71.0)	52.7 (50.1, 55.3)
RD within geomorphic surfaces	4.5 (2.5, 6.5)	40.0 (35.3, 44.6)	51.0 (45.7, 56.4)	46.5 (41.5, 51.5)	35.5 (32.4, 38.7)
RD hemlock	14.2 (9.4, 18.9)	17.7 (13.3, 22.1)	21.5 (16.6, 26.5)	24.3 (19.1, 29.5)	19.4 (17, 21.8)
RD conifers	33.9 (28.6, 39.2)	43.1 (38.4, 47.8)	47.8 (42.4, 53.1)	59.8 (54.5, 65.2)	46.1 (43.3, 48.9)
RD hardwoods	6.1 (3.9, 8.2)	9.3 (5.9, 12.8)	10.1 (6.7, 13.6)	8.6 (6.0, 11.3)	8.5 (7.1, 10.0)
Canopy cover (%)	73.2 (69.6, 76.9)	78.4 (74.7, 82.1)	79.2 (75.8, 82.5)	85.5 (81.4, 89.6)	79.1 (77.2, 81.0)
Conifer canopy cover (%)	46.7 (38.6, 54.8)	53.7 (46.5, 61.0)	53.9 (46.8, 61.0)	64.2 (57.2, 71.2)	54.6 (50.9, 58.3)
Hardwood canopy cover (%)	26.7 (19.4, 34.2)	25.8 (19.3, 32.4)	25.9 (19.0, 32.7)	22.4 (16.0, 28.8)	25.2 (21.9, 28.5)
Trees per hectare	274.4 (219.4, 329.4)	296.9 (251.9, 341.8)	412.8 (336.9, 488.7)	497.6 (416.7, 578.4)	370.4 (336.3, 404.5)
Quadratic mean diameter	37.9 (35.3, 40.5)	38.5 (36.3, 40.6)	40.2 (38.5, 42.0)	38.6 (36.6, 40.5)	38.8 (37.7, 39.8)

Table 2.7. Differences in relative density (RD) of overstory trees between different geomorphic surfaces (n=63). Differences in overstory tree relative density between geomorphic surfaces (95% CI) (left). Differences in overstory tree relative density between geomorphic surfaces (95% CI), considering only trees rooted in the geomorphic surface measured (right). Student's T statistic and p-values are shown.

	Relative density differences between geomorphic surfaces			**Relative density differences between geomorphic surfaces considering only trees rooted in geomorphic surface**		
Contrast	**Estimate**	**T**	**p≤**	**Estimate**	**T**	**p≤**
Valley - Headmost Area	-12.130 (-18.668, -5.592)	-3.65	0.001	-35.45 (-40.64, -30.26)	-13.65	0.0001
Headmost Area - Slope	-4.626 (-11.164, 1.912)	-1.39	0.165	-11.08 (-17.10, -5.10)	-3.7	0.0005
Slope - Ridge	-10.674 (-17.212, -4.136)	-3.22	0.002	4.53 (-0.83, 9.9)	1.69	0.10

Canopy cover was similar among geomorphic surfaces, although tree relative density was much lower in valleys than in surrounding slope and headmost areas (Table 2.6). The lack of differences in canopy cover between geomorphic surfaces may have been due to the contribution of shrub species over two meters in height (e.g., vine maple) to canopy cover estimates in gap areas, or to the much narrower lateral extents of canopy cover gaps associated with the most fluvially-active portions of valley surfaces in zero-order basins, in comparison to floodplains of higher-order drainages.

Herbaceous and shrub species

I collected forest floor plant species cover data on 138 confirmed plant species, including 111 herb (forb and graminoids), 21 shrub, and six seedling tree species (Table 2.8). Sword fern (*P. munitum*) had the highest cover at 19% (Table C1, Appendix C); redwood sorrel (*O. oregana*) had the second highest cover at 17%. The 0 m and 1 m lateral zones were dominated by *O. oregana*, and *P. munitum* dominated the 5 m, slope, headmost and ridge zones.

Table 2.8. Forest floor herb, shrub and seedling tree richness in each geomorphic/ lateral zone in unmanaged zero-order basins. N = 63 basins.

Geomorphic/ lateral zone	Number of plots	Number of herb species	Number of shrub species	Number of seedling tree species
0 m	295	77	17	4
1 m	196	73	15	3
5 m	192	73	18	5
Slope	127	58	16	3
Headmost	176	60	18	5
Ridge	127	55	16	2
Totals	1113	111	21	6

Indirect gradient analysis

Indirect gradient analysis identified several distinct patterns in plant species composition (Figure 2.4). Stress for a three-dimensional ordination was 17.05, lower than random expectation ($p = 0.048$) and considered "interpretable" under the stringent criteria developed by Clarke (1993). Correlations between the three axes and the original 45-dimensional space were 0.439, 0.188 and 0.180, respectively.

After rotation to maximize correlations between Axis 1 and the single most highly correlated variable (stability), parameters for stability, distance from basin center and cover by organic substrates had the strongest positive correlations with scores on Axis 1 (Table 2.9, Figure 2.5). Fluvial and hillslope disturbance measures such as surface moisture, deposition, large substrate and scour were negatively correlated with scores on Axis 1 (Table 2.9, Figure 2.5). Axis 2 represented a

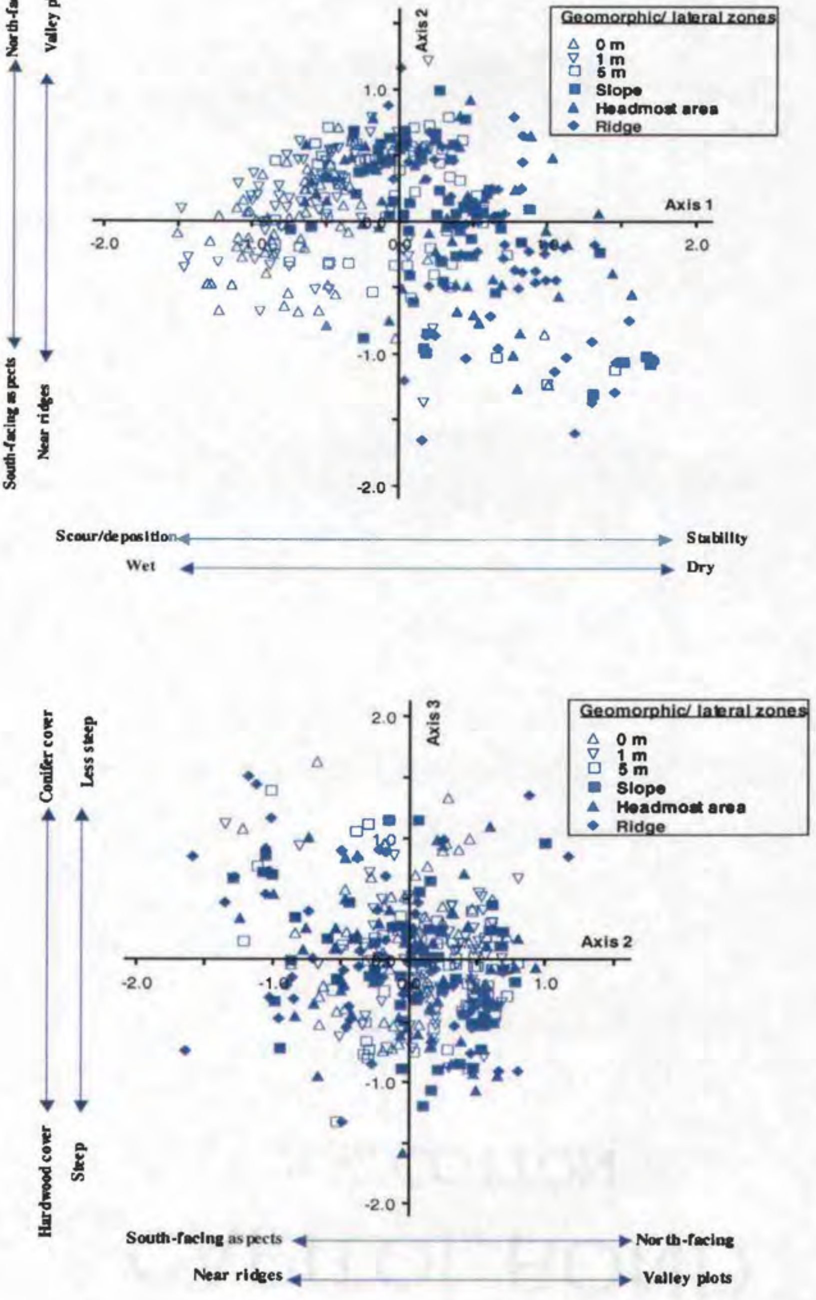

Figure 2.4. Ordination of experimental units in plant species space, for 3 ordination axes (n=375). Experimental units (points) represent plots averaged for each geomorphic/lateral zone in each basin. Geomorphic/lateral zone membership overlain on experimental units. Directional arrows indicate important environmental gradients identified through correlation analysis and mixed linear model results.

Table 2.9. Spearman's rank correlation coefficients (r) and summed coefficients of determination (R^2) between environmental parameters and axis scores from an ordination of lateral zones in plant species-space. Parameters ordered by summed R^2 values for the three ordination axes. Only parameters with correlations significant at $p \leq 0.001$ for at least one axis are shown. "ns" represents non-significance.

Environmental parameter	Axis 1	Axis 2	Axis 3	Summed R^2
Stability	0.669	ns	ns	0.448
Organic substrate	0.585	-0.123	0.148	0.379
Large substrate	-0.521	ns	-0.303	0.363
Deposition	-0.576	ns	ns	0.332
Relative density within geomorphic surfaces	0.566	ns	ns	0.320
Litter depth	0.535	ns	-0.158	0.311
Surface moisture	-0.532	ns	0.166	0.310
Conifer canopy cover	0.300	0.141	0.427	0.292
Distance from center	0.529	ns	ns	0.280
Relative density of hemlock	0.308	ns	0.421	0.272
Scour	-0.508	-0.108	ns	0.270
Relative density	0.476	0	0.170	0.256
Basin depth	-0.477	0.166	ns	0.256
Hardwood canopy cover	-0.158	-0.195	-0.401	0.224
Relative density of hardwood	ns	ns	-0.471	0.222
Plot height	0.466	ns	ns	0.217
Basin gradient	-0.183	ns	-0.416	0.206
Elevation	0.195	-0.123	0.389	0.204
Ocean distance	0.168	ns	0.417	0.202
Canopy cover	0.402	ns	ns	0.162
Large substrate	0.323	0.045	0.231	0.159
Ridge distance	-0.332	0.133	ns	0.128
Heat load index	0.211	-0.228	0.156	0.121
Basin area	ns	-0.232	ns	0.054

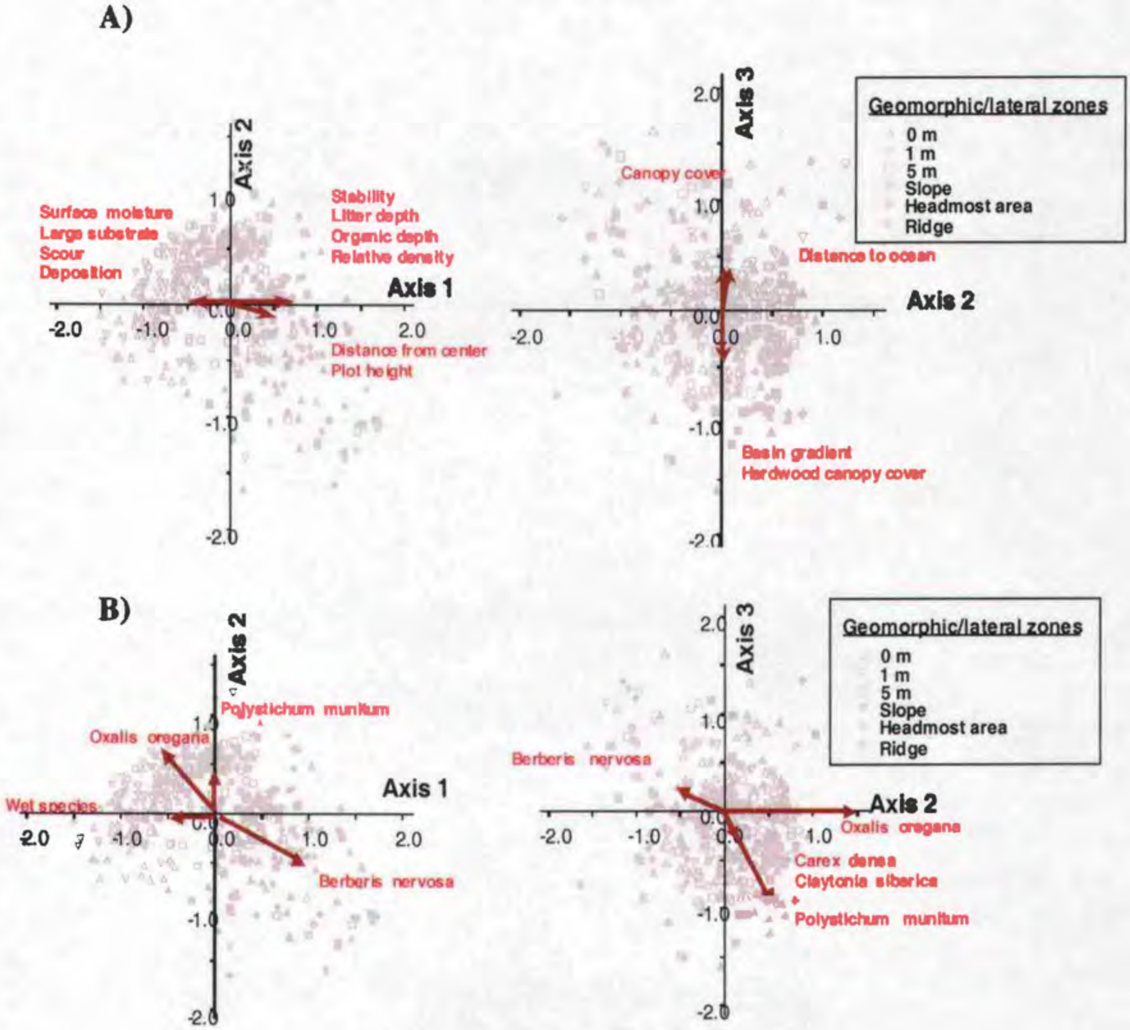

Figure 2.5. Joint plots of environmental variables and cover of plant species for an indirect ordination of lateral zones in species-space. Joint plots only depicted for parameters with $R^2 > 0.15$. Experimental units shown in gray. **A)** Correlations between environmental variables and axis scores. **B)** Correlations between individual plant covers and axis scores. "Wet species" included *Tolmiea menziesii*, *Adiantum pedatum*, *Mitella ovalis*, *Athyrium felix-feminosa*, *Mimulus dentatus* and *Blechnum spicants*.

complex gradient, weakly related to position within the basin. Correlations between environmental variables and scores on Axis 2 were relatively low, with the highest positive correlation with basin depth and the highest negative correlation with heat load index. Axis 3 represented a weak gradient in species composition related to overstory characteristics (Table 2.9, Figure 2.5). Correlations between environmental variables and scores on Axis 3 were also relatively low, including positive correlations with canopy cover of conifers and negative correlations with canopy cover of hardwoods and basin gradient.

Gradients in plant species composition across lateral zones in zero-order basins were most clear along Axis 1 (Figure 2.4). Along Axis 1, slope and ridge zones were associated with drier and more stable portions of ordination space, 0 m and 1 m zones with wetter and more disturbed ordination spaces, and 5 m and headmost zones were intermediate. Axes 2 and 3 did not clarify relationships between lateral zones.

In addition to consideration of environmental parameters and lateral zones, I investigated relationships between cover by individual plant species and species composition in experimental units (Figure 2.5). On Axis 1, cover of *Berberis nervosa* was positively correlated with axis position (r = 0.55); units with high *B. nervosa* cover thus also had high stability and low surface moisture. Cover of wet species like *Mitella ovalis* were negatively correlated with Axis 1 position (r = -0.61), and associated with zones with low stability and high surface moisture. Axis 2 helped differentiate between mesic species like *O. oregana* (r = 0.39) and drier species like *B. nervosa* (r = -0.41), although correlations with measured variables were very weak (Table 2.9). Axis 3 differentiated dry species associated with high conifer cover like *Rhododendron macrophyllum* (r = 0.24) and *B. nervosa* (r= 0.25) from mesic species associated with more open, steeper areas like *P. munitum* (r = -0.41), *Carex densa* (r = -0.30) and *Claytonia siberica* (r = -0.34).

AICc models of indirect gradient analysis axis scores

For the developed models of ordination axis score as a function of measured environmental parameters, global models for each of the three axes had moderate fit, with centered residuals and relatively constant variance. Axis 1 *a priori* ecological models had the best model fit, consistent with the strong correlations between Axis 1 scores and individual environmental parameters (Table 2.9). Axes 2 and 3 had weaker correlations with individual environmental parameters, and *a priori* ecological models had weaker fit.

Axis 1 results

Scores on Axis 1 were best predicted by ecological models supporting multiple environmental parameters (Table 2.10). The most parsimonious *a priori*

Table 2.10. Results of model selection and ranking using AICc on sets of mixed linear regression models predicting ordination score on Axis 1 as a function of environmental parameters (n=375). Models are ordered by increasing ΔAICc within *a priori* or full model sets. Only models with ΔAICc ≤ 2 are depicted. "X" represents parameters used in models, "-" represents negative direction of effect. k = the number of parameters in a model. *w*= Akaike model weight. "Cumul prob" represents the summed Akaike model weights for a model and all better models. Model fit statistics include the generalized coefficient of determination (R^2), as calculated in Nagelkerke (1991). "Range of parameter" represents the range of values taken by a parameter in the data set. Parameter predictor weights defined in methods.

		Parameters							**Model ranking / Model fit**				
Model no.	**Rank**	**Distance from center**	**Organic substrate**	**Geomorphic surface**	**Heat load index**	**Large substrate**	**Canopy cover**	**Surface moisture**	**k**	**ΔAICc**	***w***	**Cumul prob**	**R^2**
***A priori* set**													
AX15	1			*X*	*X*		*X*	*-X*	6	**0 *** **(11.50)**	**0.999**	-	0.577
Full *(a priori* and *a posteriori*) set													
1AX124	1	*X*	*X*	*X*	*X*				6	0.000	0.251	0.251	0.597
1AX130	2	*X*		*X*	*X*	*-X*			6	0.452	0.201	0.452	0.594
1AX115	3		*X*	*X*	*X*		*X*		6	0.733	0.174	0.626	0.608
1AX114	4		*X*	*X*	*X*			*-X*	6	1.992	0.093	0.719	0.605
Coefficient Range		0.003 to 0.009	0.004 to 0.009	-1.850** to 0.722	0.170 to 0.584	-0.009 to -0.004	0.002 to 0.007	-0.099 to -0.043					
Range of Variable		0-194 m	0-100%	4 categories	0-1.0	0-100%	0-100%	1-7					
Parameter predictor weights		**0.278**	**0.173**	**0.124**	**0.122**	**0.077**	**0.073**	**0.050**					

* Values presented for *a priori* set, as well as for the full (*a priori* and *a posteriori*) set (in parentheses).

** Geomorphic surface is a categorical variable. Value range given for intercept, instead of parameter coefficient.

model describing Axis 1 ordination scores (AX15; Table B1, Appendix B) was a multiple factor ecological model including a categorical term for geomorphic surface and continuous terms for heat load index, canopy cover, and surface moisture (Table 2.10). This model was over 23 AICc units from its closest competitor, and was approximately 1000 times more likely to be the best fit to the data in the *a priori* model set, based on model weight. The stability parameter was not included in the best models for Axis 1 (Table 2.10), even though it was the single parameter most highly-correlated with Axis 1 score (Table 2.9). For model AX15 geomorphic surface, a categorical parameter, had the strongest effect on plant species composition (position along Axis 1), after accounting for other parameters in the model (Table 2.10). The generalized coefficient of determination (generalized R^2, hereafter) for model AX15 was 0.577. For the *a priori* model set, the null model (AX0, Table 2.B1) was ranked 19th out of 21 (ΔAICc = 139.14), suggesting that parameters in the best model had relatively high predictive power.

The four top *a posteriori* models shared two parameters with model AX15: geomorphic surface and heat load index (Table 2.10). Results for parameter predictor weights were complementary to model ranking results. The 27 models within the 0.995 cumulative model weight for the full model set describing Axis 1 supported 11 parameters (Table 2.11). Geomorphic surface zone, heat load index, mean distance from basin center, and cover by organic substrates were the four most important parameters for prediction of plant composition (Axis 1 score), considering parameter predictor weights

Table 2.11. Parameter predictor weights for environmental parameters used in models describing ordination axis scores. Results use full model sets, for all parameters within the 0.995 cumulative model weight, for each of 3 axes. "Number of models" is the number of models in the full model set supporting each parameter. "Parameter predictor weight" represents the relative utility of a parameter in predicting the response (axis score).

Parameter	Number of models	Parameter predictor weight[1]
Axis 1		
Distance from basin center	6	0.278
Organic substrates	15	0.173
Geomorphic surface	26	0.124
Heat load index	19	0.122
Large substrates	10	0.077
Deposition	3	0.074
Canopy cover	7	0.073
Surface moisture	5	0.05
Litter depth	2	0.012
Basin area	2	0.009
Basin gradient	2	0.008
Axis 2		
Plot height	11	0.341
Heat load index	19	0.222
Distance from ridge	11	0.159
Organic depth	11	0.147
Distance from basin center	8	0.069
Basin area	5	0.038
Geomorphic surface	4	0.024
Axis 3		
Conifer canopy cover	14	0.223
Surface moisture	18	0.198
Basin gradient	19	0.188
Distance from coast	20	0.177
Geomorphic surface	3	0.046
Geologic formation	2	0.038
Hardwood canopy cover	1	0.035
Litter depth	5	0.031
Disturbance due to harvest	2	0.024
Disturbance due to roads	6	0.016
Organic substrate	1	0.012
Large substrates	2	0.010

[1] Parameter predictor weights were standardized for number of models with each parameter and normalized to sum to 1.0 (Stoddard 2000).

Axis 2 results

Axis 2 scores in the ordination of experimental units in plant species-space were best described by *a priori* ecological models with parameters related to position in the basin, judged by AICc values (Table 2.12). For Axis 2, two models had ΔAICc < 2. The best *a priori* model (AX9, Table B1, Appendix B) was only 1.11 times more likely than its closest competitor to be the best fit to the data, based on model weights. AX9 was a univariate model with a term for the negative effect of heat load index (Table 2.12). The second-best model (AX7: ΔAICc = 0.214) had a positive term for distance from ridge, and a negative term for distance from basin center. Heat load index had the strongest effect on Axis 2 score. The null model (AX0) ranked third out of 21 models (ΔAICc = 7.16), and two best models had generalized R^2 values less than 0.08, suggesting poor fit of the best models to the data.

The best *a posteriori* models shared two parameters from the best *a priori* models: a negative term for heat load index and a positive term for plot height above stream. The 25 models within the 0.995 cumulative model weight for Axis 2 supported seven parameters (Table 2.11). Based on analysis of parameter predictor

Table 2.12. Results of model selection and ranking using AICc on sets of mixed linear regression models predicting ordination score on Axis 2 as a function of environmental parameters (n=375). Models are ordered by increasing ΔAICc within *a priori* or full model sets. Only models with ΔAICc ≤ 2 are depicted. "X" represents parameters used in models, "-" represents negative direction of effect. k = the number of parameters in a model. *w*= Akaike model weight. "Cumul prob" represents the summed Akaike model weights for a model and all better models. Model fit statistics include the generalized coefficient of determination (R^2), as calculated in Nagelkerke (1991). "Range of parameter" represents the range of values taken by a parameter in the data set. Parameter predictor weights defined in methods.

		Parameters					**Model ranking**				**Model fit**
Model no.	**Rank**	**Plot height**	**Heat load**	**Ridge distance**	**Organic depth**	**Distance from center**	**k**	**ΔAICc**	***w***	**Cumul prob**	**R^2**
***A priori* set**											
AX9	1		*-X*				**2**	0.000* (9.380)	0.497	0.497	0.071
AX7	2			*X*		*X*	**3**	0.214* (9.594)	0.447	0.944	0.065
Full *(a priori* and *a posteriori*) set											
2AX9	1	*-X*	*-X*				**3**	0.000	0.277	0.277	0.120
2AX31	2	*-X*	*-X*	*X*			**4**	0.450	0.221	0.498	0.130
2AX27	3	*-X*	*-X*		*-X*		**4**	0.863	0.180	0.677	0.140
Coefficient range		-0.019 to -0.007	-0.589 to -0.120	0.003 to 0.280	-0.090 to -0.011	-0.008 to -0.004					
Range of parameter		0-76 m	0-1.0	0.0-3.0	0-15 cm	0-194 m					
Parameter predictor weights		**0.341**	**0.222**	**0.159**	**0.147**	**0.069**					

* Values presented for *a priori* set, as well as for the full (*a priori* and *a posteriori*) set (in parentheses).

weights, plot height, heat load index, distance from ridge and depth of organic material were the most important parameters for predicting Axis 2 score. These complementary results provided support for relatively simple position models including parameters for plot height and heat load index, among the models tested. However, models for Axis 2 (including the global model) had weak fit in general, and Axis 2 explained little of the variation in the original ordination space, suggesting low utility for even the best models.

Axis 3 results

For the *a priori* set of ecological models describing Axis 3 ordination scores, a single model (AX10, Table B1, Appendix B) had ΔAICc ≤ 2. This best model was over six times more likely than its closest competitor to be the best fit to the data in the *a priori* model set. This model included a single term for the negative effect of basin gradient. The null model was ranked 10th out of 21 (ΔAICc = 13.69) and the generalized $R^2 = 0.15$ for model AX10, suggesting only moderate fit of this best model to the data.

For the full model set, a single best *a posteriori* model emerged (3AX114, Table 2.13). In addition to a negative effect of basin gradient, this model contained parameters for positive effects of conifer canopy cover, surface moisture and distance from ocean. Based on analysis of parameter predictor weights for the 12

Table 2.13. Results of model selection and ranking using AICc on sets of mixed linear regression models predicting ordination score on Axis 3 as a function of environmental parameters (n=375). Models are ordered by increasing ΔAICc within *a priori* or full model sets. Only models with ΔAICc $\leq$ 2 are depicted. "X" represents parameters used in models, "-" represents negative direction of effect. k = the number of parameters in a model. *w*= Akaike model weight. "Cumul prob" represents the summed Akaike model weights for a model and all better models. Model fit statistics include the generalized coefficient of determination (R^2), as calculated in Nagelkerke (1991). "Range of parameter" represents the range of values taken by a parameter in the data set. Parameter predictor weights defined in methods.

		Parameters				**Model ranking**				**Model fit**
Model no.	**Rank**	**Conifer Canopy Cover**	**Surface Moisture**	**Basin Gradient**	**Distance from Ocean**	**k**	**ΔAICc**	***w***	**Cumul prob**	**R^2**
A priori set										
AX10	1			-*X*		**2**	0 * (20.773)	0.775	0.775	0.150
Full *(a priori* **and** *a posteriori)* **set**										
3AX114	1	*X*	*X*	-*X*	*X*	**5**	0	0.713	0.713	0.366
Coefficient range		0.002 to 0.005	0.039 to 0.092	-0.036 to -0.011	0.017 to 0.045					
Range of variable		0-100%	1.0 -7.0	3.5-42°	36-55 km					
Parameter predictor weights		**0.223**	**0.198**	**0.188**	**0.177**					

** Values presented for *a priori* set, as well as for the full (*a priori* and *a posteriori*) set (in parentheses) models within the 0.995 model weight for the Axis 3 model set, canopy cover of conifers, surface moisture, basin gradient and distance from ocean were the four most important model parameters for predicting Axis 3 ordination scores (Table 2.11). Like Axis 2, best models for Axis 3 were weak, suggesting low utility for the best model.

Direct gradient analysis: plant species in environment-space

Direct gradient analysis of plant species in environment-space identified changes in plant composition along stability and position gradients similar to those in indirect gradient analysis, and identified the relative importance of key environmental parameters in structuring plant species composition (Figure 2.6, Table 2.14). A two-dimensional ordination of species in environment-space had a stress value (dissimilarity) of 10.07, lower than stress in Monte Carlo randomized data ($p = 0.02$). After rotation to maximize correlation with stability (to facilitate comparison with indirect gradient analysis), Axis 1 had an $R^2 = 0.676$ with the original 16-dimensional environmental space and Axis 2 had an $R^2=0.272$ with the original space. The total correlation of both axes with the original plant-environment data was 0.948.

Of the 16 environmental parameters hypothesized to be important predictors of plant composition from results of indirect gradient analysis, parameters related

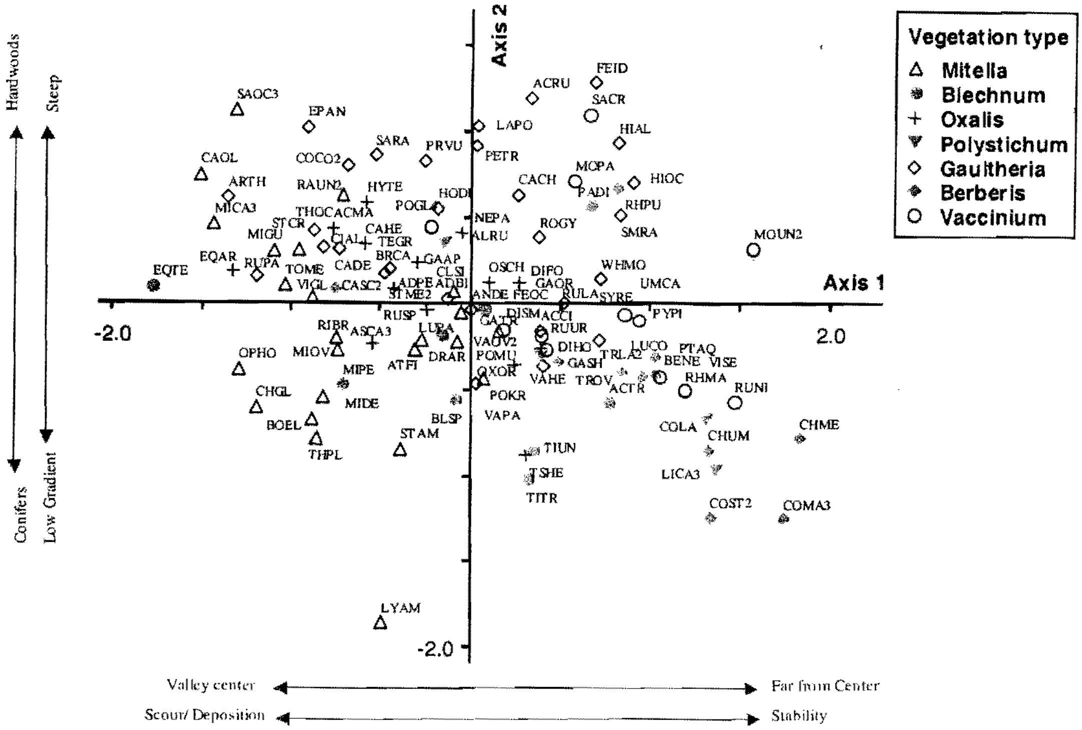

Figure 2.6. Ordination of plant species in environment-space. Points represent species. Species membership in 1 of 7 vegetation types is overlain on species points. Directional arrows indicate important environmental gradients identified from consideration of correlations between individual environmental parameters and ordination axis scores for species. See Appendix D for species codes.

Table 2.14. Spearman's rank correlation coefficients (r) and summed coefficients of determination (R^2) between 16 environmental parameters and axis scores for a direct gradient analysis of plant species in environmental-space, for 2 axes (n=104 species). "ns" represents parameters not significant at the p = 0.005 level. Parameters are ordered by coefficients for Axis 1.

Environmental parameter	Axis 1	Axis 2	Summed correlations (R^2)
Stability	0.954	ns	0.910
Relative density within geomorphic surface	0.890	ns	0.792
Distance from basin center	0.829	ns	0.687
Plot height	0.806	ns	0.650
Litter depth	0.696	ns	0.484
Organic substrate	0.630	-0.497	0.644
Organic depth	0.518	-0.692	0.747
Relative density of hemlock	0.518	-0.778	0.874
Conifer canopy cover	0.464	-0.906	1.036
Relative density of hardwood	-0.418	0.781	0.785
Hardwood canopy cover	-0.478	0.870	0.985
Basin gradient	-0.667	0.694	0.927
Average surface moisture	-0.697	-0.269	0.558
Deposition	-0.762	ns	0.581
Large substrate	-0.785	0.642	1.028
Scour	-0.930	0.277	0.942

to stability, overstory characteristics, position in the basin, and substrate characteristics had the highest correlations with axis scores in the direct gradient analysis (Table 2.14). The highest positive correlations with Axis 1 were with stability and relative density within geomorphic surfaces; the highest negative correlations were with scour and large substrate (Figure 2.6). Position on Axis 1 was also highly positively correlated with elements of geomorphic position, including distance from basin center and plot height. Axis 2 represented a gradient in overstory cover (from conifer to hardwood) and substrate (from organic to large substrate cover).

In direct gradient analysis, the positions of species in environmental space were comparable to the species composition of experimental units (plots averaged for each lateral zone) in indirect gradient analysis. In both ordinations, plant species tolerant of dry conditions, such as *B. nervosa*, were associated with drier, densely forested conditions within basins. Plants tolerant of wet conditions, such as *Tolmiea menziesii* and *M. ovalis*, were associated with wetter, disturbed areas in both ordinations (Figure 2.4; Figure 2.5). In contrast to indirect gradient analysis, ordination of plant species in environment space more clearly delineated: *i*) a seep-associated group of species including *Chrysosplenium glechomaefolium*, *Oplopanax horridum* and *M. petandra*; *ii*) a distinct species group associated with hydric conditions and dense coniferous overstory including *Lysitchiton americanum*, *Tiarella trifoliata* and *Streptopus amplexicaulis*; *iii*) a group of species associated with steep and moderately dry conditions (generally in upper slope areas), including *Festuca idahoensis*, *Actea rubra* and *Sanicula crassicaulis*; and *iv*) an extremely dry species group (generally in ridge areas) including *Corallorhiza maculata*, *Chimaphila menziesii* and *Listera caurina* (Figure 2.5).

Vegetation types in zero-order basins

Seven vegetation types were identified in zero-order basins, consisting of groups of experimental units (plots averaged for each lateral zone) with similar plant species composition (Figure 2.7). The vegetation type descriptions below integrate averages of environmental parameters for units in each type, indicator species analysis results, and field observations.

The *Mitella* vegetation type, named for *Mitella ovalis* (the species with the highest indicator value for this group), was restricted to valley geomorphic surfaces and slope areas immediately adjacent to them (0 m and 1 m lateral zones). More than 7 % of all experimental units were classified as belonging to the *Mitella* vegetation type. This type was associated with seep and splash zone areas, with high scour and saturated surfaces (Figure 2.7). Consequently, litter depth and tree relative density were low for this vegetation type. The results of indicator species analysis suggested that the *Mitella* vegetation type supported high species richness; twenty-five species were associated with the *Mitella* vegetation type (Table C1,

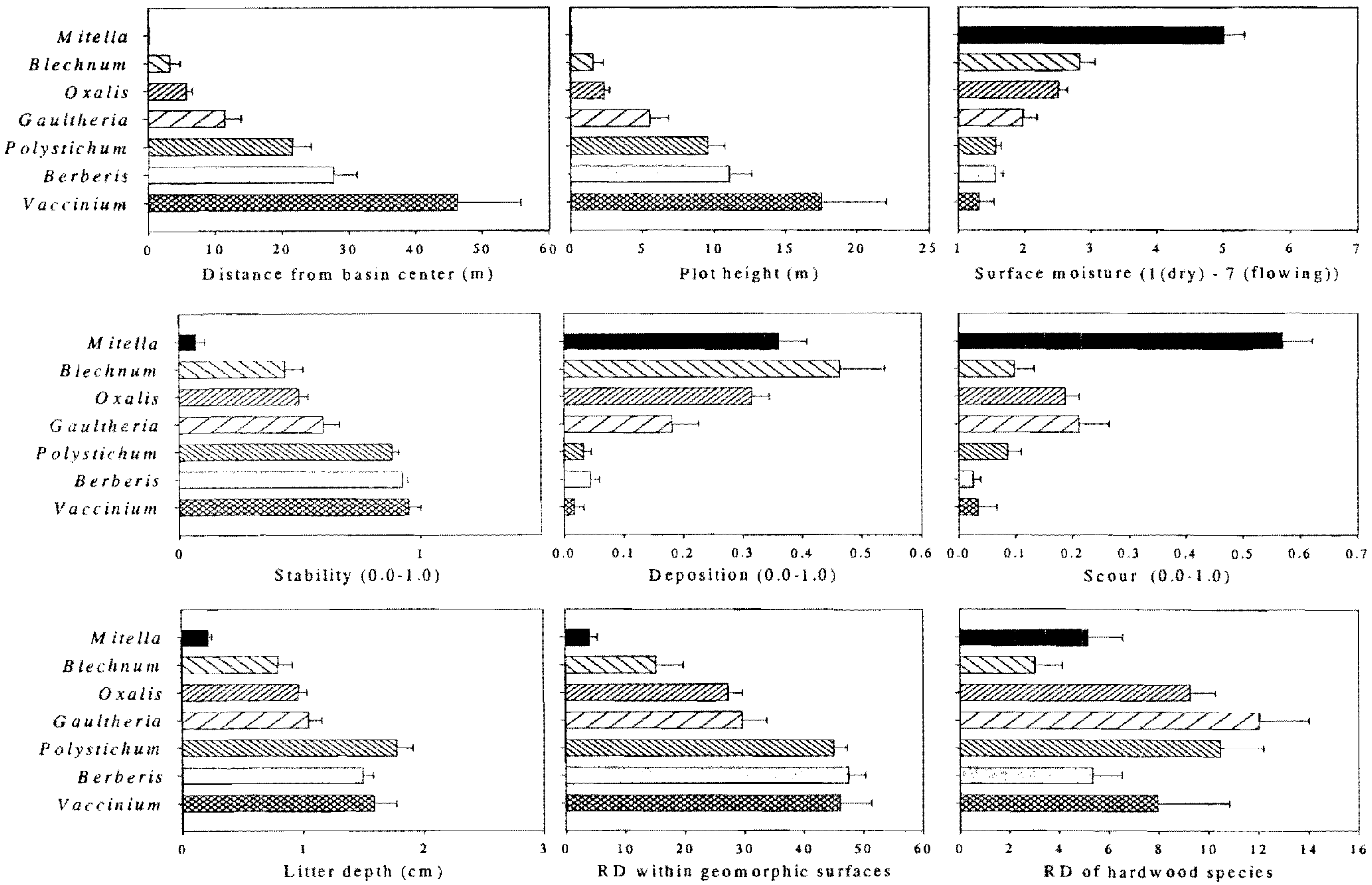

Figure 2.7. Nine environmental parameters ($\overline{x}$ + SE) for lateral zones in seven vegetation types, ordered by distance from basin center. Stability, deposition and scour represent presence/absence plot variables averaged for each lateral zone.

Appendix C), but only 13 of these species had maximum indicator values significantly higher than random expectation ($p < 0.05$; "indicator species" hereafter). Although *M. ovalis* had the highest average cover for the *Mitella* vegetation type (Table C1, Appendix C), it did not dominate plots typed as *Mitella*.

The *Blechnum* vegetation type was a splash zone and lower slope assemblage, associated principally with the 1 m lateral zone. Experimental units with this vegetation type had the highest average deposition, and 'moist' surface moisture (Figure 2.7). The *Blechnum* type was relatively simple, supporting 10 species, with only two significant indicator species. Only *Blechnum spicants* achieved an average cover over 1% in this vegetation type, and only 6.6 % of all experimental units were classified as the *Blechnum* vegetation type.

The *Oxalis* vegetation type was comparable to a riparian terrace community. Although it was most frequent in valley margins (1 m lateral zone), this type occurred in all portions of zero-order basins except ridge zones. *Oxalis* was the most common vegetation type across basins, accounting for over 33% of all experimental units. This vegetation type occurred in moderately stable, moist surfaces (Figure 2.7). The *Oxalis* vegetation type occurred where hardwood density was high compared to other vegetation types. *O. oregana* was the only indicator species, suggesting that the other 18 species associated with this type were widely-distributed within zero-order basins. *O. oregana* had the second highest cover of any forest floor species (Table C1, Appendix C).

Although the *Gaultheria* vegetation type occurred throughout zero-order basins, it was observed most frequently in mid-slope areas. Over 9% of experimental units were classified as the *Gaultheria* vegetation type. This vegetation type contained the highest density of hardwoods, and it occurred predominantly on stable slopes (Figure 2.7). The *Gaultheria* vegetation type had high species richness, with 30 associated species, but only four were indicator species.

The *Polystichum* vegetation type was primarily associated with mid-slope positions (Table C1, Appendix C). The *Polystichum* vegetation type was the second most common vegetation type in zero-order basins, including 21% of all experimental units classified. This vegetation type occurred where there was low deposition and surface moisture, and relatively high stability and overstory relative density (Figure 2.7). Litter was deepest in units in the *Polystichum* vegetation type. *P. munitum* was the only indicator species for the type, and only four species had their highest cover and frequency in this vegetation type. *P. munitum* had the highest average cover of any forest floor plant species in the zero-order basins sampled.

The *Berberis* vegetation type occurred in upper slope and ridge areas, where conditions were relatively dry. This vegetation type was relatively common; 17% of experimental units were classified as the *Berberis* vegetation type. This type occurred where litter depth and stability were high.

The *Vaccinium* vegetation type represented a forested ridge assemblage. The *Vaccinium* vegetation type occurred least frequently in zero-order basins, accounting for only 4% of all experimental units. This type occurred were surfaces were most stable and litter was relatively deep (Figure 2.7). Thirteen species had their highest cover and frequency in the *Vaccinium* vegetation type, and this vegetation type supported the second-highest number of indicator species (six species: Table C1, Appendix C).

The relationship between vegetation types and the species they supported was evaluated using an overlay of vegetation type on the direct ordination of species in environment-space (Figure 2.6). Vegetation types associated with extremes along moisture and stability gradients (Axis 1) were the most interpretable: the *Mitella* type was associated with the more disturbed, wetter portions of ordination space, while the *Polystichum*, *Berberis* and *Vaccinium* types were associated with the driest, most stable portions of the ordination on Axis 1. The *Blechnum* and *Oxalis* vegetation types did not occupy distinct environmental space in the ordination. Axis 2 in the direct gradient analysis differentiated the *Gaultheria* type, which was associated with steep vine maple dominated slopes, and the *Mitella* type, which was associated with steep, seepy areas with low conifer cover.

Indicator species analysis for geomorphic and lateral typologies

Comparison of the number and type of species associated with assemblages developed using a geomorphic surface zone typology (valley, slope, headmost, ridge) to those associated with assemblages developed using a hierarchically-nested/finer resolution lateral zone typology (0 m, 1 m, and 5 m lateral zones as well as slope, headmost and ridge zones) provided insight into species composition across geomorphic and lateral gradients in zero-order basins. For headmost, slope and ridge zones, geomorphic surface typologies had higher summed indicator values, more associated species (species with highest cover and frequency of occurrence in a zone), and similar numbers of indicator species compared to similar lateral zones (Table 2.15). However, division of valley and slope geomorphic zones into 0 m, 1m, 5 m and slope lateral zones clarified differences in plant composition in fluvial, splash zone and lower slope areas. The 0 m and 1 m lateral zones had higher summed indicator values than the valley geomorphic zone, and a larger number of indicator species.

Valley centers (0 m lateral zone) supported indicator species adapted to fluvial disturbance and inundation (e.g., *C. glechomaefolium*). Splash zones (1 m lateral zones) had species associated with stream banks and terraces, including *Blechnum spicant*, *A. filix-femina* and *O. oregana*. Comparison of indicator species for the slope geomorphic surface zone to indicators for the 5 m lateral zone and

Table 2.15. Indicator values (IV) of species for lateral and geomorphic surfaces, based on indicator species analysis. Only species with $p < 0.075$ are shown ($n = 377$ for lateral zones; $n = 252$ for geomorphic surface zones). Species are listed with the zone for which they had highest IV. Number of associated species and total sums of indicator values for each zone in each typology shown in parentheses **(bold)**.

Lateral/ geomorphic zones			**Geomorphic surface zones**		
Species	**IV**	**p**	**Species**	**IV**	**p**
***0 m* (33: 295)**			***Valley* (32: 250)**		
Mitella ovalis	35.3	0.001	Mitella ovalis	60.2	0.001
Mimulus dentatus	19.1	0.001	Tolmiea menziesii	32	0.001
Tolmiea menziesii	17.7	0.001	Athyrium filix-femina	27.6	0.001
Ribes bracteosum	9.8	0.004	Mimulus dentatus	24.6	0.001
Mitella petandra	6.4	0.007	Ribes bracteosum	18.9	0.001
Chrysosplenium glechomaefolium	6.6	0.012	Chrysosplenium glechomaefolium	12.8	0.001
Rubus spectabilis	10.8	0.017	Blechnum spicant	27	0.001
Boykinia elata	6.6	0.034	Rubus spectabilis	19.4	0.001
Tsuga heterophylla	9.2	0.059^{+}	Streptopus amplexifolius	17.1	0.001
Viola glabella	7.1	0.065^{+}	Viola glabella	13.4	0.006
***1 m* (20: 298)**			Adiantum pedatum	18.8	0.009
Blechnum spicant	30	0.001	Bromus carinatus	17	0.015
Athyrium filix-femina	23.4	0.001	Mitella petandra	7.6	0.015
Oxalis oregana	23.1	0.001	Mitella caulescens	7.1	0.015
Streptopus amplexifolius	17.1	0.001	Boykinia elata	9.5	0.037
Tiarella trifoliata var. trifoliata	11.3	0.007	Tiarella trifoliata var. trifoliata	12.5	0.056^{+}
Adiantum pedatum	10.6	0.053^{+}	Equisetum telmatiea	4.8	0.064^{+}
Slope (10: 127)			***Slope (26:468)***		
None			Polystichum munitum	37.6	0.001
***5 m* (16: 173)**			Oxalis oregana	32.6	0.001
Polystichum munitum	22.5	0.001	Trillium ovatum	22.2	0.001
Trillium ovatum	12.2	0.002	Dicentra formosa	16.6	0.002
Dicentra formosa	11.6	0.004	Disporum hookeri	20.8	0.003
Polystichum kruckebergii	7.8	0.016	Polystichum kruckebergii	10.6	0.019
			Vancouveri hexandra	13.5	0.025
			Dryopteris arguta	6.1	0.048
Headmost (14:142)			***Headmost (26:354)***		
Trientalis latifolia	9	0.001	Trientalis latifolia	9	0.037
Rhododendron macrophyllum	6.6	0.054^{+}	Carex deweyana	13.1	0.054^{+}
Ridge (18: 131)			***Ridge (23:206)***		
Berberis nervosa	29.3	0.001	Berberis nervosa	41.8	0.001
Vaccinium ovatum	12	0.004	Viola sempervirens	14	0.015
Pyrola picta	6.2	0.005	Vaccinium ovatum	13.6	0.049
Pteridium aquilinum	5.8	0.009	Pyrola picta	7.1	0.021
Smilacina racemosa	6.1	0.011	Smilacina racemosa	6.7	0.023
Viola sempervirens	8.9	0.011	Pteridium aquilinum	6.8	0.042

$^{+}$p not significant at 0.05-level.

slope zone (representing middle and upper slope areas) suggested that the most distinctive portion of slope geomorphic surfaces was the lower slope (Table 2.15). All significant indicator species from the slope geomorphic surface zone were associated with the 5 m lateral zone, while the slope lateral zone had no significant indicator species. Plant species composition was significantly ($p < 0.001$) different between zones for both geomorphic and lateral typologies (Table 2.16). For effect sizes in MRPP, values of $A \geq 0.3$ are quite strong (B. McCune, pers. comm.). The effects of geomorphic surface zones and lateral zones on species composition were thus moderately strong, but were smaller than the effect of individual zero-order basins on species composition (Table 2.16). The geomorphic surface zone typology had a slightly larger effect size on plant assemblages within zero-order basins.

Table 2.16. Comparison of the effect of geomorphic surface zones, lateral zones, and zero-order basins on plant species composition, using multi-response permutation process (MRPP). "N range" represents the range in sample size per class. T is the test statistic. "*A*" is the chance-corrected within-group agreement, an estimate of effect size (within-group homogeneity compared to random expectation).

Classification parameter	Groups	N range	T	A	p <
Geomorphic surface zones	4	63	-47.721	0.186	0.0001
Lateral zones	6	61-63	-48.698	0.177	0.0001
Zero-order basin	63	6	-20.599	0.286	0.0001

Plant diversity in zero-order basins

Plant species richness (N0) peaked in sites 5 m from basin center (5 m lateral zone). Other basin areas had lower richness (Figure 2.8, Figure 2.9). In contrast, diversity of common plant species (N1) was highest in valley centers (0 m lateral zone) and second-highest in areas 1 m from basin center (1 m lateral zone). Diversities of very common species (N2) were similar for all areas within zero-order basins.

Species area curves (Figure 2.9) reflected richness relationships in lateral zones, with the 5 m zone having highest richness and ridge zones having lowest richness, across a range of sampling intensities. Species area curves implied a moderate number of rare species in all lateral zones, with well over 80 plots required to approach the total species richness in the full sample for any lateral zone.

Shrub assemblages in zero-order basins

Shrub species provided approximately 13.8 % cover in zero-order basins, led by drier, evergreen species (Table 2.17). Ridges had the highest shrub cover,

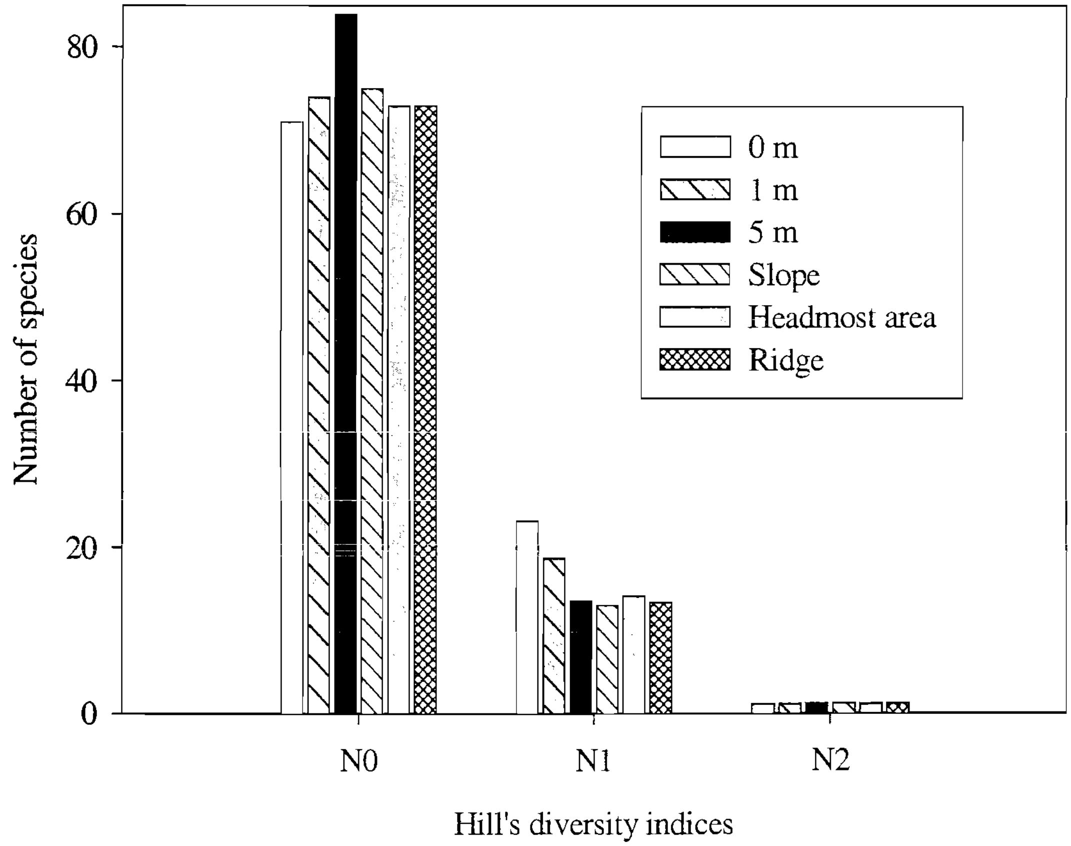

Figure 2.8. Plant species richness and diversity in zero-order basin geomorphic/lateral zones. N0 is species richness, N1 is exp (-Shannon's Index), N2 is the reciprocal of Simpson's Index. Richness and diversity produced using plant plot data corrected for unequal sample size, averaged for each of 6 geomorphic/lateral zones in 63 zero-order basins.

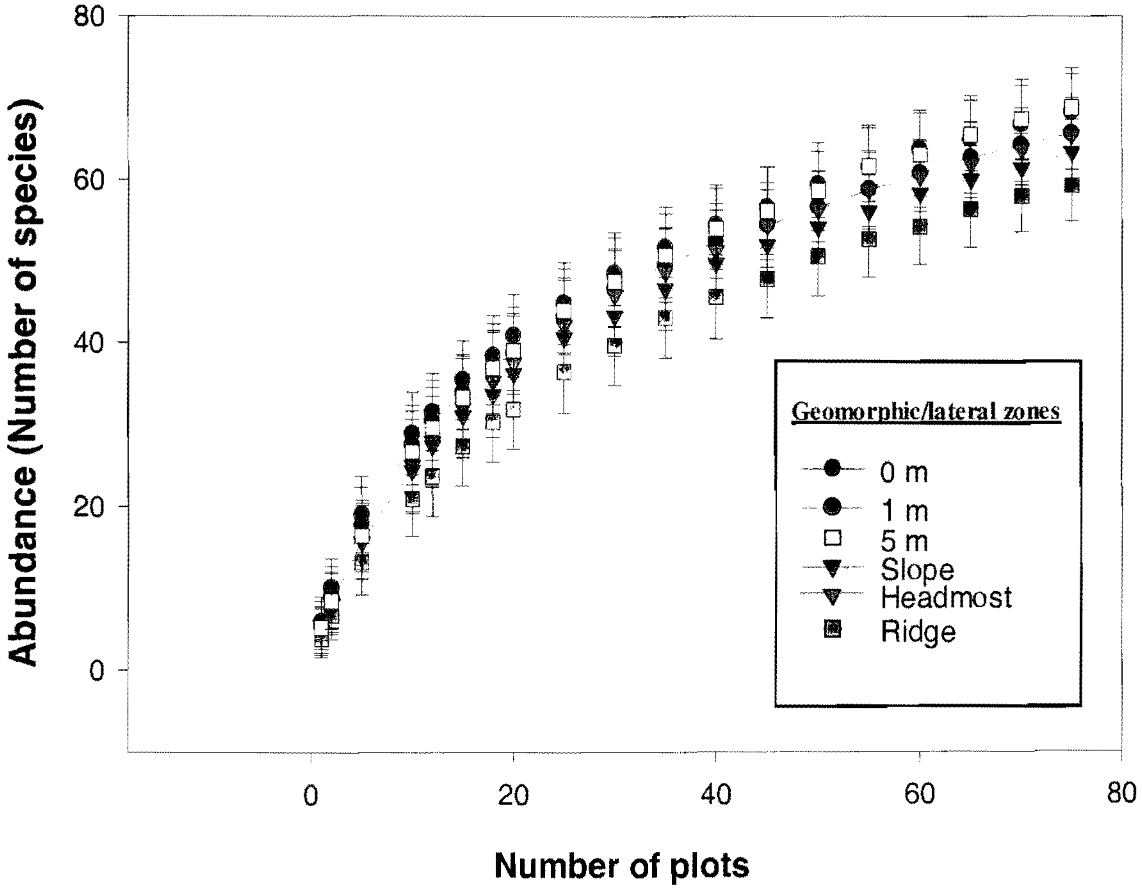

Figure 2.9. Species-area curves for six geomorphic/lateral zones. Species abundance ($\overline{x}$ + SD) as a function of number of plots sampled, across 63 zero-order basins. Each plot was 2 m^2.

Table 2.17. Percent cover of shrub species (95% confidence intervals) in 4 geomorphic surface zones in zero-order basins. Species arranged in order of decreasing total cover (n = 63).

Shrub species	Moisture class[1]	Valley	Headmost	Slope	Ridge	Basin mean
Berberis nervosa	D	0.3 (0, 0.6)	4.41 (3.12, 5.7)	4.06 (3.1, 5.01)	11.35 (8.61, 14.1)	3.9 (3.31, 4.49)
Rubus spectabilis	W	2.81 (1.56, 4.05)	0.37 (0.01, 0.72)	1.3 (0.69, 1.9)	0.21 (-0.11, 0.53)	1.38 (0.95, 1.81)
Gaultheria shallon	M	0.54 (0.25, 0.83)	1.6 (0.77, 2.42)	1.23 (0.68, 1.77)	3.01 (1.18, 4.84)	1.32 (0.96, 1.68)
Vaccinium parvifolium	M	1.27 (0.8, 1.75)	1.4 (0.7, 2.09)	1.48 (0.83, 2.14)	0.35 (0.04, 0.67)	1.27 (0.95, 1.59)
Ribes bracteosum	W	2.99 (1.78, 4.21)	0.25 (-0.1, 0.6)	0.9 (0.41, 1.39)	0.08 (-0.08, 0.23)	1.25 (0.85, 1.65)
Acer circinatum	M	0.84 (0.37, 1.31)	1.59 (0.69, 2.49)	1.07 (0.66, 1.48)	1.03 (0.12, 1.94)	1.12 (0.81, 1.43)
Vaccinium ovatum	D	0.64 (0.24, 1.03)	1.24 (0.4, 2.07)	0.4 (0.14, 0.65)	4.15 (1.56, 6.74)	1.09 (0.71, 1.48)
Rhododendron macrophyllum	D	0.08 (-0.03, 0.19)	1.26 (0.47, 2.04)	0.76 (0.32, 1.19)	1.18 (0.41, 1.95)	0.73 (0.47, 0.99)
Holodiscus discolor	M	0.24 (-0.06, 0.53)	0.8 (0.13, 1.47)	0.64 (0.17, 1.12)	0.35 (-0.1, 0.81)	0.53 (0.28, 0.79)
Rubus parviflorus	M	0.49 (-0.06, 1.03)	0.39 (-0.04, 0.82)	0.1 (-0.06, 0.25)	0	0.27 (0.07, 0.46)
Corylus cornuta	M	0.13 (-0.07, 0.32)	0.34 (-0.08, 0.75)	0.36 (-0.09, 0.82)	0	0.25 (0.05, 0.45)
Whipplea modesta	M	0.01 (-0.01, 0.02)	0.14 (0.02, 0.26)	0.23 (-0.07, 0.53)	0.31 (0.1, 0.53)	0.16 (0.04, 0.27)
Rubus laciniatus	D	0.09 (-0.02, 0.21)	0.19 (0.01, 0.38)	0.13 (0.03, 0.24)	0.12 (-0.06, 0.29)	0.13 (0.07, 0.2)
Rubus ursinus	D	0.05 (-0.01, 0.1)	0.12 (0.02, 0.22)	0.09 (0.02, 0.16)	0.04 (-0.04, 0.12)	0.08 (0.04, 0.12)
Sambucus racemosa	M	0.05 (-0.02, 0.12)	0.07 (-0.07, 0.22)	0.11 (-0.11, 0.33)	0	0.07 (-0.02, 0.16)
Rosa gymnocarpa	D	0	0.13 (-0.02, 0.28)	0.03 (-0.02, 0.08)	0.13 (-0.1, 0.37)	0.06 (0.01, 0.11)
Toxicodendron diversilobum	D	0	0.22 (-0.07, 0.52)	0	0	0.05 (-0.02, 0.13)
Oplopanax horridum	W	0.14 (-0.13, 0.42)	0	0.03 (-0.02, 0.07)	0	0.05 (-0.03, 0.13)
Rubus nivalis	D	0	0.07 (-0.07, 0.22)	0.01 (-0.01, 0.04)	0.04 (-0.04, 0.12)	0.03 (-0.01, 0.06)

Table 2.17. (continued)

Shrub Species	**Moisture class**[1]	**Valley**	**Headmost**	**Slope**	**Ridge**	**Basin mean**
Rhamnus purshiana	M	0	0.01 (-0.01, 0.02)	0.05 (-0.05, 0.15)	0	0.02 (-0.02, 0.06)
Rubus leucodermis	D	0	0	0.04 (-0.04, 0.11)	0	0.01 (-0.01, 0.04)
Oemleria cerasiformis	M	0	0	0	0.04 (-0.04, 0.12)	0 (0, 0.01)
Symphoricarpos albus	M	0	0.02 (-0.02, 0.06)	0	0	0 (0, 0.01)
Wet species total		5.94 (4.03, 7.86)	0.62 (0.13, 1.11)	2.22 (1.37, 3.07)	0.29 (-0.06, 0.65)	2.68 (2.03, 3.33)
Mesic species total		2.18 (1.23, 3.12)	3.38 (2.14, 4.63)	2.97 (1.91, 4.02)	1.02 (0.43, 1.62)	2.62 (2.06, 3.18)
Dry species total		2.53 (1.71, 3.36)	10.61 (8.23, 13)	7.82 (6.34, 9.3)	21.09 (16.72, 25.47)	8.5 (7.49, 9.5)
Shrub species total		10.65 (8.35, 12.95)	14.61 (11.78, 17.44)	13.01 (11.03, 14.98)	22.41 (17.92, 26.9)	**13.79 (12.5, 15.09)**

[1] Moisture classes include wet (W), mesic (M), and dry (D). Moisture classes were subjectively assigned, based on shrub assignments to vegetation types with average surface moistures of > 2 (wet), 1.5-2 (mesic) or < 1.5 (dry)

followed by headmost areas and slope zones. Valley surfaces had the lowest shrub covers. *B. nervosa* was the most commonly observed shrub species, with almost 4% cover; it realized its highest cover on ridges (11.3 %) and its lowest cover in valleys (0.3%). *R. spectabilis* accounted for < 1.4 % cover in zero-order basins, but it had greatest cover (2.8 %) in valley floors. *Ribes bracteosum* had the highest cover of any shrub in valley geomorphic surfaces (almost 3%), and was frequently associated with seepy depositional surfaces.

Shrub species associated with relatively dry conditions had the highest percent cover across basins, and were the most prevalent in ridge zones (Table 2.17). The cover of shrub species associated with wet conditions was highest in valley geomorphic surfaces. Mesic shrub species occurred across geomorphic surface zones. Both wet and mesic species averaged < 3% cover across the basins studied.

DISCUSSION

Strong spatial patterning was evident for plants in unmanaged zero-order basins in the Oregon Coast Range. Overstory, herbs and shrubs showed distinct associations with geomorphic and lateral zones, suggesting that these areas harbor plant assemblages distinct from both downstream riparian and surrounding hillslope communities.

Overstory patterns in zero-order basins

Zero-order basin overstories were more similar to upland areas (Spies 1991) or to overstories in first-order riparian systems in the southern Coast Range (Pabst and Spies1999) than to larger-order riparian overstories (Nierenberg and Hibbs 1999). The top three coniferous species and the top hardwood species in terms of basal area in zero-order basins were the same top species identified in mature upland areas in the Oregon Coast Range (Spies 1991). Zero-order basins supported higher densities of conifer species, and lower densities of hardwoods, particularly red alder, than larger-order riparian systems (Nierenberg and Hibbs 1999, Pabst and Spies 1999). Red alder dominates larger-order riparian systems (Nierenberg and Hibbs 1999); hardwood communities in zero-order basins were predominantly big leaf maple, with much lower basal area cover than in larger basins. These results suggest that there is a reduction in hardwood density moving upstream in drainage basins, analogous to reductions documented moving laterally away from fluvial centers (Nierenberg and Hibbs 1999, Pabst and Spies 1999), and a change in overstory species composition.

Valley and headmost geomorphic surfaces (convergent surfaces) in zero-order basins had distinctly different overstory structure than surrounding areas. Relative densities of valley and headmost surfaces were significantly lower than surrounding slopes and ridges; similar results were found by Kikuchi and Miura (1993) for zero-order basins in Japan. Differences in structure across geomorphic surfaces were not as dramatic as in larger riparian systems; the "treeless" overstory type identified by Nierenberg and Hibbs (2000) in unmanaged riparian floodplains was patchily distributed in zero-order basin valleys and headmost areas, spatially compressed into a small lateral band surrounding valley fluvial centers. This lateral band did not extend to mid-slope positions (an average of 24 m from basin center). Although there were significant differences in overstory structure between geomorphic surfaces, there were negligible differences in canopy cover. Fluvial disturbance is less intense in zero-order basins than in downstream systems; this may allow overstories and tall shrubs to "close" over disturbed surfaces, thus minimizing differences in canopy cover between valley and slope surfaces.

Forest floor vegetation in zero-order basins

Environmental gradients and disturbance processes are the two principal factors structuring plant composition in forested landscapes of the Pacific Northwest (Wimberly and Spies 2001, Ohman and Spies 1998). Correlation analysis and empirical modeling of the relationship between environmental parameters and plant ordination scores suggested that plant species composition was most strongly associated with parameters related to position within the basin (related to fluvial, hillslope, and microclimate processes), and overstory characteristics, affecting both shading and organic substrate deposition. Environmental parameters associated with plant species composition in zero-order basins acted at different spatial scales. At smaller spatial scales (circa 2 m^2), lateral distance from basin center, plot height, substrate characteristics and stability were some of the most important factors related to species composition. Geomorphic surface zone was an intermediate-scale expression of geomorphic position, and was associated with a strong gradient in species composition. Overstory tree density and canopy cover were additional intermediate-scale parameters important in predicting plant species composition. Basin aspect (heat load index) and basin gradient were larger spatial scale parameters which were strongly associated with plant species assemblages.

The relationship between natural disturbance rates and magnitudes and plant composition in zero-order basins was not directly measured. Disturbances in zero-order basins, including fire and landsliding, would be predicted to affect substrates, overstory composition and hydrologic function in basins, aspects of which were measured. The relative importance of disturbances, anthropogenic or natural, in comparison to environmental gradients in structuring plant communities in zero-order basins is unclear.

Several studies have suggested the importance of geomorphic (Spies and Barnes 1985, Gregory et al. 1991, Pabst and Spies 1998) and lateral (Pabst and Spies 1999, Nierenberg and Hibbs 2000) surfaces in organizing species composition. Results from this study support the importance of geomorphic surfaces as a conceptual framework for organizing plant composition in zero-order basins, and as a driver of environmental gradients in zero-order basins. This study documented the importance of three particular geomorphic surfaces within zero-order basins for support of plant species diversity and distinct plant assemblages: valley center and splash zone areas within and adjacent to valleys, lower slope surfaces, and (possibly) headmost areas.

Valley floors supported lower tree density than surrounding areas, high frequencies of scour and deposition, and the highest surface moisture in zero-order basins. The high diversity of microsites in valley surfaces associated with scour and deposition may have led to higher plant diversity (Gregory et al. 1991, Pabst and Spies 1998). Valley floors supported the highest plant species diversity in zero-order basins, and the largest number of significant indicator species. Within valleys, valley centers (0 m lateral zones) included hydrophytes and stoloniferous species capable of surviving higher disturbance levels or recolonizing quickly. Assemblages in the splashzone (1 m lateral zone) included species generally associated with moist habitats, but included more perennials and species with well-developed root systems.

Several authors have suggested the importance of hillslope-constrained portions of headwater systems close to fluvial center, in support of species diversity. Olson et al. (2000) found that the near-stream environment ("inner gorge", areas $\leq$ 15 m from basin center) was distinct from upland conditions in both microclimate and microsite variables. Findings from this study appear consistent with findings in Olson et al. (2000), but suggest spatial compression of inner gorges in zero-order basins.

Considered jointly, lateral zones within 5 m of basin center supported 17 of the 24 indicator species identified in zero-order basins, although these areas made up a small fraction of total basin area. The 5 m lateral zone contained four of the top five indicator species from the slope geomorphic zone, while slope lateral zones (representing mid-slope areas) supported no significant indicator species. This suggests that the lower slope (the "transition slope" identified by Pabst and Spies (1998)) provides distinct environmental conditions within these basins. The 5 m lateral zone also supported the highest species richness in zero-order basins. The high richness of the 5 m lateral zone suggests that it may provide intermediate disturbance levels (Connell 1978), or an optimal combination of soil hydration, limited disturbance, and higher light levels than denser mid-slope areas.

Headmost areas had fluvial regimes and overstory relative densities intermediate between valley floors and surrounding slope surfaces, and they were distinct from either. However, headmost area plant composition was relatively indistinct and variable in ordination space. Species most strongly associated with headmost areas included *Trientalis latifolia*, *R. macrophyllum* and *C. deweyana*, but none of these species had high maximum indicator values, and all three of these species are found in a range of mesic to dry habitat types across the landscape. Diversity of headmost areas was not different from other geomorphic surfaces. It therefore appears that headmost areas supported overstory structure distinct from surrounding geomorphic surfaces, but plant composition was similar.

Vegetation types in zero-order basins

Classification of species into vegetation types was useful in understanding the ecological patterns in zero-order basins. Vegetation types: *i*) made it easier to identify strong gradients in species composition related to surface moisture, scour, and plot height which were obscured in continuous gradient analysis; *ii*) facilitated comparison to vegetation studies in larger riparian basins (below); and *iii*) suggested management units for plant assemblages in zero-order basins. The most distinct differences between vegetation types were differences in position within basins (i.e. distance from basin center and plot height) and surface moisture.

Comparison of zero-order vegetation types to plant species groups identified in larger-order riparian systems by Pabst and Spies (1998) clarified the range of microhabitat types present in zero-order basins. Gravel bar groups (*Glyceria, Petasites, Urtica*) and open/disturbance area species groups (*Rubus ursinus*) identified by Pabst and Spies (1998) did not occur in unmanaged zero-order basins. The *Mitella* vegetation type that I identified overlapped the *Chrysosplenium* and *Tolmiea* groups identified by Pabst and Spies (1998), associated with seeps and moist habitats. Broad mesic groups like the *Oxalis* and

Gaultheria vegetation type were comparable to the *Acer circinatum* group and *Rubus spectabilis* species group identified by Pabst and Spies (1998), but for the absence of *Rubus spectabilis*. In general, zero-order basins appeared to support a broader range of dry vegetation types, and fewer fluvial groups than larger riparian systems. Pabst and Spies (1998) suggested that in moving from larger to smaller stream orders, geomorphic surfaces and fluvial processes become spatially compressed and tightly juxtaposed, obscuring riparian patterns in biological diversity described by Gregory et al. (1991). My results from zero-order basins appeared consistent with this hypothesis. The *Oxalis* and *Gaultheria* vegetation types occurred with similar frequencies in all six lateral zones. Many individual species also were present across the entire lateral gradient.

Vegetation types may act as both an integrator of environmental gradients and as a delineator of the lateral and longitudinal extent of geomorphic processes within zero-order basins. The *Mitella* and *Blechnnum* vegetation types, for example, were tightly tied to moisture and fluvial disturbance, and could potentially serve as delineators of the longitudinal initiation points or lateral extent of fluvial processes in the absence of other indicators. At a finer scale, the *Blechnum* vegetation type was weakly associated with scour but strongly associated with deposition, highlighting its potential as a delineator of the lateral extent of splash zone conditions. Unfortunately, relationships for drier groups were not as distinct.

Although the seven vegetation types identified in zero-order basins were relatively distinct, they would not serve as precise indicators for the plant species they contained. Vegetation types supported similar number of indicator species to the assemblages associated with geomorphic surface and lateral zone typologies, and had similar or higher summed indicator values. However, mesic vegetation types (e.g., *Oxalis, Gaultheria*) were not strong groups, with few significant indicator species and many generalist species. There were few species that occurred exclusively within any vegetation types; only four species had maximum indicator values > 50. These results suggest that vegetation types would make relatively poor indicators predicting the occurrence of individual plant species. The similar low number of indicator species for geomorphic and lateral zones suggest that these zones are not distinctive enough for specialist species occur. Therefore, plant species and vegetation types within zero-order basins would probably be relatively poor indicators for other taxa, at the spatial scale at which data was analyzed. Reasons for the lack of strong indicator plant species may be the ephemeral nature of distinctive fluvial habitats, excluding hydrophytic plant species, the ameliorating effect of coniferous overstories, or that environmental conditions present in zero-order basins occur elsewhere in forested landscapes.

Shrub assemblages in zero-order basins

Shrub species composition and cover in zero-order basins were more similar to conditions in upland areas than riparian areas. Zero-order basins had lower shrub cover than larger-order riparian basins, particularly by riparian associated species. Nierenberg and Hibbs (1999) found extensive treeless areas in unmanaged terraces and floodplains in riparian zones of the Oregon Coast Range. Salmonberry often dominated these treeless areas. Salmonberry is the most abundant shrub species in most Coast Range riparian forests, accounting for over 25% cover in riparian areas (Pabst and Spies 1998), and thus salmonberry exerts biotic control over herb composition and tree regeneration in riparian systems (Hibbs and Giordano 1996, Pabst and Spies 1998). Across zero-order basins, total shrub cover was only 14%, and salmonberry cover in valley floors averaged < 3%. The low cover in zero-order basins by shrub species associated with wet conditions is more comparable to shrub composition in upland areas (Spies and Franklin 1991), and may be due to the reduced and spatially compressed fluvial regime in these areas. *B. nervosa*, a shrub associated with dry conditions, had the highest cover in zero-order basins. The moderate cover by predominantly evergreen shrubs in unmanaged zero-order basins may have a significant effect on forest floor herbaceous vegetation, litter composition and downstream nutrient transport.

Study limitations

The sample population for this study included 63 unmanaged zero-order basins, within 0.8 km of paved surfaces. The spatial scope of inference would include the full study area (850 km^2 of the upper Coquille River Basin), because randomization was used and the entire area is similar in geology and climate. Tentative extrapolation could be made to other zero-order basins in the mid-Coast Range of Oregon with similar environmental conditions. There are limitations on inference from this study, associated with geomorphology and disturbance regime in the sample. Inference would not include hollows terminating in second-order or larger systems or cliff areas, which could make up a sizeable portion of zero-order basins in some habitats. Less than 10% of the zero-order basins I initially selected as study sites were deleted from the study due to cliff walls.

More importantly, the sample population did not include managed sites; study objectives were developed principally to characterize an environmental baseline for plant composition in zero-order basins. Thus no inference can be made to conditions or plant associations in managed zero-order basins. Because I did not control for natural fluvial or hillslope disturbance, the sample reflected the range of natural disturbance conditions in unmanaged zero-order basins.

Forest management implications

Findings from this study may serve several functions relevant to management of headwater areas, including: *i*) providing a baseline of plant assemblages and plant-environment relationships against which to compare management effects or to direct management in zero-order basins; *ii*) designating the longitudinal and lateral extent of riparian influence in headwater areas; *iii*) providing vegetation types useful in rapid assessment and mapping of zero-order basin plant assemblages; *iv*) providing predictions for the effects of management on plant composition; and *v)* suggesting a role of zero-order basins in supporting biotic diversity in forested landscapes.

This study of plant composition in unmanaged zero-order basins provides a baseline for evaluating plant composition in zero-order basins in contexts where disturbance may mask subtle environmental gradients (Adams and Bury 2002). Such baseline studies are imperative for landscape-level management of plant diversity and plant assemblages. Results from this study provide information on individual plant species, species richness, vegetation types and overstory tree characteristics of zero-order basins in the central Coast Range of Oregon, which would be useful in assessing effects of management in these basins and in directing levels of management.

Results of this study would assist in delineation of longitudinal and lateral extents of riparian conditions in headwater areas. Several plant species (e.g., *M. ovalis*, *C. glechomaefolium*, *O. horridum*) strongly associated with Oregon Coast Range headwater riparian communities (Pabst and Spies 1998) penetrate zero-order basins, along fluvial gradients. Fluvial vegetation types, including the *Mitella* and *Blechnum* types, were found in valley and lower slope surfaces, but rarely occurred in headmost, mid-slope and ridge surfaces. Laterally, fluvial vegetation types were identified principally within five meters of basin center. These results suggest that within drainages, environmental conditions supporting riparian communities continue upstream into zero-order basins. Management to minimize impacts to riparian plant communities might focus on areas close to basin center (the "inner gorge" identified by Olson et al. 2000) and mostly (but not exclusively) downstream of the initiation of scour and deposition.

Vegetation types have been suggested for use in gauging productivity, regeneration success and habitat potential in managed landscapes (Spies and Barnes 1985, Christy et al. 1998). Vegetation types identified in zero-order basins would assist managers in delineating the extent of fluvial processes, delineating plant assemblages associated with geomorphic surfaces, and in rapid assessment and mapping of community types (Spies and Barnes 1985) within zero-order basins. Because these vegetation types contained multiple species and represented averages for lateral zones, vegetation types incorporated broader environmental influences and might provide more stable delineations than seasonally or spatially variable parameters like flow status or substrate characterizations.

Because the sample population did not include managed sites, relationships between management levels in zero-order basins and plant composition could not be considered. However, considering the results of empirical modeling of plant-environment associations in this study, I hypothesize that management activities that influence fluvial or hillslope processes or overstory densities in zero-order basins will lead to changes in plant composition. Because of the correlations between measured and unmeasured environmental parameters in this observational study, hypotheses regarding the effects of changes in individual parameters on plant composition cannot be made.

Although the plant species identified in zero-order basins are not rare in the landscape, vegetation types identified in zero-order basins were distinct. Zero-order basins supported a range of vegetation types, including both types similar to riparian assemblages and distinct vegetation types. These distinct vegetation types suggest that a unique set of fluvial and hillslope processes shape the biotic communities in zero-order basins. This unique set of physical processes and the environmental conditions associated with them may support other taxa adapted to conditions in zero-order basins, including sensitive taxa.

Due to their geomorphology and landscape position, zero-order basins may play a key role in maintaining beta diversity in upland forested hillslopes. Hillslopes near ridgelines are topographically the driest portions of landscapes. Zero-order basins support riparian plant species close to ridgelines (mean distance from ridgeline to initiation of scour and deposition = 165.5 m), and juxtapose these riparian species with species associated with extremely dry conditions, thus greatly increasing plant species diversity in hillslopes as a whole. Current species diversity in steep, forested landscapes may partially be a function of the high frequency of zero-order basins in these landscapes.

The importance of zero-order basin fluvial and hillslope processes, and the environmental conditions associated with them, in maintaining biotic diversity in entire forested landscapes is not understood. The effect of management activities on zero-order basin biotic communities and thus on the beta diversity of forested hillslopes is also uncertain: the sensitivity to anthropogenic disturbance of plants and other taxa in zero-order basin with naturally high disturbance frequencies has not been investigated. A fuller understanding is needed of the physical processes acting on plants and other taxa in zero-order basins, the role of these basins in maintaining species diversity across landscapes, and the effects of forest management on these processes. Where maintaining native biodiversity is a management goal, it would be prudent to maintain a range of disturbance states in zero-order basins in forested landscapes comparable to the historic range of natural variability in basin disturbance in this ecoregion.

Conclusions

The key role of zero-order basins in transporting coarse substrate and wood down gradient to larger-order systems has been shown (May 2001, Benda 1988). Results from this study suggest that zero-order basins are also be important in support of distinct plant assemblages, as the final upstream extension of riparian plant species, and in maintenance of beta diversity in steep forested landscapes. Plant composition in zero-order basins followed strong environmental gradients, principally related to geomorphic position. Areas within 5 m of valley center supported distinct physical properties, the highest plant diversity, and the most distinct plant assemblages in zero-order basins. Information on the presence and spatial patterning of plant species in zero-order basins may be useful in management of biotic resources in steep, forested landscapes of the Pacific Northwest.

CHAPTER 3. AMPHIBIAN ASSEMBLAGES IN ZERO-ORDER BASINS IN THE OREGON COAST RANGE

INTRODUCTION

In western North America, headwater drainages make up a large proportion of the forested landscape (Hack and Goodlett 1960, Benda 1990, Appendix V-G in USDA and USDI 1994). Because of their frequency and aerial extent in mountainous forest landscapes, their role in transport of materials down-gradient to higher-order systems (Benda 1990, May, 2001), and their influence on downstream water quality (FEMAT 1993, Beschta et al. 1987), it is probable that small headwater drainages are important in the maintenance of ecosystem integrity, a common objective for forestry practices in the Pacific Northwest.

Management to meet requirements of federal biodiversity policies requires maintenance and restoration of habitat to support well-distributed populations of native species within autonomous geophysical landscape units, such as riparian areas (FEMAT 1993). A significant component of ecosystem management in drainage basins in the Pacific Northwest has involved the installation of riparian buffers, areas where disturbance from forest management is reduced to minimize impact to riparian species. Buffers have traditionally been established based on stream size and fish usage (Belt and O'Laughlin 1994), extending some pre-determined distance laterally from fluvial center. Differences in management practices across land ownerships in the Pacific Northwest (Gregory 1997), particularly in smaller basins (Table 3.1), have resulted in scrutiny of resources in headwater areas, and reassessment of ecological values warranting protection. For basins supporting ephemeral streams in particular, protection of native ecosystem resources is negligible in current management guidelines, while installation of downstream protections has left these headwater areas open to continued anthropogenic disturbances. Ephemeral systems, also called zero-order basins, dominate the drainage area of most soil-mantled hillslopes (Hack and Goodlett 1960, Benda 1990, Kikuchi and Miura 1993). Zero-order basins are hillslope units where flow lines converge on a hollow (Tsukamoto, Ohta and Noguchi 1982), including catchment areas above sustained scour and deposition as well as intermittent scour areas, extending from ridgelines down to the initiation of first-order streams. Zero-order basins may include areas defined as hollows (Montgomery and Dietrich 1989, Benda 1990), ephemeral or intermittent streams or the uppermost portions of first-order streams (USDA USDI 1994). Zero-order basins have been studied for their unique physical characteristics, including their disturbance regime (Reneau and Dietrich 1990, May 2001) and moisture relations (Dietrich et al. 1997). Although studies have characterized vertebrate

Table 3.1. Comparison of riparian zone management practices and species of concern for perennial and intermittent stream types. Comparisons of management in forested mountain streams of the Pacific Northwest (adapted from Young 2000), and amphibian species of concern identified in zero-order basins in the study area. Intermittent basins include both 1st - and 2nd-order stream systems, and zero-order basins.

	Basin type			
	Perennial	**Intermittent**		
Provincial/ State government	**(> 2nd-order)**	**(1st - 2nd-order)**	**(Zero-order)**	**Species of concern[1]**
British Columbia	20-m buffer; 20-m man. zone	No buffer; 20-m man. zone	None	Tailed frog Pacific giant salamander
US Federal lands (NFP Lands)	1-2 site-potential tree heights	1site-potential tree height	Variable by slope/ geology	Tailed frog S. torrent salamander Dunn's salamander Clouded salamander
Washington State/Private	No buffer; 7.5 - 30-m man. zone	None	None	Dunn's salamander
Oregon State/Private	6 m buffer; 30-m man. zone	6 m buffer; 15-m man. zone	None	Tailed frog S. torrent salamander Clouded salamander
California State/Private	45-m man. zone	15-m man. zone	None	Tailed frog S. torrent salamander

[1] Species designated sensitive or threatened by provincial, state or federal governments.

(McComb et al. 1993) and plant (Pabst and Spies 1998, Nierenberg and Hibbs 1999) usage of unmanaged headwater riparian areas, no studies have been conducted to characterize species assemblages in unmanaged zero-order basins specifically. The upper limits of riparian species in drainage basins have not been well-defined. Furthermore, there may be a close association between abiotic and biotic patterns and processes in zero-order basins, resulting in biological diversity patterns in headwater systems that may be organized by geomorphic processes (Kovalchik and Chitwood 1990, Gregory et al. 1991, Pabst and Spies 1998). In particular, amphibian headwater species patterns may reflect shaping by these abiotic processes (e.g., Dupuis and Bunnel 2000, Wilkins and Peterson 2000).

Amphibian species may be key components for forest management consideration within zero-order basins. Amphibians have relatively high biomass in headwater stream systems (Bury 1988, Vesely 1997), and have been proposed as environmental indicator species (Vitt et al. 1990, Welsh and Droege 2001), due in part to their associations with late successional forests and sensitivity to management activities (Bury and Corn 1988, Welsh 1990, Blaustein et al. 1995). The relatively low vagility and peripatry of many forest-associated amphibians lead to a relatively tight coupling of densities to habitat elements commonly-influenced by forest management, such as downed wood volumes and overstory conditions (Corn and Bury 1989, FEMAT 1993).

Amphibian assemblages have been characterized in both managed (Vesely 1997, Wilkins and Peterson 2000, Olson et al. 2000, Stoddard 2001) and unmanaged (Bury et al. 1991, Welsh and Lind 1991, Adams and Bury 2002) headwater streams. Preliminary results of Olson et al. (2000) show changes in amphibian assemblages as streams changed from perennial systems to channels above water, from aquatic and splash zone species to species favoring drier habitat elements. However, Olson et al. (2000) did not consider unmanaged systems, and they did not clearly define species assemblages associated with zero-order basins and their geomorphic surfaces. Studies of amphibian fauna in unmanaged systems can provide a baseline for evaluating species composition and ecosystem integrity in contexts where disturbance may mask subtle environmental gradients (Adams and Bury 2002).

This study examines geomorphic, spatial, and habitat associations of amphibians in unmanaged zero-order basins in the Oregon Coast Range. Specifically, I investigate (*i*) amphibian species-specific spatial distribution patterns along longitudinal and lateral gradients, and relative to three geomorphic surfaces (valley, headmost and slope zones); (*ii*) empirical models to quantify amphibian species-specific associations with environmental parameters; (*iii*) patterns of amphibian assemblage composition in zero-order basins relative to environmental parameters; and (*iv*) forest management implications of the resulting amphibian species' habitat relationships and amphibian assemblage compositions in zero-order basins.

MATERIALS AND METHODS

Study Area

The study area was chosen based on land ownership, the presence of large unmanaged areas, a relatively high density of first-order systems (over 13 first-order streams/km^2), and similarities in landscape attributes including vegetation, geology, elevation and marine influence. Work was conducted on United States federal lands administered by the Coos Bay District of the Bureau of Land Management (BLM) in the central Oregon Coast Range (Figure 3.1). The study area encompassed approximately 850 km^2 of the headwaters of the Coquille River Basin (4767N to 4798N UTM, 418E to 445E UTM). The area is underlain by uplifted sea floor sediment and basalt, with geologic formations composed of sandstone and sandy siltstone (USDI 2000).). Soils in study sites included principally series in the Preacher-Bohannon and Umpcoos-Rock Outcrop units. The area is deeply dissected by stream networks, including many steep headwater channels. Within the Coast Range physiographic province, maximum air temperatures seldom exceed 30° C, and minimum air temperatures rarely fall below freezing (USDI 2000). Most precipitation occurs as rainfall, ranging from 1397

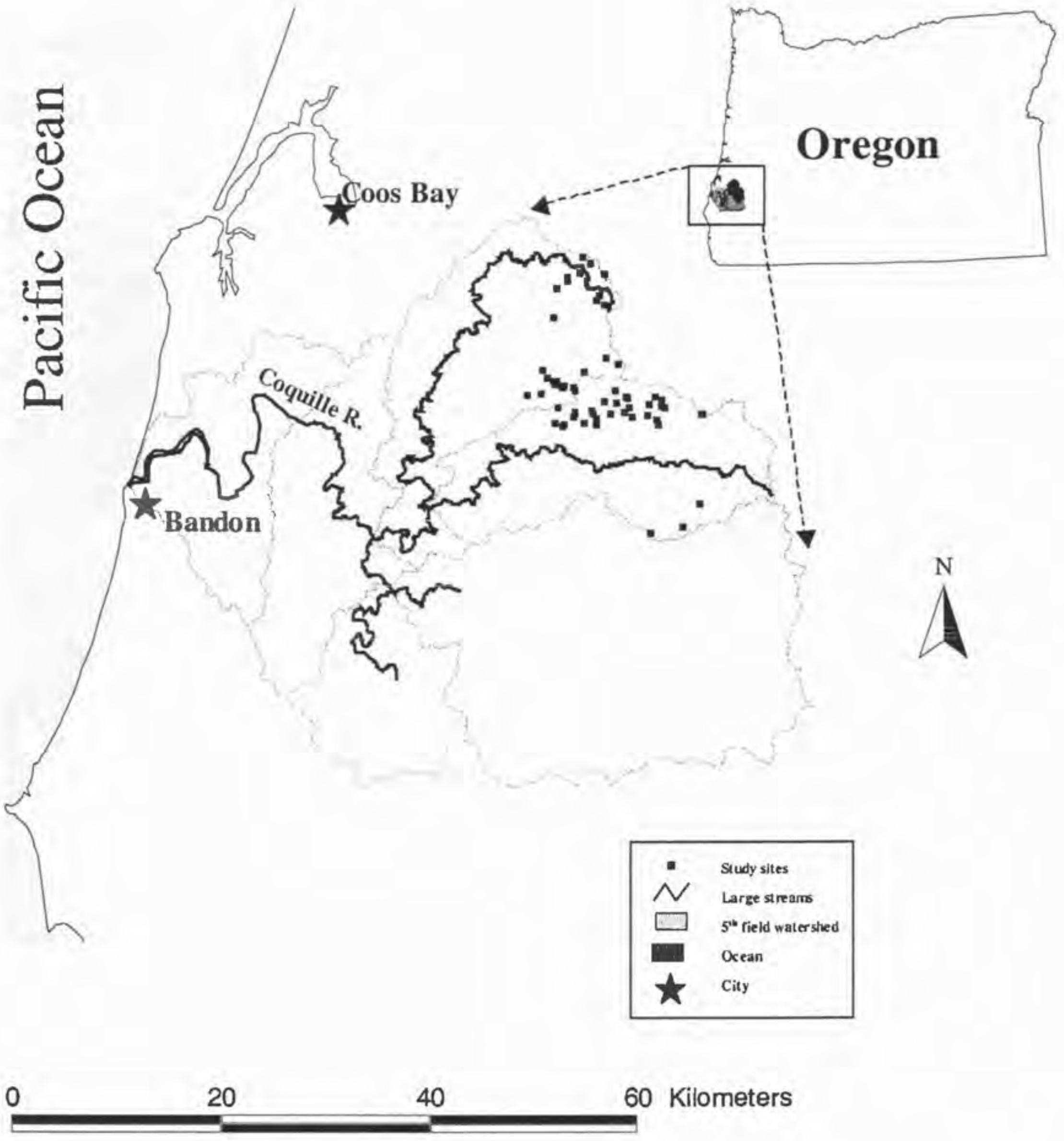

Figure 3.1. Location of study area and 63 study sites within the Coquille Basin, southwestern Oregon.

mm to over 3810-mm annually (OSU 1982). The area is deeply dissected by stream networks and has a drainage density of 2.9 km of streams per km^2, ca 76% of which are 1st-and 2nd-order systems (USDI 2000).

This area is in the western hemlock (*Tsuga heterophylla* (Raf.) Sarg.)) zone (Franklin and Dyrness 1969). Forested upland areas are dominated by Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and western hemlock. Forest floor species include evergreen huckleberry (*Vaccinium ovatum* Pursh), salal (*Gaultheria shallon* Pursh), sword fern (*Polystichum munitum* (Kaulf.) Presl) and oxalis (*Oxalis oregana* Nutt.). Riparian areas support principally hardwood overstory trees including red alder (*Alnus rubra* Bong). Riparian terrace species include salmonberry (*Rubus spectabilis* Pursh) and stinking black currant (*Ribes bracteosum* Dougl.).

Study sites

Within the study area, 222 zero-order basins within unmanaged stands were identified from geographic information system (GIS) maps of land ownership, stand ages, roads, contour crenulations (produced by 10-m digital elevation models), and first-order systems. A set of selection criteria was applied *a priori* to all zero-order basins within the study area to identify suitable sites. Sites disturbed by management activities, sites > 0.8 km from a transportation corridor, and zero-order basins that did not terminate at the tip of a first-order channel (Dietrich et al. 1987) were eliminated. Preliminary observations suggested that zero-order basin habitat parameters varied with differences in slope and aspect. I therefore stratified zero-order basins into high (> 39°) and low (< 39°) slope classes, and into south and west-facing (120°-300°) and north and east-facing (301°-119°) aspect classes. All 222 systems were numbered, and a random number generator was used to determine order of sites visited, alternating by slope/aspect class. The sample population analyzed in this report includes the first 63 randomly selected zero-order basins from the inference population of 222 zero-order basins.

Data collection

In the field, I delineated the extent of each zero-order basin as areas extending downslope from the ridgeline to the point where fluvial scour became clearly more continuous than discontinuous (estimated visually over a channel length of 15 m), often at the junction with another zero-order drainage. Within delineated zero-order basins, I established a longitudinal axis along and parallel to the most fluvially active portion of the basin (Figure 3.2). I considered this

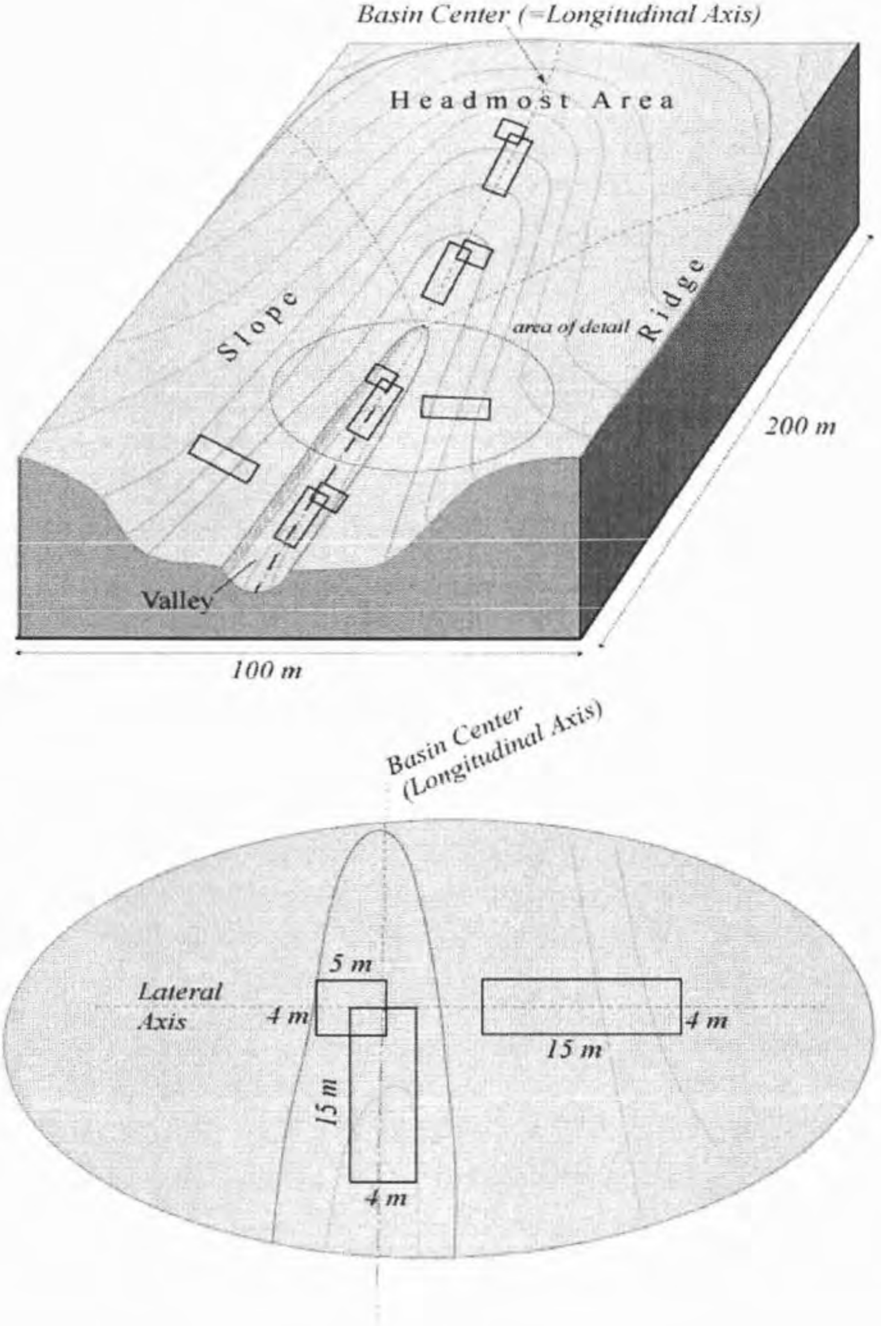

Figure 3.2. Schematic of geomorphic surfaces and amphibian transect set up within zero-order basins.

longitudinal axis basin center. Measurements of distance-from-ridge to sampling transect were measured along this axis. Lateral measurements of distance from basin center were measured perpendicular to this axis (Figure 3.2, detail area).

Several authors (Hack and Goodlet 1960, Gregory et al. 1991, Pabst and Spies 1998) have suggested that community patterns and biological diversity in headwater streams are organized by geomorphic surfaces shaped by geomorphic processes. Within zero-order basins I delineated three geomorphic surfaces: valleys, headmost areas, and slopes (Figure 3.2). I defined valley geomorphic surfaces as convergent areas below (downstream of) the first evidence of scour and deposition. I defined headmost zones as convergent, filled valley areas above the first evidence of scour and deposition, extending to a topographic break. Headmost zones were inclusive of both hollows and source areas, as defined by Montgomery and Dietrich (1989). I defined slope geomorphic surfaces as non-convergent, planar surfaces, extending laterally from valley floors to ridgelines.

I established six amphibian sampling transects within each zero-order basin, two in each geomorphic surface (Figure 3.2). Transects in valley and headmost zones included a 15-m x 4-m section centered on basin center and extending upstream along the longitudinal axis, and a 5-m x 4-m section established perpendicular to the longitudinal axis at the upstream end of the longitudinal transect. This design was chosen to compare amphibian densities in valley surfaces to densities in lower slope geomorphic surfaces ("transition" slopes, as defined in Pabst and Spies 1988). Due to section overlap, the survey area within each of these amphibian transects was 76 m^2. Transects within slope geomorphic surfaces were placed perpendicular to the first and final in-valley transects, on opposite sides of the basin. Each slope transect consisted of one 15-m x 4-m section (60 m^2). Where the lateral distance from basin center to ridgeline was > 30 m, the start point of slope transects was established halfway between basin center and ridgelines, perpendicular to the longitudinal axis. Where total slope length was < 30 m, the start points of slope transects were placed 5 m from basin center.

I surveyed for amphibians from March through June in 2000 and 2001. I sampled amphibians in each transect using time-constrained searches of all cover objects and litter (Corn and Bury 1991) for a maximum of 30 minutes, not including animal processing time. I measured 31 environmental variables (Table 3.2) within zero-order basins that may be important in structuring amphibian assemblages. These data were collected at plot, transect and zero-order basin spatial scales. At the plot scale, data were collected for three substrate, two downed wood, and nine overstory parameters. Overstory variables were measured using variable-radius sampling in one plot per geomorphic surface. At the amphibian transect scale, data were collected on two positional, one surface moisture, and four scour and deposition parameters. Binary parameters for the presence/absence of saturation, scour, deposition, and stability in individual plots became proportions when averaged for lateral or geomorphic zones. At the zero-order basin level, I collected data on geomorphic surface, basin gradient, basin

Table 3.2. Description of habitat parameters collected at the plot, transect, or zero-order basin scale, covariates, and references for importance of ecological variables, and species associated with them.

Parameter	**Code**	**Units**	**Description**	**Ref.**[1]	**Species**[2]
Transect scale					
Ridge distance	DISTRIDG	m	Ridgeline to plot slope distance, divided by distance from ridgeline to initiation of scour.		A B C D^- E^-
Distance from center	DISTC	m	Perpendicular slope distance from center of the basin to plot location.	1, 2, 3, 4	C^- D E
Surface moisture	MOISTR	1-7	Integer index of plot moisture, modeled on categories developed by Crisafulli (Olson et al. 1999). Values range from 1 ('dry') to 7 ('flowing').	4, 7	A C
Saturation	SATUR	0, 1	Presence/ absence of field-estimated 'saturated' conditions.	4	A B C D^- E^-
Scour	SCOUR	0, 1	Presence/ absence of scour (removal of above ground vegetation and litter).	4	A B C
Deposition	DEPOSIT	0, 1	Presence/ absence of deposition (material from outside of the plot mobilized by fluvial or hillslope disturbance.	7	A B C
Stability	STABLE	0, 1	Presence/ absence of stable conditions (no scour or deposition).		C^- D^- E
Plot Scale					
Large substrate	LRGSUB	%	Visual estimate of % of plot surface obscured by gravel, cobble, boulders, or bedrock (substrates > 5 mm).	2,5	A B C D^- E^-
Organic substrate	ORGSUB	%	Visual estimate of % of plot surface obscured by litter, organic material, bark, or downed wood.	5,2	C D^- E
Litter depth	LITTER	cm	Litter depth averaged from five points/plot.	2,5	A^- B^- C $^-D^-$ E

Table 3.2. (continued)

Parameter	Code	Units	Description	Ref.[1]	Species[2]
Downed wood volume	CWDM3HA	m^3/ha	Volume of downed wood, calculated from visually estimated downed wood length and diameter.	1,2,5	A B C D E
Downed wood frequency	WOODFREQ	0-1	Presence/ absence of downed wood.	1,2,5	D
Canopy cover	CCTOT	%	Percent of view screen obscured in a canopy viewer (Mueller-Dombois and Ellenburg 1974) stationed at plot center.	5	A B C D E
Large overstory	BA70	m^2/ha	Basal area of trees over 70 cm in diameter.	2,5	A B C D E
Relative density	RD	0-100	Tree density metric calculated from basal area and quadratic mean diameter (Curtis 1982), using basal area from variable-radius overstory plots and visually estimated diameters.	3	C
Relative density within geomorphic surface	RDIN	0-100	Relative density (similar to Curtis 1982), calculated using only trees rooted in the same geomorphic surface as the variable-radius plot.		A^- B^- C D E
Relative density of hemlock	RDTSHE	0-100	Relative density (similar to Curtis (1982)), calculated using only western hemlock trees in variable-radius overstory plots.		A^- B^- C^- D E
Relative density of hardwood	RDHW	0-100	Relative density (similar to Curtis (1982)), calculated using only hardwood species in variable-radius overstory plots.		A B C D^- E^-
Snag density	SNAGS	m^2/ha	Snags/ha, calculated from variable-radius overstory plots	5	D
Fern cover	FERNS	%	% of plot surface obscured by ferns.	2,5	A B D
Shrub cover	SHRUBS	%	% of plot surface obscured by shrubs.	3	A^- B^- C^- D^-
Basin level					
Geomorphic surface	GEOSRF	Cat.	Three classes: valley, headmost area and slope.		C D E

Table 3.2. (continued)

Parameter	**Code**	**Units**	Description	**Ref.**[1]	**Species**[2]
Basin gradient	GRADE	°	Gradient (slope) of zero-order basin, calculated using difference in elevation and measured length of basin.	2,5,7	A B C D E
Feature depth	DEPTH	m	Difference in elevation between the midpoint of the geomorphic surface and the surrounding ridgeline.		A B E^-
Heat load index	HEATNDX	0-1	Relative measure of solar gain, calculated using the formula: 1-cos(aspect-45)/2 (Beers et al. 1966). 0 represents cool (45°) aspects, 1.0 represents warm (225°) aspects.	2,5,7	A^- B^- C^- D^- E^-
Basin area	AREA	ha	Area potentially contributing surface flow to the point of initiation of scour and deposition in a zero-order basin. Generated in ARC/INFO, using flow direction and accumulation algorithms and a 10-m digital elevation model.		A B C D^- E^-
Covariates					
Day number	DAY	0-180	Number of days from January 1 to survey date.		A^- B^- C^- D^- E^-
Relative humidity	RH	%	Relative humidity of transect area (sling psychrometer).		A B C D E
Temperature	TEMPF	°F	Temperature of transect area.		A B C D E
Elevation	ELEV	m	Zero-order basin ridge elevation (altimeter).	7	A^- B^- C^- D^- E^-
Ocean distance	DISTOCN	km	Distance from ocean, derived from ARC/INFO GIS coverages of the study area.		A^- B^- C^- D^- E^-
Stand age	AGE	years	Stand age of forested areas in the zero-order basin, derived from ARC/INFO GIS coverages of the study area.	2,5	A B C D E

[1] Key literature suggesting that the parameter may be related to amphibian density. Reference codes include: 1) Leonard et al. 1993; 2) Blaustein et al. 1995; 3) Vesely 1997; 4) Bury et al. 1991; 5) Corn and Bury 1991; 6) Bury and Corn 1988; 7) Bury, Corn and Aubry 1991.

[2] Species for which the parameter was used in habitat-association models. Species codes include: A) Southern torrent salamander; B) Dunn's salamander; C) western red-backed salamander; D) clouded salamander; E) ensatina . “-” represents parameters with a hypothesized negative effect on species capture.

depth, heat load index (a cosine transformation of basin aspect), and flow area above the initiation of scour and deposition. Data collected on covariates included date of survey, relative humidity, temperature, stand age and distance from ocean.

Statistical Analyses

Spatial distribution patterns

I used several analyses to examine the longitudinal and lateral distribution patterns of amphibian species. First, between-species, I compared proximity to ridgeline to determine the relative longitudinal extents of amphibians in zero-order basins. I considered the shortest slope distance along the longitudinal axis from ridgeline to a species capture in a zero-order basin as that species' proximity to ridgeline. I made between-species comparisons of proximity to ridgeline, using a general linear model (PROC GLM, SAS Institute 1999) with natural log of proximity to ridgeline as the response, and species as the explanatory variable. I quantified the size of differences in proximity to ridgeline between species using pair-wise means comparisons with a Tukey-Kramer adjustment for unplanned comparisons.

Similarly, I contrasted species' use of areas along lateral axes using between-species comparisons of maximum distance from basin center for each zero-order basin. I analyzed differences using a general linear model with the natural log of maximum distance from basin center to capture as the response, and species as the explanatory variable. I quantified the size of differences between species using pair-wise means comparisons with a Tukey-Kramer adjustment for unplanned comparisons.

Within-species, I compared differences in captures in each of three lateral zones, to examine species-specific penetration of "dry" and "moist" habitats. For this analysis I summed species captures made in each of three lateral zones: 0-2 m, 2- 5 m, and > 5 m (slope transect data) from basin center. I quantified differences in amphibian capture between lateral zones using log-linear regression models (PROC GENMOD, SAS Institute 1999), because amphibian species captures were collected as count data. Lateral zone was the explanatory variable and captures was the response for each model, for each species. I used an exchangeable correlation structure to model spatial autocorrelation between lateral zones within a zero-order basin. I included an offset to account for different sampling effort between lateral zones. Model goodness of fit was assessed using estimated deviance/degrees of freedom (df) and comparison of model predicted values to actual values.

Geomorphic surface zones integrate longitudinal and lateral environmental gradients in zero-order basins, and I hypothesized that species' densities would differ among geomorphic surfaces. Within-species, I quantified differences in amphibian captures between geomorphic surfaces using log-linear regression models (PROC GENMOD, SAS Institute 1999). For this analysis, I summed transect capture data for each geomorphic surface zone (valley, headmost and slope) in each zero-order basin. Geomorphic surface zone was the explanatory variable, and number of captures per geomorphic surface zone was the response, for each species. As in within-species lateral analyses, I used an exchangeable correlation structure to model spatial autocorrelation between geomorphic surface zones within a zero-order basin, and included an offset to account for different sampling effort.

For log-transformed responses in each of the above analyses, differences between groups (between species or between geomorphic or lateral zones) became ratios of median responses after back-transformation. Confidence intervals surrounding 1.0 implied no significant difference between groups.

Species-habitat models

For each amphibian species with > 50 captures, I developed sets of empirical log-linear regression models (PROC GENMOD, SAS Institute 1999) describing amphibian capture rates in unmanaged zero-order basins as a function of geomorphic position, surface moisture, substrate, canopy cover, downed wood and overstory parameters. For this analysis, amphibian captures were summed and environmental parameters were averaged for each geomorphic surface in each zero-order basin. I assessed spatial autocorrelation between geomorphic surfaces using generalized estimating equations (PROC GENMOD, SAS Institute 1999), and included an offset in models to account for the different amounts of area sampled in the different geomorphic surfaces.

I used an information-theoretic approach to model development and selection (Burnham and Anderson 1998), based on careful *a priori* development of models and inference based on model likelihood. Model sets represented competing hypotheses on the environmental drivers of amphibian species density in zero-order basins, using different combinations of explanatory variables. I developed *a priori* sets of ecological models from existing literature describing amphibian habitat associations (Table 3.2) and from general ecological theories (e.g., microclimate concepts (canopy cover, transect depth), island biogeography concepts (basin area, large overstory)). I constrained parameter number to a maximum of five per model, to allow tractability and the ability to discern between different processes. I used a $\log_e$ transformation for parameters hypothesized to have a threshold effect (Franklin et al. 2000) on amphibian captures (e.g., wood volume). Where Spearman rank correlations between variables were > 0.6 within a model, I subjectively eliminated correlated variables. Because ecological models were not hierarchically nested (Burnham and Anderson 2001), I developed a single global model containing the majority of the uncorrelated parameters used in each model set, to assess model fit and overdispersion for the model set. A null model, a model with only an intercept and no explanatory variables, was included to determine if any of the collected variables gave better fit to the response variable (amphibian captures) than consideration of the response mean alone.

For each model set, I used Akaike's Information Criterion (AIC), an estimate of Kullback-Liebler distance (the loss of information when a model is used to approximate truth), for model selection and ranking (Burnham and Anderson 1998). For model selection, the model with the smallest AIC value was judged the best approximation for the information in the data, relative to the models considered. Models within 2 AIC units of the best approximating model were considered reasonable competitors. Following model ranking, models within 2 AIC units of the best model were investigated for model fit by evaluating model deviance/df, by comparison of best models to the rank of the null model, and by comparison of predicted values to observed data in best models.

I used several measures to assess the strength of evidence for individual models in a set, including ΔAIC, the difference between the AIC value for a given model and the model with the lowest AIC value in the set. ΔAIC values can be used to compute Akaike weights (*w*), estimates of the relative likelihood of each model, given the likelihood of the full set of candidate models (Burnham and Anderson 2001).

For models within 2 AIC units of the best model, I developed estimates of the unconditional sampling variation of model parameters, and used it to adjust 95% confidence intervals for model parameters (Burnham and Anderson 1998). I interpreted adjusted confidence intervals for parameters from best models with consistent and strong effects on amphibian captures. I compared the relative importance of model parameters in each model set by computing parameter predictor weights (Burnham and Anderson 2001), an indicator of the importance of individual parameters in predicting response, considering the entire model set. Predictor weights were calculated by summing the Akaike weights of the models in which a parameter occurred. Model weights were adjusted (w') to account for different numbers of models with a given parameter following Stoddard (2001), using the formula:

$$w' = (\text{no. models/no. models with the variable}) \times (1/\text{no. variables}) \times w$$

Ordination

I examined the dominant gradients in amphibian species composition in zero-order basins using ordination. I used nonmetric multidimensional scaling (NMS; Mather 1976) in PC-ORD (McCune and Mefford 1997) to perform an indirect gradient analysis of experimental units (captures summed for each geomorphic surface in each zero-order basin) in amphibian species-space. I used a Sorenson distance measure, and detrended correspondence analysis (Hill and Gauch 1980) to establish starting coordinates for the ordination. Interpretation of ordination axes was facilitated by consideration of Spearman rank correlations between environmental parameters and axis scores. The final ordination was rotated to maximize correlations between axis 1 and the environmental variable with the single highest correlation with the ordination space. Ellipses were drawn around areas in ordination space with highest density for each species.

Development of amphibian species assemblages

I used indicator species analysis (Dufrene and Legendre 1997) to quantify the degree of association between amphibian species and geomorphic surface zones and lateral zones in zero-order basins. Indicator species analysis combines information on the abundance of a species in a class relative to its abundance in all classes with consistency of occurrence of a species in a class to provide an indicator value, the percent of perfect indication of a species for a particular class. I examined amphibian assemblages associated with each zone of each classification scheme, considering only species whose maximum indicator values were significantly higher than values from Monte Carlo simulations (2000 iterations, 0.05 level).

I compared the effectiveness of geomorphic surface zones and lateral zones in explaining amphibian species distributions by comparing the number of significant indicator species associated with each zone in each classification scheme, and the size of maximum indicator values. I used the sum of species' indicator values for each zone as a criterion to compare classification schemes for their ability to explain species distributions (Dufrene and Legendre 1997). I used a multi-response permutation procedure (MRPP: Biondini et al. 1988) to test the effect of geomorphic surface zones and lateral zones on species composition. MRPP is a non-parametric technique for testing a hypothesis of no significant difference between groups. I used MRPP in PC-ORD (McCune and Mefford 1997) with Sorenson distance and rank transformation of the distance matrix to address loss of sensitivity due to community heterogeneity. I estimated effect size using chance-corrected within-group agreement (*A*), an estimate of within-group homogeneity compared to random expectation.

RESULTS

I surveyed 382 transects in 63 unmanaged zero-order basins, capturing a total of 865 amphibians of 8 species: western red-backed salamander (*Plethodon vehiculum* (Cooper); southern torrent salamander (*Rhyacotriton variegatus* Stebbins and Lowe); Dunn's salamander (*Plethodon dunni* Bishop); clouded salamander (*Aneides ferreus* Strauch); ensatina (*Ensatina eschscholtzii* Gray); Pacific giant salamander (*Dicamptodon tenebrosus* Good); tailed frog (*Ascaphus* *truei* Stejneger), and Northwestern salamander (*Ambystoma gracile* (Baird)) (Table 3.3). Only terrestrial (adult) tailed frogs were observed, whereas Pacific giant salamanders included both terrestrial and aquatic forms. Captures averaged over 6.3 (95% confidence interval (CI): 5.48, 7.26) detections/surveyor hour. Amphibian densities were highly variable by species and by geomorphic surface (Table 3.3). Average amphibian diversity (Shannon index, H') in zero-order basins was relatively low. Average diversity in valley geomorphic surfaces was 0.33 units higher (95% CI: 0.16, 0.50) than in headmost surfaces. Average amphibian diversity in headmost areas was 0.13 units higher than slope areas, but this trend was not significant (95% CI: -0.05, 0.30). Four of the eight amphibian species identified in zero-order basins are considered species of concern by state or federal governments in all or parts of their ranges (Table 3.1).

Spatial patterns in amphibian assemblages

Species associated with riparian and seep habitats, including Pacific giant, torrent and Dunn's salamanders, occurred further from ridgelines than species associated with upslope conditions like clouded salamander and ensatina (Table 3.4). Mean minimum longitudinal distances from ridgeline to capture ranged from 104.5 m (95% CI: 81.8, 127.2) for ensatina to 174.6 m (95% CI: 139.2, 210.0) for

Table 3.3. Total number of herpetofauna captures (**bold**), densities, richness and diversity for each geomorphic surface, and species proximity to ridgeline (95% CI) and distance from basin center (95% CI). Densities (mean number of captures/ 1000 m^2 searched) provided only for species with over 30 captures (95% CI). Diversity (H') is mean of Shannon Index (95% CI).

Species	**Geomorphic surface**			**Total**	**Spatial metrics**	
	Valley	**Headmost**	**Slope**		**Proximity to ridgeline**	**Distance from basin center**
	(n=63)	(n=63)	(n=63)		(n = 12-52)[1]	(n = 12-52)[1]
Western red-backed salamander	**88**:9.31 (6.65, 11.97)	**101**:11.14 (7.85, 14.44)	**92**:12.36 (9.45, 15.28)	**281**	139.40 (109.00, 169.80)	21.27 (16.98, 25.56)
Southern torrent salamander	**139**:16.06 (10.63, 21.5)	**27**:2.35 (0.43, 4.27)	**2**:0.3 (-0.12, 0.72)	**168**	174.60 (139.20, 209.99)	1.89 (-0.06, 3.84)
Dunn's salamander	**121**:12.85 (9.48, 16.22)	**34**:3.13 (1.46, 4.81)	**5**:0.61 (0.08, 1.14)	**160**	170.71 (142.90, 198.53)	3.40 (1.81, 5.00)
Clouded salamander	**28**:2.8 (1.66, 3.95)	**64**:8.83 (5.64, 12.02)	**37**:4.75 (2.84, 6.66)	**129**	112.09 (91.63, 132.55)	14.28 (9.85, 18.72)
Ensatina	**5**:0.38 (-0.01, 0.78)	**40**:5.68 (3.36, 8.01)	**32**:3.93 (2.23, 5.63)	**77**	104.53 (81.81, 127.24)	14.86 (9.71, 20.00)
Pacific giant salamander	**32**:3.17 (1.68, 4.66)	**2**:0.28 (-0.11, 0.67)	**1**:0.11 (-0.10, 0.33)	**35**	174.5 [1](137.53, 211.47)	0.38[1] (-0.26, 1.01)
Tailed frog	**5**	**1**	**1**	**7**		
Plethodontid juveniles (< 15 mm)	**7**	**0**	**0**	**7**		
Northwestern salamander	**0**	**1**	**0**	**1**		
Southern alligator lizard	**0**	**1**	**0**	**1**		
Total captures	425	270	170	**865**		
Number of transects	136	119	127	382		
Richness	7	8	7			
Diversity (H')	0.89 (0.76, 1.01)	0.56 (0.42, 0.69)	0.49 (0.31, 0.55)			

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[1] Sample sizes (n) for spatial metrics are variable, depending on species' presence in zero-order basins

Table 3.4. Between-species ratios of median proximity to ridgeline (95% CI) and median maximum distance from center (95% CI). Results are ordered by size of proximity to ridgeline ratio (n = 63). "A" indicates aquatic life form; "T" indicates terrestrial life form.

Species 1	Species 2	Proximity to ridgeline	Distance from center
Pacific giant (A)	Ensatina	1.92 (1.02, 3.63)*	0.17 (0.06 , 0.42)*
Pacific giant (A)	Clouded	1.75 (0.93, 3.23)	0.17 (0.07, 0.43)*
Pacific giant (A)	W. red-backed	1.59 (0.87, 2.91)	0.1 (0.04 , 0.23)*
Pacific giant (A)	Dunn's	1.11 (0.6, 2.04)	0.47 (0.19 , 1.15)
Pacific giant (A)	Pacific giant (T)	1.11 (0.5, 2.47)	0.41 (0.11 , 1.54)
Pacific giant (A)	Southern torrent	1.1 (0.59, 2.05)	1.88 (0.59 , 5.97)
Pacific giant (T)	Ensatina	1.73 (0.9, 3.33)	0.41 (0.13 , 1.31)
Pacific giant (T)	Clouded	1.56 (0.82, 2.94)	0.42 (0.13, 1.33)
Pacific giant (T)	W. red-backed	1.43 (0.76, 2.67)	0.24 (0.08 , 0.73)*
Southern torrent	Ensatina	1.75 (1.14, 2.7) *	0.22 (0.11, 0.43)*
Southern torrent	Clouded	1.59 (1.05, 2.38) *	0.23 (0.12, 0.43)*
Southern torrent	W. red-backed	1.45 (0.98, 2.13)	0.13 (0.07, 0.23)*
Southern torrent	Pacific giant (T)	1.02 (0.53, 1.96)	0.53 (0.17, 1.70)
Southern torrent	Dunn's	1.01 (0.68, 1.52)	0.61 (0.33, 1.13)
Dunn's	Ensatina	1.72 (1.15, 2.63) *	0.36 (0.19, 0.68)*
Dunn's	Clouded	1.56 (1.06, 2.33) *	0.37 (0.20, 0.68)*
Dunn's	W. red-backed	1.44 (0.99, 2.07)	0.21 (0.12 , 0.36)*
Dunn's	Pacific giant (T)	1.01 (0.53, 1.89)	0.87 (0.28, 2.70)
W. red-backed	Ensatina	1.2 (0.81, 1.82)	1.72 (0.93, 3.23)
W. red-backed	Clouded	1.1 (0.75, 1.61)	1.79 (0.99, 3.23)
Clouded	Ensatina	1.1 (0.72, 1.69)	0.97 (0.50, 1.87)

* $p \leq 0.05$ for individual two-species comparison, after Tukey-Kramer adjustments

torrent salamander. Five of 21 between-species comparisons for longitudinal proximity of amphibian species to ridgeline were significant. The median proximity to ridgeline of aquatic Pacific giant salamanders was approximately 1.9 times larger than that of ensatina. Torrent and Dunn's salamanders, usually associated with fluvial environments, occurred over 1.5 times farther from ridgelines than clouded salamander and ensatina, usually associated with upslope environments. The other 16 between-species comparisons were not significant.

Although patterns in species maximum distance from basin center were comparable to species proximity to ridgeline, differences between species in maximum distance from basin center were stronger, and the spatial patterning of western red-backed salamander relative to other amphibians was clarified (Table 3.4). Mean maximum distances from basin center ranged from 0.4 m (95% CI: -0.3, 1.0) for aquatic forms of the Pacific giant salamander to 21.3 m (95% CI: 17.0, 25.6) for western red-backed salamander. The median maximum distances from basin center for Pacific giant, torrent and Dunn's salamanders were less than half that of ensatina and clouded salamanders. In contrast to results for proximity to ridgeline, western red-backed salamander occurred significantly farther from basin center than Pacific giant, torrent and Dunn's salamanders (Table 3.4).

Within-species, capture rates differed among lateral zones for four of the five amphibians with over 50 captures (Table 3.5). Median capture rates of torrent salamander were over six times higher in areas within 0-2 m of the center of zero-

Table 3.5. Ratios of median species captures between lateral zones and between geomorphic surface zones, for 5 species, with 95% confidence intervals (n=189). **Bold** indicates significant contrasts ($p<0.05$). Model fit statistics include an estimate of deviance divided by degrees of freedom (Dev/df).

	Lateral zone contrasts			**Geomorphic surface zone contrasts**		
	Model fit	**Ratios**		**Model fit**	**Ratios**	
Species	**Dev/ df**	**0-2 m/ 2-5 m**	**2-5 m / > 5 m**	**Dev/ df**	**Valley/ Headmost**	**Headmost / Slope**
Southern torrent[1]	1.36	**6.08** **(2.58, 14.34)**	**13.77** **(1.63, 116.27)**	1.80	**4.95** **(2.20, 11.13)**	**11.65** **(2.36, 57.55)**
Dunn's	1.07	1.52 (0.92, 2.53)	**9.09** **(3.26, 25.36)**	1.25	**3.10** **(1.75, 5.49)**	**6.12** **(2.12, 17.03)**
W. red-backed[2]	1.56	**0.49** **(0.37, 0.65)**	**1.55** **(1.10, 2.17)**	1.69	0.78 (0.54, 1.13)	0.96 (0.70, 1.32)
Clouded	1.44	**0.53** **(0.27, 0.85)**	**2.10** **(1.02, 3.45)**	1.38	**0.38** **(0.26, 0.55)**	1.60 (0.95, 2.72)
Ensatina	1.06	1.19 (0.30, 1.45)	1.53 (0.39, 1.79)	1.02	**0.10** **(0.03 – 0.30)**	1.16 (0.71, 1.90)

[1] Lateral model included year (2000, 2001) as a covariate. Geomorphic model included day number as a covariate.
[2] Lateral model included day number as a covariate.

order basins than in areas 2-5 m from basin center, and over 13 times higher in the 2-5 m zone than in the > 5 m zone. Dunn's salamander capture rates were similar in the first five meters from basin center. However, Dunn's salamander median capture rates were over nine times higher in areas 2-5 m from basin center than in areas > 5 m from center (slope zone). Western red-backed salamander and clouded salamander captures were both higher in the 2-5 m zone than in either the 0–2 m or > 5 m lateral zones. There were no differences in captures between the three lateral zones for ensatina.

Within-species, capture rates differed among lateral zones for four of the five species with over 50 captures (Table 3.5, ratios in bold show significant contrasts). Median capture rates of torrent salamander were over six times higher in areas within 0-2 m of the center of zero-order basins than in areas 2-5 m from basin center, and over 13 times higher in the 2-5 m zone than in the > 5 m zone. Dunn's salamander capture rates were similar in the first five meters from basin center. However, Dunn's salamander median capture rates were over nine times higher in areas 2-5 m from basin center than in areas > 5m from center (slope zone). Western red-backed salamander and clouded salamander captures were both higher in the 2-5 m zone than in either the 0–2 m or > 5 m lateral zones. There were no differences in captures between the three lateral zones for ensatina. For the five models, estimated deviance/df ranged from 1.06 (ensatina) to 1.56 (western red-backed), suggesting moderately low overdispersion and adequate model fit.

Spatial autocorrelation between lateral zones was quite low, ranging from 0.04 (torrent) to 0.21 (western red-backed).

Log linear models of amphibian capture rates as a function of geomorphic surface zone were significant in four of the five species tested (Table 3.5). Median capture rates for torrent salamanders were almost five times higher in valley zones than in headmost zones, and over 11.5 times higher in headmost zones than in slope zones. Dunn's salamander captures were over three times higher in valley zones than in headmost zones, and over six times higher in headmost zones than in slope zones. There were no differences in captures of western red-backed salamander between geomorphic surface zones. Clouded salamander captures in valley zones were less than half those in headmost zones. There was a trend of more clouded salamander captures in headmost than in slope zones. Similarly, median ensatina captures in valley zones were one tenth those in headmost zones, but captures in headmost zones were not different than slope zones. Estimated deviance/df was 1.8 for torrent salamander, suggesting moderately poor model fit. Spatial autocorrelation between geomorphic surfaces was modest, ranging from 0.014 (torrent) to 0.231 (clouded).

Amphibian associations with environmental parameters

Empirical models of amphibian capture rates as a function of sets of environmental variables were developed for the five species with > 50 captures. Model number ranged from 28 models for torrent salamander to 30 models for western red-backed and clouded salamanders including the global model, a null model, and five covariate models (Tables E1-E5, Appendix E). Spatial autocorrelation between geomorphic surfaces was relatively low (0.02 to 0.17). The scale parameter (a measure of overdispersion) was 1.1 for the global models for ensatina, torrent and Dunn's salamander, 1.22 for western red-backed and 1.3 for clouded salamander, implying moderately good model fit. Additionally, sample size was less than 25 times larger than parameter number for most models. I therefore used a version of AIC incorporating both a quasi-likelihood modification and a small sample size modification, referred to as QAICc. Best models for each species are presented below (Table 3.6); complete *a priori* model sets for each species are shown in Appendix E.

Torrent salamander

The model set describing torrent salamander captures as a function of environmental variables included parameters directly or indirectly linked to the

Table 3.6. Results of model selection and ranking for models predicting amphibian captures as a function of environmental variables. Results include model parameters, model fit statistics, and estimated slope parameters (95% CI) for log linear regression models with $\Delta QAICc \leq 2$, for 5 species (n = 126 for southern torrent and Dunn's salamander and ensatina, 189 for western red-backed and clouded salamander). "k" represents the number of parameters in a model. "*w*" is Akaike model weight. Model fit statistics include deviance/degrees of freedom (Dev/df). Parameter slope estimates provided in model order, significant parameters shown in **bold.** Environmental parameter codes provided in Table 3.2.

Species Model no.	MODEL	k	ΔQAICc	w	Dev/ df	Estimated slope parameters (95% CI)
Southern torrent salamander models						
RV18	**GRADE** + HEATNDX + DISTRIDG + **SATUR**	5	0	0.844	1.48	β_1= -7.543 (-8.607, -6.502)
						β_2= 0.024 (0.002, 0.046)
						β_3= -0.469 (-0.977, 0.039)
						β_4= -0.094 (-0.532, 0.345)
						β_5= 3.937 (3.184, 4.69)
Dunn's salamander models						
PD11	**SHRUBS** + **CCTOT** + **SATUR** + LRGSUB	5	0	0.903	1.33	β_1= -5.375 (-6.484, -4.306)
						β_2= 0.013 (0.005, 0.021)
						β_3= -0.012 (-0.024, -0.001)
						β_4= 1.689 (1.154, 2.224)
						β_5= 0.006 (-0.004, 0.016)
Western red-backed salamander models						
PV7	**SATUR + LRGSUB**	3	0	0.337	1.63	β_1= -4.63 (-4.872, -4.391)
						β_2= -0.892 (-1.366, -0.440)
						β_3= 0.013 (0.006, 0.021)
PV19	**GRADE**+**AREA**+ HEATINDEX + DISTC + LN(DISTRIDG)	6	0.708	0.237	1.62	β_1= -5.127 (-5.648, -4.615)
						β_2= 0.036 (0.017, 0.055)
						β_3= -0.307 (-0.51, -0.103)
						β_4= 0.127 (-0.4, 0.655)
						β_5= 0.006 (-0.009, 0.021)
						β_6= 0.006 (-0.325, 0.337)
PV15	**LRGSUB** + **SATUR** + RDHW + CCTOT	5	1.729	0.142	1.63	β_1= -5.078 (-6.081, -4.132)
						β_2= 0.016 (0.006, 0.024)
						β_3= -0.946 (-1.432, -0.460)
						β_4= -0.008 (-0.022, 0.005)
						β_5= 0.006 (-0.005, 0.018)
Clouded salamander models						
AF16	**GEOSRF**	3	0	0.31	1.38	β_1= -5.33 (-5.784, -4.942)
						β_2= Cat.

Table 3.6. (continued)

Species Model no.	MODEL	k	ΔQAICc	w	Dev/ df	Estimated slope parameters
Clouded salamander models (continued)						
AF19	**GEOSRF**+SATUR+**LN(BA70)** +WOODFREQ+ LRGSUB	7	0.840	0.204	1.34	β_1= -7.004 (-8.84, -5.299) **β_2= Cat.** β_3= 0.806 (-0.119, 1.731) **β_4= 0.437 (0.01, 0.864)** β_5= 0.094 (-0.748, 0.936) β_6= -0.006 (-0.021, 0.01)
AF17	**GEOSRF** + AREA + GRADIENT + HEATINDX	6	1.811	0.125	1.36	β_1= -4.526 (-5.39, -3.684) **β_2= Cat.** β_3= -0.047 (-0.252, 0.158) β_4= -0.024 (-0.054, 0.006) β_5= -0.523 (-1.191, 0.144)
Ensatina models						
EE4	**RDIN** + CCTOT	3	0	0.194	1.21	β_1=-8.348 (-10.686, -6.32) **β_2= 0.019 (0.006, 0.031)** β_3=0.025 (-0.002, 0.052)
EE10	**RDTSHE** + CCTOT + LITTER	4	0.361	0.162	1.2	β_1= -7.248 (-9.524, -5.277) **β_2= 0.019 (0.007, 0.031)** β_3=0.019 (-0.001, 0.051) β_4= -0.156 (-0.587, 0.274)
EE21	**RDIN** + **CCTOT** + LITTER + STABLE	5	0.794	0.13	1.19	β_1= -8.33 (-10.83, -6.16) **β_2= 0.015 (0.002, 0.029)** **β_3= 0.026 (0.001, 0.054)** β_4= -0.368 (-0.868, 0.055) β_5= 0.598 (-0.388, 1.696)
EE11	**LRGSUB** + RDHW + SATUR	4	0.810	0.129	1.2	β_1= -4.964 (-5.34, -4.617) **β_2= -0.037 (-0.063, -0.014)** β_3= 0.014 (-0.007, 0.035) β_4=-1.184 (-2.971, 0.603)
EE7	CCTOT + LITTER +**ORGSUB**	4	1.502	0.092	1.21	β_1=-8.548 (-11.068, -6.335) **β_2= 0.025 (0.001, 0.053)** β_3=-0.3 (-0.755, 0.088) **β_4= 0.023 (0.007, 0.039)**
EE20	CCTOT + ORGSUB + DISTC + GRADE	5	1.969	0.072	1.2	β_1=-7.69 (-10.358, -5.29) β_2=0.023 (-0.001, 0.051) β_3=0.016 (-0.002, 0.034) β_4=-0.009 (-0.037, 0.015) β_5=-0.031 (-0.064, 0.001)

presence of seeps, saturated conditions, larger substrate (gravels, talus), and shading (Table E1, Appendix E). For torrent salamanders, only valley and headmost zones were modeled, because only two captures occurred in slope zones. The most parsimonious model for torrent salamander captures in zero-order basins (RV18, Table E1; Table 3.6) included terms for basin gradient, heat load index, distance from ridge (corrected for distance from ridge to scour initiation) and saturation. The Akaike weight of this model was 0.84. The model was over five QAICc units from its closest competitor, and 12.41 times more likely to be the best model for the data. All models within a 99.5% confidence set of cumulative model weights contained the saturation parameter.

In the best model (RV18), a change from dry to saturated conditions resulted in a 51.3-fold (95% CI: 24.14, 108.89) increase in median capture numbers, after accounting for the other factors in the model. An increase in basin gradient of 1° was associated with a 2.4% (95% CI: 0.24, 4.7) increase in capture number, after accounting for the other factors in the model. The direction of effect for saturation and basin gradient were both positive, as predicted. Normalized parameter predictor weights (Table 3.7) suggested that basin gradient and heat load index were the most important variables in the model set for predicting torrent salamander captures.

The global model was initially ranked above all other models, due to a very high number of parameters. This model was not consistent with analysis goals, and was eliminated from consideration. The null model was ranked 26th out of the

Table 3.7. Parameter predictor weights from empirical models for five salamanders, for all parameters within the 0.95 confidence set of model weights, normalized to sum to 1.0. Parameter predictor weights are defined in methods.

Environmental parameters	Southern torrent	Dunn's	Western red-backed	Clouded	Ensatina
Geomorphic parameters					
Geomorphic surface				0.273	
Basin area		0.006	0.131	0.125	
Basin gradient	0.438		0.142	0.094	
Heat load index	0.438		0.131	0.085	
Ridge distance	0.063	0.003	0.072		
Distance from center			0.101		
Fluvial and hillslope parameters					
Saturation	0.058	0.101	0.131	0.102	0.056
Deposition		0.002			
Stability				0.088	0.038
Large substrates	0.004	0.097	0.156	0.053	0.162
Litter depth					0.068
Organic substrate					0.055
Overstory parameters					
Canopy cover		0.231	0.028		0.093
Large overstory		0.010	0.0291	0.0851	
Relative density within geo. surf.					0.203
Relative density of hardwoods		0.001	0.079		0.162
Relative density of w. hemlock					0.101
Downed wood volume		0.003		0.024	0.062
Downed wood frequency				0.071	
Shrub cover		0.545			

remaining 27 models (ΔQAICc = 176.19, Table E1), implying good fit of most models. However, the best model had moderately high deviance/df, and only moderate fit of observed to predicted values. These results temper support for optimal fit of a model of torrent salamander captures as a function of gradient, heat load index, distance from center of basin and saturation.

Dunn's salamander

The model set for Dunn's salamander included parameters directly or indirectly linked to saturation, large substrate and vegetative shading (Table E2, Appendix E). For Dunn's salamander, only valley and headmost zones were modeled, because only five captures occurred in slope zones.

The most parsimonious model for Dunn's salamander captures in zero-order basins (PD11, Table E2; Table 3.6) included terms for shrub cover, canopy cover, saturation and large substrate. This model had an Akaike weight over 0.9, was over 5.8 QAICc units from its closest competitor, and was 18 times more likely to be chosen as the actual best model in the set. In the single best model for Dunn's salamanders, an increase of 1% in shrub cover was associated with a 1.3% (95% CI: 0.48, 2.12) increase in median number of captures, after accounting for other factors in the model. An increase in canopy cover of 1% resulted in a 1.2% (95% CI: 0.1, 2.34) decrease in median captures, after accounting for the other factors in the model. A change from dry to saturated conditions resulted in a 5.4-fold (95% CI: 3.17, 9.24) increase in captures, after accounting for the other factors in the model. The positive direction of effect for saturation was consistent with expected results. The negative effect of canopy cover and positive effect of shrub cover were not consistent with expectation, and may be due to an association of Dunn's salamander with fluvially-disturbed, open, riparian shrub-dominated areas within stands with otherwise high canopy cover. Normalized parameter predictor weights supported the positive effect of shrub cover and saturation and the negative effect of canopy cover as the most important model parameters for predicting Dunn's salamander captures (Table 3.7).

The single best *a priori* model for predicting Dunn's salamander captures had a weight of 0.90 and deviance/df of 1.33. The null model was ranked 25th out of 29 models (ΔQAICc = 62.64, Table 3.A2), and there was a moderately strong relationship between model predictions and observed values. There is thus moderately good support for a model of Dunn's salamander captures as a function of shrub and canopy cover, saturation, and large substrate.

Western red-backed salamander

The model set for the western red-backed salamander included parameters for surface moisture, organic substrates, large substrate, downed wood, and overstory characteristics (Table E3, Appendix E). The most parsimonious model for western red-backed salamander captures in zero-order basins (PV7, Table E3, Appendix E; Table 3.6) included terms for saturation and large substrate. This model was less than 0.71 QAICc units from its closest competitor, and only 1.42 times more likely to be the best fit to the data. Two other models were within 2 QAICc units of the top-ranked model (Table 3.6).

The saturation parameter occurred in two of the models with ΔQAICc < 2, with a coefficient range of –1.43 to -0.44. In the highest ranked model (PV7), change from dry to saturated conditions was associated with a 2.44-fold decrease (95% CI: 1.55, 3.92) in median number of captures, after accounting for large substrate. For model PV7, an increase of 1% in large substrate cover was associated with a 1.5% (95% CI: 0.6, 2.1) increase in median captures. For model PV19 (Table E3), an increase in basin gradient of 1° was associated with a 3.67% (95% CI: 1.71, 5.65) increase in captures, after accounting for other factors in the models. In model PV19, a 1 ha increase in basin area was associated with a 35.9% (95% CI: 10.88, 66.55) decrease in captures, after accounting for other factors in the models. The negative direction of effect for saturation and basin area in top models were not consistent with *a priori* predictions that western red-backed salamander would choose wetter portions of zero-order basins. Positive association with large substrate and basin gradient followed expectation. Normalized parameter predictor weights supported large substrate, basin gradient, saturation, basin area and heat load index as the five most important variables for predicting western red-backed salamander captures (Table 3.7).

The null model was ranked 23rd out of 30 models (ΔQAICc = 14.93, Table E3) and there was a moderately strong relationship between model predictions and observed values. However, the best models had moderately high deviance/df (1.63) and there was wide discrepancy among top models, with no clearly superior single model or parameters. This suggested only moderate support for a model of western red-backed captures as a function of saturation and large substrate.

Clouded salamander

The model set for the clouded salamander included parameters for geomorphic zone, downed wood, large substrate, and overstory characteristics (Table E4, Appendix E). Three models within the *a priori* model set had ΔQAICc < 2 (Table 3.6). The most parsimonious model for clouded salamander captures in zero-order basins (AF16, Table E4; Table 3.6) was a univariate model with a categorical variable for geomorphic surface, with a weight of 0.316. This model was less than one QAICc unit from its closest competitor, and only 1.52 times more likely to be the best fit to the data in the model set. All three models with ΔQAICc < 2 supported the geomorphic surface parameter. For the single best model in the model set, change from valley to headmost zone was associated with a 36% (95%

CI: 14.8, 98.5) increase in median capture rates (Table 3.6). Differences in captures between other geomorphic zones were not significant. For model AF19 (Table E4), a 2-fold change in basal area of trees over 70 cm was associated with a 35.16% (95% CI: 0.67, 81.47) increase in median capture rates, after accounting for other factors in the models. Normalized parameter predictor weights supported changes in geomorphic surface, basin area and saturation as the most important parameters for predicting clouded salamander captures. The positive relationship between large overstory and clouded salamander captures was expected.

The null model was ranked 14th out of 31 (ΔQAICc = 7.83, Table E4). *A priori* models had moderate deviance/df (1.34-1.37), and there was a weak relationship between model predictions and observed values for the best *a priori* model (AF16). There was no clearly superior *a priori* model, and no distinct subset of important parameters other than geomorphic surface. This suggests relatively weak support for a model of clouded salamander captures as a function of geomorphic surface.

Ensatina

The model set for ensatina captures included parameters for surface moisture, substrate composition, downed wood, and overstory characteristics (Table E5, Appendix E). Only headmost and slope zones were modeled, since only five captures occurred in valley zones. The most parsimonious model for ensatina captures in zero-order basins (EE4, Table E5; Table 3.6) had a model weight of 0.19 and included terms for relative density of trees within the geomorphic surface and canopy cover. This model was less than 0.4 QAICc units from its closest competitor, and only 1.2 times more likely to be the best fit to the data. Five other models were within 2 QAICc units of the top-ranked model. For the six models for ensatina salamanders with ΔQAICc < 2, five parameters were significant in at least one model (Table 3.6). Relative density within geomorphic surfaces occurred in two of the top models, with a transformed coefficient range of 0.002 to 0.031. In the highest ranked model (EE4), a one unit increase in relative density within geomorphic surfaces was associated with a 1.87% increase (95% CI: 0.57, 3.18) in median capture rates, after accounting for canopy cover. For model EE10, an increase of one unit in relative density of hemlock was associated with a 1.92% (95% CI: 0.65, 3.20) increase in median ensatina captures, after accounting for other model parameters. The positive direction of effect for overstory measures and organic substrate were consistent with hypothesized relationships for ensatina. Normalized parameter predictor weights supported relative density within geomorphic surface, large substrate, relative density of hardwoods, relative density of hemlock and canopy cover as the five most important variables for predicting ensatina captures in zero-order basins.

The top *a priori* models had deviance/df less than 1.25, however the null model was ranked 16th out of 29 (ΔQAICc = 9.73, Table E5). The best *a priori* model had a moderately weak relationship between model predictions and observed values. In the best model, canopy cover had a coefficient range including zero. These findings suggest relatively weak support for a model of ensatina captures as a function of relative density of trees within the geomorphic surface and canopy cover.

Ordination

Ordination of geomorphic surfaces in amphibian species-space clarified the dominant gradients in amphibian composition in zero-order basins (Figure 3.3). A three-dimensional NMS solution had "stress" (a measure of dissimilarity between the original data and the reduced ordination space) of 12.7, and appeared stable within 100 iterations. Final ordination stress was within levels considered "interpretable" under the stringent criteria developed by Clarke (1993). For interpretation, the 3-dimensional ordination was rotated such that the interpretable portion was in two dimensions. Ordination distances in this 2-dimensional space had a summed correlation to the original seven-dimensional space of 0.727. The third axis had a correlation to the original seven-dimensional space of 0.178. The ordination was rotated to maximize correlations between Axis 1 and the stability parameter. With this rotation, Axis 1 was positively associated with stability ($r = 0.611$), relative density within geomorphic surfaces ($r = 0.618$), and overstory basal

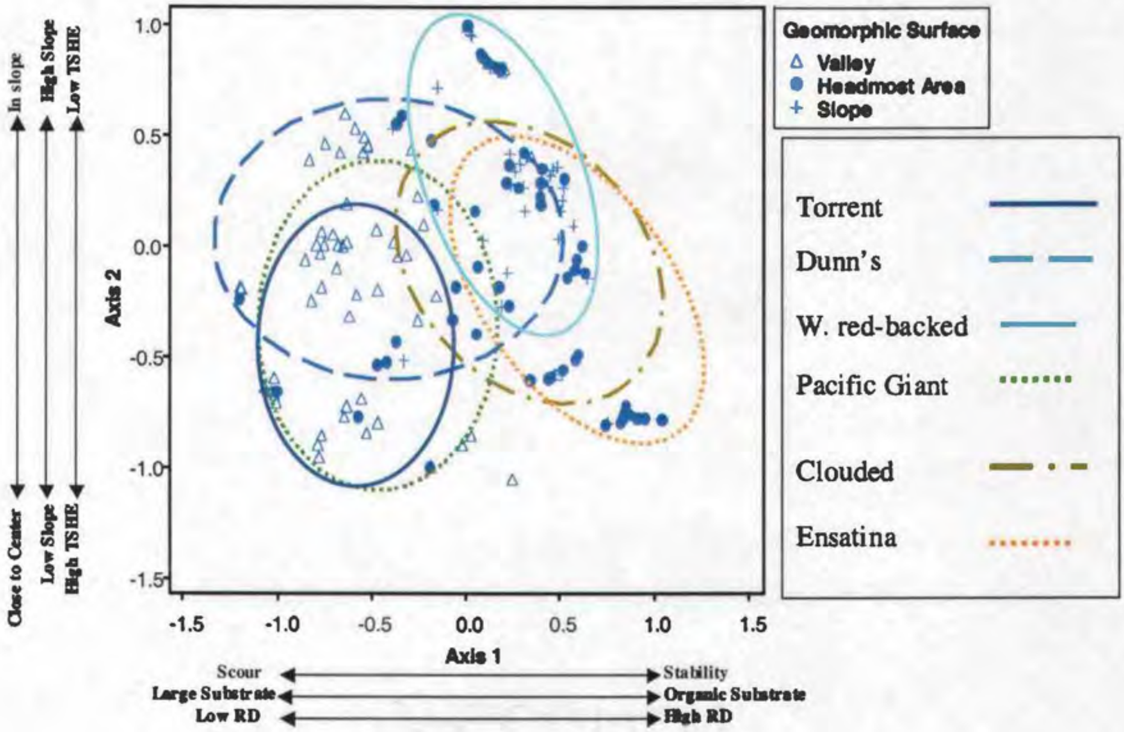

Figure 3.3. Ordination of experimental units along two axes in amphibian species-space (n = 176). Experimental units (points) are amphibian transects, averaged for each geomorphic surface in a basin. Geomorphic surface membership is shown, overlain on points. Ellipses are drawn around points with highest densities of respective species. Directional arrows indicate important environmental gradients identified through correlation analysis.

area (r = 0.470) (Figure 3.3). Axis 1 was negatively associated with surface moisture (r = -0.550), scour (r = -0.574), and large substrate cover (r = -0.477). Correlations between environmental variables and scores on axis 2 were relatively low, including positive correlations with basin gradient (r = 0.284) and distance from center (r = 0.199), and negative correlations with relative density of hemlock (r = -0.212). These correlations were all significant (p < 0.001).

Torrent, Dunn's and Pacific giant salamanders were tightly coupled in ordination space, in areas of the ordination associated with fluvial/hillslope disturbance and surface moisture. Clouded salamander and ensatina had highest densities at the opposite end of the dominant gradient, associated with surface stability and dense overstory. Western red-backed salamander was peripheral in ordination space, associated with steep areas far from fluvial center. There was much more overlap in amphibian composition between slope and headmost zones than between these and the more distinct valley zones in ordination space.

Development of geomorphic and lateral zone species assemblages

Indicator species analysis supported the importance of geomorphic surfaces shown in earlier analyses, clarified the hierarchical importance of lateral zones within geomorphic surfaces, and showed assemblages associated with each zone in each of the two classification schemes (Table 3.8). For the geomorphic surface

Table 3.8. Indicator values of species for geomorphic surface zones and lateral zones, developed using indicator species analysis. "Max. indicator value" represents the percentage of perfect indication of a species for the group it was most strongly associated with. "p" is the proportion of shuffled data matrices having max. indicator values as high as or higher than the original data (Monte Carlo test). **"Σ IV"** is sum of species indicator values for each class, shown in **bold**. N = 176 for geomorphic surface zones, 166 for lateral zones.

Geomorphic surface zones	**Max. indicator value**	**p**	**Lateral zones**	**Max. indicator value**	**p**
Valley			**0-2 m**		
Dunn's	56.7	0.001	Southern torrent	57.3	0.001
Southern torrent	52.7	0.001	Dunn's	49.4	0.001
Pacific giant (A)	19.4	0.001	Pacific giant (A)	15.3	0.005
Pacific giant (T)	11.3	0.004	Tailed frog	7.1	0.035
Σ IV: 184			**Σ IV: 174**		
Headmost			**2-5 m**		
Clouded	29.8	0.002	No significant species		
Ensatina	24.4	0.003			
Σ IV: 87			**Σ IV: 62**		
Slope			**> 5 m**		
W. red-backed	31.4	0.055	No significant species		
Σ IV: 70			**Σ IV: 55**		

classification scheme, three species were significant indicators for valley zones, including both terrestrial and aquatic forms of the Pacific giant salamander. Clouded and ensatina salamanders were significant indicators for headmost zones. These species had higher densities in and fidelity to headmost areas than to other geomorphic surfaces, forming a unique assemblage associated with headmost areas. Western red-backed salamander was only a marginally significant indicator for slope zones, consistent with its high densities in all three geomorphic zones. Indicator species analysis results for the lateral zone classification scheme clarified the hierarchical nesting of lateral differences in amphibian composition within geomorphic surfaces (Table 3.8). Four species were significant indicators for the 0-2 m lateral zone. Only torrent salamander had a higher individual maximum indicator value in the lateral zone classification scheme, consistent with its strong ties to fluvial characteristics present at fluvial center. Clouded salamander, ensatina and western red-backed salamander were not significant indicators for any lateral zone, implying that these species were present across lateral zones in zero-order basins. These results are comparable to contrasts from log linear models, and suggest that these terrestrial-breeding amphibians assort more by geomorphic surface than by proximity to fluvial center.

The geomorphic surface zone classification scheme had higher summed indicator values than the most similar lateral zone for each zone (Table 3.8). Significance test results and estimates of effect sizes for the two different classification schemes using MRPP provided similar results. There were significant differences in amphibian species distributions between zones in both classification schemes (T values: -20.98 and –27.85, $p < 0.0001$). The geomorphic surface zone classification scheme had a slightly higher chance-corrected within-group agreement ($A = 0.153$) than the lateral zone scheme ($A = 0.116$). The results of indicator species analysis and MRPP suggest that differences in geomorphic surface are more important than lateral zone distinctions in structuring amphibian assemblages in zero-order basins.

DISCUSSION

The implementation of buffer protection in western North American riparian areas (Table 3.1) since the 1950's (Gregory 1997) has modified management in forested landscapes. However, zero-order basins have traditionally been treated as upland forest. If zero-order basins provide unique resources, such as critical habitats for riparian species, management activities in these areas could have adverse effects on biotic resources. Within zero-order basins, this study determined the upper limits, spatial patterning and habitat features associated with amphibians, a taxon that may have unique ties to this portion of the forested landscape. Although the scope of inference for these findings is limited to unmanaged zero-order basins within the study area, these results have implications regarding the role of zero-order basin geomorphic and lateral zones in supporting amphibian assemblages which likely extend from the western portions of northern California to British Columbia. Results from this study may be considered reference conditions against which findings from basins with forest management can be weighed.

Although a few studies have documented use of unmanaged headwater basins by amphibians (Bury et al. 1991, Adams and Bury 2002), amphibian assemblages in unmanaged zero-order basins have not been previously characterized. The amphibian species I detected are found throughout the Coast Range of Oregon, and four of eight species I observed have status of concern in all or parts of their ranges in the Pacific Northwest (Table 3.1). All eight species have been found to have some associations with components of older forest ecosystems, and all but ensatina have been rated to have medium to high viability risk during regional status assessments (review in Blaustein et al. 1995).

Zero-order basins in this study supported four species traditionally associated with riparian habitats: Pacific giant, torrent and Dunn's salamanders, and tailed frogs (Nussbaum 1983, Bury et al. 1991, McComb et al. 1993). No larval tailed frogs were observed. Aquatic forms of the Pacific giant salamander were captured over 1.4 times further from ridgelines (downstream) than any other amphibian. I observed two amphibian species traditionally associated with upland areas in zero-order basins: clouded salamander and ensatina (Corn and Bury 1991, Welsh and Lind 1991). Clouded salamander is of particular interest because it is less frequently documented in forest landscape studies. Western red-backed salamander has been found in both upland (McComb et al. 1993) and riparian (Vesely 1997) areas. In this study of zero-order basins, western red-backed salamander had the highest densities of any amphibian in headmost and slope geomorphic surfaces (drier portions of zero-order basins), and did not appear to be a riparian obligate.

Pond breeding amphibians such as red-legged frog (*Rana aurora* Baird and Girard), rough skinned newt (*Taricha granulosa* (Skilton)), and (except for one capture) northwestern salamander were not observed in the zero-order basins I studied, although they were observed in the surrounding landscape.

The relatively high detection frequencies (over 6.3 animals/ person hour) in this study suggest that zero-order basins may represent important amphibian habitats. Average densities for torrent, Dunn's, western red-backed, clouded and ensatina salamanders (Table 3.3) in zero-order basins were higher than captures reported by Vesely (1997) for unmanaged riparian buffers in the Oregon Coast Range. Densities of upland species in zero-order basins, particularly western red-backed salamanders, were lower than densities reported by others (Corn and Bury 1991, Davis 1996). Densities for aquatic species in zero-order basins were also lower than those suggested for stream habitats in the Pacific Northwest (Bury et al. 1991). However, caution should be exercised in comparing density results among studies, due to differences in effort, methodology and sampling design.

Spatial patterning of amphibians in zero-order basins

The densities of riparian- and upland-associated amphibian species in zero-order basins followed spatial and environmental gradients. Amphibian species with life history ties to fluvial conditions (Pacific giant, torrent and Dunn's salamanders) occurred farther from ridges (i.e. downstream) than other amphibians. Amphibians requiring perennial flow were restricted to the extreme lower ends of zero-order basins, while torrent salamander was able to use habitat areas above the initiation of fluvial scour and deposition, associated with seeps. Pacific giant, torrent and Dunn's salamanders occurred significantly closer to the center of basins than western red-backed, clouded, ensatina salamanders. Torrent salamander, an aquatic species associated with oxygenated flowing systems, was strongly associated with the 0-2 m lateral zone. Dunn's salamander had little difference in captures within the first 5 m, consistent with current understanding regarding its splash zone life history. Both clouded and western red-backed salamanders had their highest densities in areas 2-5 m from center, but indicator species analysis found no significant indicator species for the 2-5 m or > 5 m zones. These results suggest that the highest amphibian biodiversity in zero-order basins occurs in areas close to the fluvial center, and that there is little difference in amphibian assemblages in areas > 2 m from the center of the basin. These results are comparable to preliminary findings of Olson et al. (2000) who found strong reductions in relative humidity and changes in other environmental parameters outside of a zone 15 m from center in headwater stream inner gorges. These cool, moist zones appear to be amphibian diversity hotspots.

Geomorphic surface zones integrate longitudinal (valley vs. headmost areas) and lateral (valley and headmost areas vs. slope zones) differences in amphibian composition. Log linear regression models showed torrent and Dunn's salamander were much more common in valley floors, less so in headmost areas, and functionally absent from slopes. Indicator species analysis supported riparian species (torrent, Dunn's, Pacific giant) as strong indicators for valley geomorphic surfaces, particularly in the 0-2 m lateral zone. Western red-backed salamander was a marginally significant indicator species for slope areas, but there were no differences between western red-backed salamander captures in the three geomorphic surfaces. No other species were uniquely associated with slope surfaces.

Indicator species analysis supported clouded and ensatina salamanders as strong indicators for headmost areas. Both clouded salamander and ensatina achieved their highest densities in headmost areas. Headmost areas had the highest amphibian richness, and higher densities of riparian species than slope areas. Amphibian diversity in headmost geomorphic surfaces was lower than valley surfaces, and not significantly higher than slope areas. These results suggest that headmost areas, drainage areas above scour and deposition, support a marginally distinct, patchily distributed (Gregory 1991) amphibian assemblage, comparable in richness to higher-order riparian systems downstream, inclusive of some riparian species.

Amphibian associations with habitat parameters in zero-order basins

Several species-habitat models indicated associations between amphibian taxa and abiotic conditions, while others indicated strong associations with late successional forest characteristics, such as the basal area of large overstory trees.

Torrent salamander

Torrent salamanders had a strong association with saturation and basin gradient, and a weak positive association with distance from ridge and large substrate. Welsh and Lind (1996) suggested that, at a microhabitat scale, torrent salamanders are associated with seep habitats and a mix of coarse substrates. Such conditions occur both above and below the initiation of fluvial scour and deposition in zero-order basins.

Dunn's salamanders

Captures of Dunn's salamander were positively associated with saturation, shrub cover and (weakly) large substrates, and negatively associated with overstory cover. Vesely (1997) also found positive associations between shrub cover and Dunn's salamander densities, and both Lee (1997) and Vesely (1997) found negative correlations between Dunn's salamander density and coniferous overstory cover in headwater streams. In zero-order basins, higher cover of shrubs and low canopy cover may be associated with scarps and recent slumps, areas often associated with fluvial disturbance and moist talus (Naiman et al. 2000).

Clouded salamander

Clouded salamander captures were positively associated with changes from valley to headmost surfaces. Others have found positive association between clouded salamander and talus (Corn and Bury 1991) and downed wood (Corn and Bury 1991, Butts and McComb 2000). Although there was not a strong relationship between the volume or frequency of downed wood and clouded salamander captures in this study, 108 of 129 captures of clouded salamander were made in, on, or under downed wood. Levels of downed wood in the unmanaged zero-order basins I investigated were relatively high compared to the range investigated by Butts and McComb (2000); thus, amounts of downed wood may not have limited clouded salamander densities in any of the sites studied.

Ensatina

Captures of ensatina were positively associated with organic substrates, overstory density (particularly western hemlock), and distance from fluvial center. These findings are comparable to other studies that showed ensatina was associated with fine woody debris (Nussbaum et al. 1983, Vesely 1997), tree density (Welsh and Lind 1991, Vesely 1997), and upland conditions (Bury and Corn 1988, McComb et al. 1993). The presence of an upland associated species like ensatina in zero-order basins, including moderate densities in areas under 5 m from fluvial center, suggest an intermediate position of zero-order basins between riparian and upland systems.

The relationships I found between individual amphibian species and environmental parameters in zero-order basins were consistent with amphibian studies conducted in other geomorphic contexts. However, in zero-order basins, fluvial and upslope habitat elements were more spatially compressed, closely juxtaposed, and patchy (Gregory et al. 1991, Pabst and Spies 1998), at both small and intermediate scales. This appeared to lead to closely juxtaposed and less distinct amphibian assemblages. The effects of this juxtaposition are clear in ordination results, with the overlap in species composition in slope and headmost plots, and in the indistinct lateral assemblages produced using indicator species analysis.

Conclusions

The role of headwater drainages, including zero-order basins, in forest ecosystems is under investigation in western North America. These areas are important in the transport of inorganic substrate and large wood down gradient to higher-order systems, principally through debris flows (Benda 1990, May, 2001). Headwater systems influence downstream water quality (Beschta et al. 1987, FEMAT 1993), and support distinct invertebrate (Dietrich 1992) and fish (Hubble 1994) faunas. Preliminary studies have shown distinct amphibian faunas in managed headwater Oregon Coast Range streams (Olson et al. 2000, Stoddard 2001) and intermittent Oregon Cascade Range streams (Lee 1997). This study is the first to document the composition and habitat associations of amphibian assemblages in unmanaged zero-order basins.

In considering the results of log linear regression models, empirical habitat models, and indicator species analysis, unmanaged zero-order basins in the south-central Oregon Coast Range appeared to support three amphibian assemblages; (*i*) a valley assemblage, supporting seep, splash zone and fluvial species (torrent, Dunn's and Pacific giant salamander), favoring fluvially disturbed areas 0-5 m from the basin center; (*ii*) a headmost assemblage, supporting clouded salamander (especially in areas 2-5 m from center) and ensatina (in drier areas); and (*iii*) a slope assemblage, associated with western red-backed salamander in "transition" slope areas (2-5 m lateral zone) and ensatina in mid-slope, drier areas (> 5 m lateral zone). Although these assemblages may have utility for management, caution should be exercised in their application. Although there were distinct differences in the densities of amphibian species across geomorphic surfaces, each species was observed in each of the surfaces. Western red-backed salamander, for example, was ubiquitous. Also, the distinctness of these assemblages may be highly dependent on season. During sustained periods of high relative humidity and moderate temperature, or during potential dispersal seasons of the species' life history, these assemblages may become indistinct. During summer months, if animals are near the surface, amphibian assemblages may become more compressed, with animals closer to fluvial centers. Habitat utilization throughout the entire life history of most forest amphibians in the Pacific Northwest is largely conjecture. Potential dependencies on portions of the forest landscape for particular life history functions (e.g., breeding, foraging, dispersal, summer/winter refugia) are unknown.

Although amphibian usage of basin areas above sustained fluvial scour and deposition has been considered (Olson et al. 2000), the upper limits of riparian species in drainage basins has not been well defined. From this study, it appears that at least two fluvially dependent species, torrent and Dunn's salamanders, penetrate drainage basins above the start of scour and deposition. These species had mean proximity to ridgelines of approximately 170 m and minima of 36 m and

46 m from ridgelines, respectively, whereas the distance to start of flow averaged over 180 m in zero-order basins.

Geomorphic surfaces in zero-order basins are unique on the forested landscape, shaped by a distinct fluvial and hillslope disturbance regime. These geomorphic surfaces provide a unique patch size and spatial arrangement of habitat features on the forested landscapes of the Pacific Northwest. The spatially compressed, closely juxtaposed, and patchy (Gregory et al. 1991, Pabst and Spies 1998) habitat features associated with geomorphic surfaces in zero-order basins leads to amphibian assemblages which are less distinct but comparable in richness and abundances to larger riparian drainages.

Forest management implications

Buffers have been suggested as techniques to minimize impact to stream-dependent (Kelsey 1995) and terrestrial (Vesely 1996) riparian amphibians. Currently, buffers are not required in zero-order basins. The results of this study show that riparian-associated amphibians (e.g., torrent salamander) and sensitive amphibians (e.g., clouded salamander) utilize zero-order basins, and that the densities of these species are related to habitat variables including relatively invariant parameters (e.g., basin gradient and aspect), and parameters affected by management including large substrates and overstory conditions. Management activities that affect substrate and overstory composition in headwater areas have been shown to have negative effects on amphibian densities (Bury and Corn 1988, Kelsey 1995). Considering these findings, where protection of amphibian species in zero-order basins is a priority, special management practices such as reserved areas within a landscape context, long rotations, or higher overstory retention might be needed to ensure maintenance of amphibian species in forested landscapes. Cissel et al. (1998 and 1999) have developed landscape-level (subdrainage-level) reserve concepts, but without considering zero-order basins as specific design elements.

If zero-order basins were included in subdrainage reserves, both patch reserves (including entire zero-order basins) and linear buffers might be useful in minimizing the effects of management activities on amphibian species. Patch reserves, encompassing entire zero-order basins and having species objectives as a key priority, would minimize impacts from timber harvest and road installation on: *i*) species associated with headmost areas (clouded salamander); *ii*) amphibian species utilizing drier portions of zero-order basins (ensatina); and *iii*) species associated with fluvial environments (torrent, Dunn's, and Pacific giant salamanders). Linear buffers established along the longitudinal axes of zero-order basins could provide refugia and aquatic connectivity for amphibian species associated with fluvial environments, and upland species distributed across zero-order basins, but having distinct peaks in density in the lower transition slope (western red-backed and clouded salamanders). The dimensions of reserved areas in zero-order basins could be designed to minimize management effects on fluvial and hillslope disturbance regimes and the microhabitat features such as seeps, talus piles (Welsh and Lind 1991) and downed wood aggregations (May 2001) that result from them. Consideration of microclimatic gradients associated with zero-order basin geomorphology and edge effects associated with adjacent forest management also would be needed.

Zero-order basins are much smaller than the riparian systems downstream, and occur in steep areas frequently not amenable to forestry; thus, establishment of zero-order basin refugia likely would require a smaller modification of management activities than traditional riparian management.

CHAPTER 4. SYNTHESIS

BACKGROUND AND OBJECTIVES

Zero-order basins, drainage areas extending from ridgelines down to the initiation of first-order streams (Tsukamoto et al. 1982), are a prominent geomorphic feature of hillslopes in mountainous, forested areas (Hack and Goodlett 1960, Kikuchi and Miura 1993). As the uppermost portions of headwater systems, zero-order basins play a role in the transport of coarse wood and substrates to larger-order systems (Benda 1990, May 2001). Because of their frequency in the landscape, position within drainage networks, geomorphology, and unique fluvial and hillslope processes, it is probable that zero-order basins play a role in the maintenance of ecosystem function and species diversity in the Pacific Northwest. However, very little information exists on the biotic components of zero-order basins, or the physical role of these features in support of ecological systems.

The key environmental factors structuring zero-order basin biotic communities affect the composition of both plant and amphibian assemblages. The objective of this synthesis is to integrate information on plant and amphibian assemblages in zero-order basins, providing a comprehensive characterization of biotic communities and the environmental parameters associated with them in these basins. I investigate similarities in the spatial, geomorphic and environmental gradients ordering plant and amphibian composition in zero-order basins, and develop management implications using this information. The information in this synthesis comes from analysis of 63 unmanaged zero-order basins, established in the headwaters of the Coquille River Basin, described in Chapters 2 and 3.

COMPARISONS OF PLANT AND AMPHIBIAN ASSEMBLAGES IN ZERO-ORDER BASINS

Geomorphic and spatial relationships of plant and amphibian taxa

Plant and amphibian assemblages were patterned along geomorphic and lateral gradients in zero-order basins. Valley geomorphic surfaces were biotically distinct for both plant and amphibian assemblages (Table 4.1; methods described in Chapters 2 and 3, and in Dufrene and Legendre (1997)). Both taxonomic groups had the largest number of associated species and the largest number of significant indicators species ($p < 0.05$) in valley zones. Plant species found principally in valley surfaces included shrubs associated with seep areas (*Oplopanax horridum* and *Ribes bracteosum*), and stoloniferous herbs (*Chrysosplenium glechomaefolium* and *Mitella ovalis*). Amphibian species found principally in valley surfaces included species associated with seeps and springs, torrent and Dunn's salamanders.

Table 4.1. Indicator values of plants and amphibians for geomorphic surfaces, based on indicator species analysis (n = 252 for plants, 176 for amphibians). Only species with significant indicator values ($p \leq 0.05$) are shown. Number of associated species and total sums of indicator values shown for each zone **(bold)**.

Plant species			**Amphibian species**		
Species	**Indicator Value**	**p**	**Species**	**Indicator Value**	**p**
Valley **(32: 250)**			*Valley* **(4:184)**		
Mitella ovalis	60.2	0.001	Dunn's	56.7	0.001
Tolmiea menziesii	32	0.001	Southern torrent	52.7	0.001
Athyrium filix-femina	27.6	0.001	Pacific giant (A)	19.4	0.001
Mimulus dentatus	24.6	0.001	Pacific giant (T)	11.3	0.004
Ribes bracteosum	18.9	0.001			
Chrysosplenium glechomaefolium	12.8	0.001			
Blechnum spicant	27	0.001			
Rubus spectabilis	19.4	0.001			
Streptopus amplexifolius	17.1	0.001			
Viola glabella	13.4	0.006			
Adiantum pedatum	18.8	0.009			
Bromus carinatus	17	0.015			
Mitella petandra	7.6	0.015			
Mitella caulescens	7.1	0.015			
Boykinia elata	9.5	0.037			
Headmost **(26:354)**			***Headmost*** **(2 : 87)**		
Trientalis latifolia	9	0.037	Clouded	29.8	0.002
Carex deweyana	13.1	0.054	Ensatina	24.4	0.003
Slope **(26:468)**			***Slope*** **(1: 70)**		
Polystichum munitum	37.6	0.001	Western red-backed	31.4	0.055
Oxalis oregana	32.6	0.001			
Trillium ovatum	22.2	0.001			
Dicentra formosa	16.6	0.002			
Disporum hookeri	20.8	0.003			
Polystichum kruckebergii	10.6	0.019			
Vancouveri hexandra	13.5	0.025			
Dryopteris arguta	6.1	0.048			
Ridge **(23:206)**			***Ridge***		
Berberis nervosa	41.8	0.001	Not sampled		
Viola sempervirens	14	0.015			
Vaccinium ovatum	13.6	0.049			
Pyrola picta	7.1	0.021			
Smilacina racemosa	6.7	0.023			
Pteridium aquilinum	6.8	0.042			

Within geomorphic surfaces, lateral distance from basin center (Figure 3.2, Chapter 3) had a moderately strong effect on both plant and amphibian species composition. Olson et al. (2000) found that the near-stream environment, areas within 15 m of stream center in headwater areas, was distinct from upland conditions in both microclimate and microsite variables. Plant species in zero-order basins had highest richness in lateral zones 5 m from center, and highest species diversity in fluvial centers. Plant species diversity and richness in areas over 5 m from basin center were distinctly lower. For amphibians, fluvial associates (Pacific giant, torrent, and Dunn's salamanders) were functionally absent from slope surfaces > 2 m from center. Terrestrial species like western red-backed and clouded salamanders had highest densities in areas 2-5 m from center. Only ensatina had more captures in areas > 5 m from center. Findings from zero-order basins thus appear consistent with findings by Olson et al. (2000) and Pabst and Spies (1998), and support an "inner gorge" effect continuing from first-order streams into zero-order basins.

Amphibians appeared to have a distinct assemblage associated with headmost areas in zero-order basins, in contrast to plant species. Clouded salamander and ensatina were indicator species for headmost areas, having both higher captures in, and fidelity to, headmost areas in zero-order basins (Table 4.1). No plant species were restricted to headmost areas. Only two of the 138 identified plant species in zero-order basins were significant indicators for headmost areas.

Maximum indicator values for these two plant species were low, and these species occurred widely in other habitats.

Torrent and Dunn's salamanders, both strongly associated with fluvial conditions in valley surfaces, also occurred in headmost areas. The *Mitella* and *Blechnum* vegetation types were functionally absent from headmost areas. These types were associated with moist fluvial conditions and perhaps with a relatively strong light environment, conditions mostly lacking in headmost areas. The stronger associations of fluvial amphibians like torrent and Dunn's salamander with headmost areas may have been due to the seasonally-available water or the presence of coarse substrates in these areas, two habitat elements shown to be related to the capture rates of these species in zero-order basins (Chapter 3).

Plant and amphibian species supported distinct adaptations to the geomorphic and lateral zones in which they occurred, and were strongly associated with distinct microclimatic conditions in these areas. For species associated with areas near basin center, these requirements included the need for cold, aerated water (torrent salamander), a year-long gilled larval stage (Pacific giant salamander), and stoloniferous root systems and splashcup dispersal (e.g., *Mitella* ovalis, *C. glechomaefolium*). Adaptations to drier slope surfaces included the use of subterranean burrows (ensatina), use of large downed wood pieces with buffered interior microclimates (clouded salamander), and woody habit and evergreen leaves (e.g., *Berberis nervosa*, *Viola sempervirens*).

Plant and amphibian associations with environmental variables

Both plant and amphibian taxonomic groups followed spatial and geomorphic gradients in zero-order basins. Plant species composition was most strongly associated with geomorphic position, including distance from basin center, geomorphic surface zone, plot height and heat load index (a cosine transformation of basin aspect) in ordinations. Substrate (especially organics) and canopy cover were of secondary importance. Plant vegetation types showed strong differences in mean distance from center, as well as in surface moisture, stability and overstory density measures.

I compared the positions of plant and amphibian taxa along environmental gradients simultaneously, using bivariate plots (Figure 4.1, Figure 4.2). Bivariate plots were constructed using five environmental parameters that were shown to be important in ordering both plant vegetation types and amphibian species in Chapters 2 and 3, through the correlation of environmental parameters with ordination axes, and high parameter predictor weights in empirical models. I plotted means for subjectively chosen pairs of these key environmental variables, for each of seven plant vegetation types and seven amphibian species.

Considering a bivariate plot of stability and canopy cover, there appeared to be three distinct plant/amphibian groups; (*i*) a "wet" group with low stability (high scour and deposition) and comparatively low canopy cover, supporting fluvial taxa

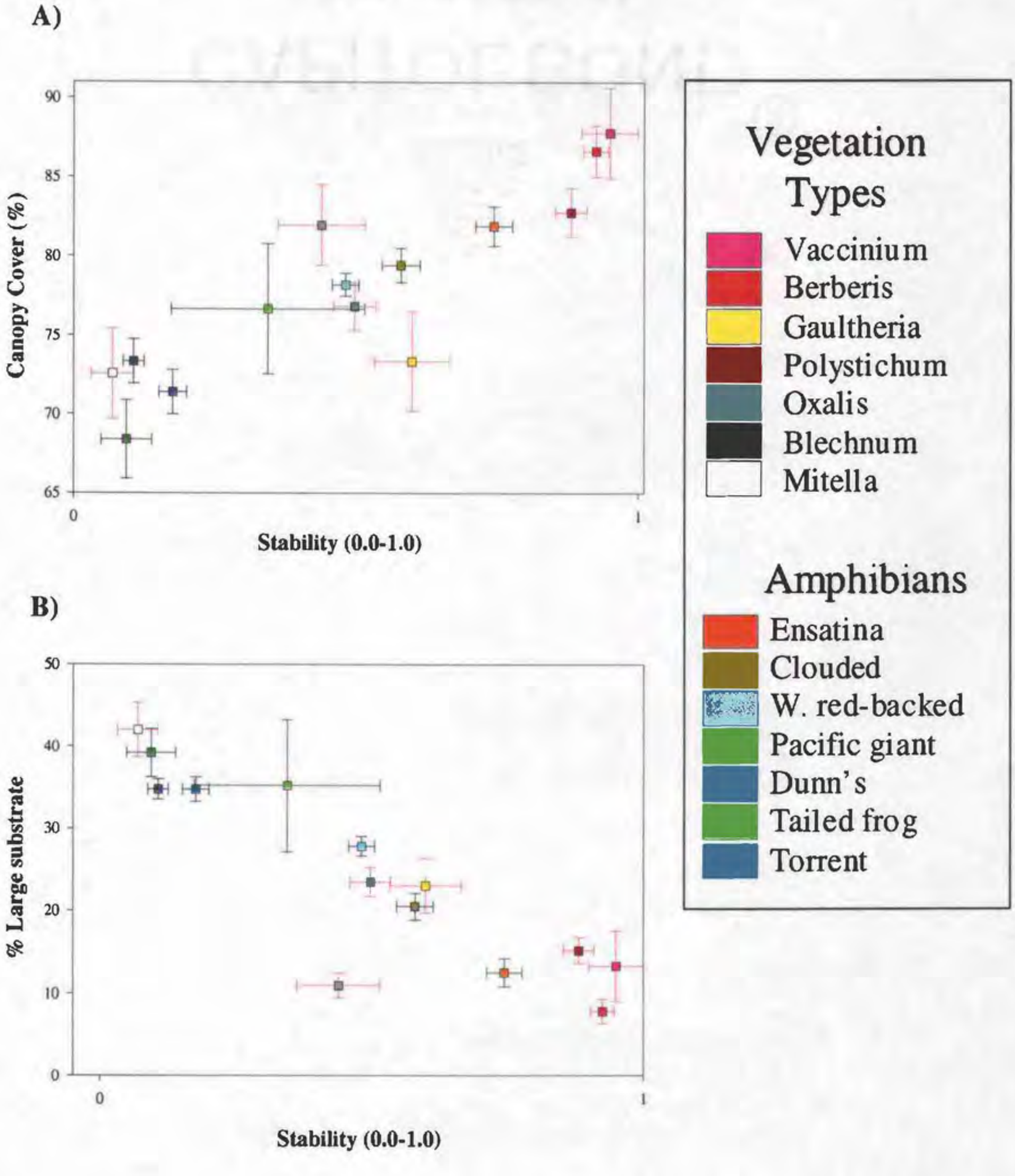

Figure 4.1. Bivariate differences in levels of key environmental parameters between 7 plant vegetation types (red error bars) and 7 amphibian species (black error bars). Bivariate plot of means ($\overline{x}$ + SE) for (A) stability and canopy cover and (B) stability and percent cover of large substrates, for plant vegetation types and amphibians.

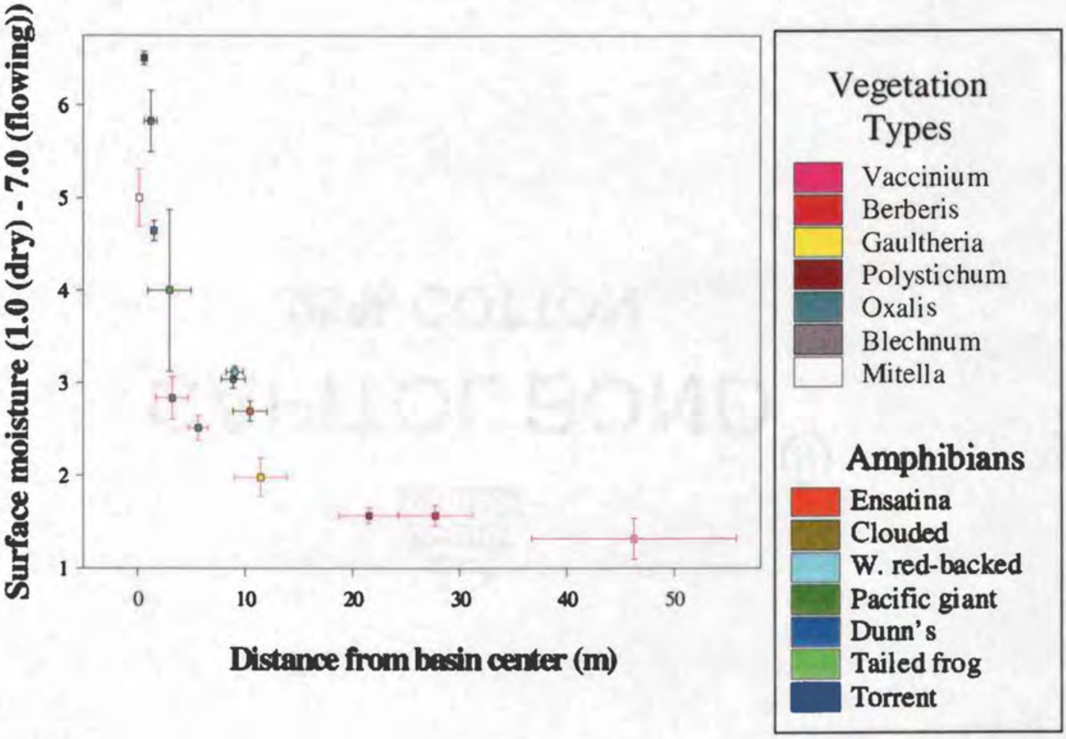

Figure 4.2. Bivariate plot of means ($\overline{x}$ + SE) for distance from basin center and surface moisture for 7 plant vegetation types (red error bars) and 7 amphibian species (black error bars).

including the *Mitella* vegetation type, as well as torrent, Dunn's and Pacific giant salamanders; (*ii*) a "mesic" group including the *Blechnum*, *Oxalis* and *Gaultheria* vegetation types, as well as tailed frogs (adults only), western red-backed and clouded salamanders; and (*iii*) a "dry" group associated with high stability and canopy cover, including the *Polystichum*, *Berberis* and *Vaccinium* vegetation types, as well as ensatina. Comparison of bivariate plots for distance from center and surface moisture (Figure 4.1), and stability and cover by large substrate (Figure 4.2) showed similar groupings.

Plants in zero-order basins appeared to have wider environmental breadth across moisture gradients than amphibians (Figure 4.2, Table 4.1). Consideration of mean distance from basin center for the two taxonomic groups suggested that amphibians were functionally constrained to areas within 10 m of basin center, although sampling extended laterally over 22 m from basin center (start point of 15 m slope transect averaged 17 m (95% CI: 14.6, 19.4) from basin center). Amphibian sampling was discontinuous in slope areas, and did not include sampling in ridge areas, so direct comparison of the two taxa is not possible. Amphibians were not sampled in ridge surfaces, because preliminary observations suggested this taxon had negligible densities in these units; plants of course had cover in these areas, including the second-highest number of significant indicator species. Plants had their second-highest number of associated species, and their highest summed indicator values in mesic slope areas. Amphibians had only one species, western red-backed salamander, weakly associated with slope areas (Table 4.1). There is some suggestion that torrent and Dunn's salamander may exclude western red-backed salamander from moist microhabitats (Petranka 1998).

In addition to spatial and geomorphic gradients, individual amphibian species also were associated with particular habitat features. Empirical models of captures suggested some partitioning in moisture regimes, use of large substrates, and overstory cover. In general, amphibian species had stronger ties to unique, discrete microhabitat elements (e.g., clouded salamander and downed wood, or torrent salamander and saturated non-organic substrates), defying categorization along continuous environmental gradients. However, four of five amphibian species analyzed showed strong differences in use of lateral and geomorphic surfaces. These lateral and geomorphic gradients were associated with levels of microhabitat or microclimatic conditions favorable to particular amphibians.

Differences in autecology between taxonomic groups

Aside from the obvious differences in functional roles, life history, biomass, and densities, plant and amphibian taxonomic groups differ in ways that influenced species presence within basins. Within basins, the mobility of amphibians potentially allows them to follow seasonally variable fluvial and microclimatic gradients, while plants must occupy temporally non-optimal areas, once established. At a broader spatial/temporal scale, many plant species have more effective dispersal than amphibians, which have relatively low vagility and high site fidelity compared to other vertebrates (Olson et al. 2001). The same habitat features may affect plant and amphibian taxa in fundamentally different ways, conceptually leading to different autecological responses. For example, changes in overstory leading to an increase in the light environment may initially cause a positive response by many plants, but a decrease in moisture levels and an increase in temperatures, leading to a negative response for amphibians (e.g., Plethodontids such as torrent salamanders).

The much higher plant species richness in zero-order basins may tend to smooth taxonomic responses to environmental gradients. This could lead to continuous changes in plant species composition across environmental gradients, whereas the lower amphibian richness would necessarily result in more discrete changes in species composition with changes in environmental parameters. Plant species richness in basins and the weaker associations between plant species and geomorphic surfaces (especially slopes and headmost areas) suggested that plant species assemblages may divide microhabitats in zero-order basins (niche space) more finely than amphibian assemblages.

Bioindicator species within zero-order basins

Several studies have demonstrated the possibility of using the richness of one taxonomic group as an indicator for richness/diversity in a second group (Pearson and Cassola 1992, Carroll and Pearson 1998). I investigated whether plant vegetation types might be indicators for amphibian species in zero-order basins using correlation analysis and indicator species analysis (Dufrene and Legendre 1996).

I calculated Spearman's rank correlations between the seven vegetation types (*Mitella*, *Blechnum*, *Oxalis*, *Polystichum*, *Gaultheria*, *Berberis*, and *Vaccinium*) and six amphibians with over 30 captures (Pacific giant (aquatic and terrestrial forms), torrent, Dunn's, western red-backed, and clouded salamanders, and ensatina) identified in zero-order basins. Five of 49 correlations were significant, showing patterns of associations between taxa with moisture dependencies. Captures of torrent salamander were correlated with the frequency of the *Mitella* vegetation type ($r = 0.39$, $p < 0.0001$) and the *Blechnum* type ($r = 0.25$, $p < 0.0006$). Captures of Dunn's salamander were associated with the frequency of the *Mitella* vegetation type ($r = 0.31$, $p < 0.0001$) and the *Gaultheria* type ($r = 0.15$, $p < 0.04$). Ensatina captures were correlated with the *Berberis* vegetation type ($r = 0.22$, $p < 0.003$). None of these correlations was particularly strong. Other vegetation types did not show distinct patterns with amphibian species.

I next used indicator species analysis (Dufrene and Legendre 1996) to calculate the degree of indication of six amphibians (N > 30) for each of seven vegetation types. For each amphibian species, I identified its maximum indicator value, the percent of perfect indication of that amphibian for the vegetation type with which it was most strongly associated, and evaluated its statistical significance using a Monte Carlo method, similar to analyses in Chapters 2 and 3 (Table 4.2). As in the correlation analysis above, relationships between moist taxa were the strongest. Amphibian species associated with fluvial conditions (torrent, Pacific giant and Dunn's salamanders) were moderately weak indicators for the *Mitella* and *Mitella/ Gaultheria* types. Other relationships were not significant. Indication of drier amphibian species for the *Vaccinium* vegetation type is surprising considering its near restriction to upper slope and ridgeline areas, which were not sampled for amphibians.

Overall, both vegetation types and amphibian species followed stability, lateral, and substrate gradients, suggesting that plant vegetation types might act as indicators for amphibian species at small spacial scales (e.g., geomorphic surfaces). However, results from indicator species analysis suggested that amphibian species were relatively weak indicators for plant vegetation types, and correlation between amphibian captures and frequency of vegetation types was low or not significant. These results suggest that vegetation types would make poor indicators for amphibian fauna in zero-order basins. Note also that any serious use of plants as bioindicators would need to consider effects of sampling scale and spatial autocorrelation (Carroll and Pearson 1998).

Table 4.2. Maximum indicator values of amphibian species for plant vegetation types in zero-order basins. "Max IV" represents maximum indicator value, the percent of perfect indication of an amphibian species for the vegetation type it was the best indicator for. "p" represents the proportion of tests larger than the Max IV from a Monte Carlo test. "Summed IV's" represent the sum of indicator values for 6 amphibian species (including Pacific giant as both aquatic (A) and terrestrial (T) forms) for each vegetation type. Mixed vegetation types represent situations where two vegetation types were present in a geomorphic surface.

Vegetation type Amphibian species	Max IV	p	Summed IV's
Mitella			111
Southern torrent salamander	25.2	0.026	
***Mitella/ Gaultheria* mix**			109
Pacific giant salamander (A)	23.2	0.041	
Dunn's	19.9	0.074	
***Oxalis* mix**			61
W. red-backed	10.5	0.722	
Vaccinium			156
Clouded	15.9	0.158	
Pacific giant salamander (T)	11.6	0.262	
Ensatina	11.2	0.385	

ECOLOGICAL ROLES OF ZERO-ORDER BASINS IN FORESTED LANDSCAPES

Several significant ecological roles have been identified for headwater drainages, including zero-order basins. Headwater drainages are important in the transport of inorganic substrate and large wood down-gradient to higher-order systems, principally through debris flows (May, 2001). Headwater drainages influence downstream water quality (Beschta et al. 1987, USDA USDI 1993), support invertebrate (Dietrich 1992), fish (Hubble 1994) and other biotic functions (Reid and Ziemmer 1994). In addition, results from my surveys of zero-order basins in the central Coast Range of Oregon (Chapters 2 and 3) suggest that these features support species diversity comparable to downstream riparian systems, provide habitat for fluvially-adapted (riparian) plant and amphibian taxa, and may provide habitats distinct from either near-stream riparian areas or surrounding hillslopes.

Amphibian richness in unmanaged zero-order basins in my study area included eight species, a number comparable to or higher than other headwater systems studied in the Oregon Coast Range (Vesely 2000, Stoddard 2001, Bury et al. 1991). Plant alpha diversity (the diversity of geomorphic surfaces in zero-order basins), measured as N1 (Hill 1973), ranged from 13 to 23 for plants in zero-order basins, a comparable range to Coast Range riparian systems (Pabst and Spies 1998).

Plant beta diversity (the diversity of entire zero-order basins) also was moderately high, due to the apparent spatial compression, tight juxtaposition and patchy distribution of fluvial and terrestrial habitats. Valley geomorphic surfaces averaged under five meters in width in zero-order basins, much smaller than 1st order and larger valley floors measured by Pabst and Spies (1998), implying spatial compression of fluvial processes and juxtaposition of adjacent slopes within five meters of basin center. The seep and intermittent flow conditions in zero-order basins appeared to lead to variation in microsite substrate and fluvial compositions, and these zones had higher species diversity than surrounding hillslopes (Gregory et al. 1991). The diversity of zero-order basins may also increase the diversity of surrounding forested hillslopes, by incorporating plant and amphibian species usually associated with riparian areas into ridgeline topographic positions.

In addition to acting as the uppermost part of a continuum between riparian and hillslope systems, zero-order basins provided habitat conditions that were distinct from either. Headmost areas supported convergent topography, discontinuous saturated large substrates, and overstories that were significantly less dense than surrounding hillslopes. Although plant composition showed only weak differentiation in headmost areas, clouded salamanders and ensatinas were significant indicators for headmost surfaces.

Other roles for zero-order basins in steep forested landscapes remain to be studied, including their role as refugia from aquatic predators, and as potential dispersal corridors. Zero-order basins may provide refugia from lotic predators for fluvially-adapted species not needing perennial flows, such as torrent and Dunn's salamanders. Predation by fish may be an important factor in ordering lotic salamander assemblages (Petranka 1983, Lowe and Bolger 2001). Pacific giant salamander also may affect the distribution of torrent salamander through predation (Welsh 1993). In this study, valley zones with or without aquatic forms of the Pacific giant salamander did not differ in the frequency of torrent salamander (56% and 41%, respectively). However, the spatial scale of refugia in systems with patchily-distributed fluvial conditions may be smaller than the scale of geomorphic surfaces examined.

Zero-order basins also may provide dispersal corridors to other drainages for riparian species, by continuing fluvial, substrate and possibly microclimatic gradients to the proximity of ridgelines. Dispersal from fluvial environments in one drainage to another drainage would require movement through < 340 m of mesic habitats through headmost areas, or < 100 m of drier habitats across slope surfaces, on average, during the periods I sampled (March through June). During wetter periods, movement between basins may be entirely through moist or saturated areas. Torrent salamander, a species with strong ties to fluvial environments (Petranka 1998), was observed over 40 m from basin center in zero-order basins (pers. obs.). The role of zero-order basins in dispersal has not been studied. Additional questions to be addressed include the effects of seasonal changes and natural and anthropogenic disturbance on plant and amphibian composition in zero-order basins.

FOREST MANAGEMENT IMPLICATIONS

In addition to the implications for forest management from the analyses of plant and amphibian taxa separately (Chapters 2 and 3), consideration of plants and amphibians together led to several synthetic forest management implications. These include the importance of: *i*) zero-order basins in supporting riparian communities; *ii*) key geomorphic surfaces within zero-order basins; and *iii*) fluvial and hillslope processes in these features.

Riparian communities penetrate zero-order basins. Zero-order basins surveyed in this study supported two distinctly riparian plant vegetation types (*Mitella* and *Blechnum*), a number of hydric plant species (e.g., *Lysitchiton americanum*), and several amphibian species associated with lotic and splash zone habitats (Pacific giant, torrent and Dunn's salamanders). These species and types were most commonly associated with valley floors, but also were observed in headmost areas and transition slope surfaces, following fluvial and substrate conditions such as high surface moisture and large particle size. For management, this suggests that riparian communities extend into zero-order basins, to the initiation point of scour and above; zero-order basins would thus be part of any management for aquatic functions and values in drainage basins.

Both plant and amphibian species had "hot spots" of species diversity and high species indicator values in zero-order basin inner gorges, areas within 5 m of valley center. There was weaker support for the distinctness of assemblages in headmost and ridge geomorphic surfaces, while mid- and upper slope surfaces supported generalist species and relatively low diversity. Maintenance of zero-order basin hotspots could be incorporated in basin-level management, to maintain the diversity of entire forested hillslopes in the Pacific Northwest.

Both plant and amphibian taxa supported some species responding across the range of most environmental parameters. For example, ensatina was associated positively with organic material and negatively with large substrates, while southern torrent salamander was positively associated with large substrates and negatively associated with organics. The *Mitella* vegetation type was associated with relatively high surface moistures and low overstory relative densities, while the *Berberis* vegetation type was associated with high relative densities and low surface moistures. At finer resolution, although both the *Mitella* and *Blechnum* vegetation types were associated with moderately high scour and deposition, the *Mitella* type was much more common in scoured areas, and the *Blechnum* type had much higher average deposition. The continuous responses of these taxonomic groups along environmental gradients implies that biotic communities respond to the full range of fluvial and hillslope processes present in unmanaged zero-order basins. Because of the correlations between measured and unmeasured environmental parameters in this observational study, hypotheses regarding the effects of changes in individual parameters on plant or amphibian composition in zero-order basins cannot be made. However, considering the results of empirical modeling for plant and amphibian association with environmental parameters, significant modification of environmental gradients in zero-order basins, including removal of canopy cover, reduction in basal area of large overstory trees, and modification of substrate characteristics (e.g., significant decrease in the amount of large substrates), would be predicted to alter the composition of plant and amphibian assemblages in zero-order basins.

CHAPTER 5. SUMMARY OF FINDINGS

The following represents a summary of findings from a survey of plant and amphibian assemblages in 63 unmanaged zero-order basins in the central Coast Range of Oregon. The findings of this research represent the first comprehensive characterization of plant and amphibian assemblages in zero-order basins, and contribute to the understanding of headwater ecosystems in forested landscapes of the Pacific Northwest. Findings are summarized by taxonomic group, with an initial summary of geomorphology findings as background, and synthetic findings and forest management implications.

Zero-order basin geomorphology

1. Zero-order basins are frequent geomorphic features in forested mountain landscapes, averaging over 18/ km^2 in the headwaters of the Coquille River Basin. Zero-order basins in the study area averaged just over 1 ha in size above the initiation point of scour, and covered less than 1% of the landscape.

2. The four geomorphic surfaces in zero-order basins (valleys, slopes, headmost areas, and ridges) differed in gradient, overstory characteristics, downed wood and fluvial disturbance levels. Differences in these and other characteristics

formed the basis of environmental gradients that were associated with changes in plant and amphibian species composition in zero-order basins.

Plant assemblages in zero-order basins

3. Zero-order basins were comparable to hillslope areas in overstory species composition, supporting principally conifers (Douglas-fir, western hemlock and western red cedar). Convergent geomorphic surfaces (valleys and headmost areas) had significantly lower relative densities than slope and ridge surfaces.

4. Shrub assemblages in zero-order basins were intermediate between hillslope and riparian assemblages in species composition and cover, with moderate total cover (14 %) led by Oregon grape (*Berberis nervosa*), a dry evergreen species. Salmonberry (*Rubus spectabilis*), a riparian shrub, provided the second highest cover (< 3% cover).

5. Zero-order basin plant composition was most associated with spatial position within the basin, following gradients in distance from basin center, differences between geomorphic surface zones, and basin aspect. Substrate and overstory characteristics were also important in predicting plant species composition.

6. Fluvially active and splash zone areas within valley surfaces and lower slope surfaces (inner gorges) were identified as “hotspots”, supporting the highest plant species richness and diversity in zero-order basins, and the strongest indicator species values (highest species cover and fidelity).

7. Plant vegetation types differed in key environmental characteristics including surface moisture, scour, and height above stream. The most distinctive vegetation types were the *Mitella* and *Blechnum* types in moist valley zones, and the *Vaccinium* type in extremely dry conditions (ridges).

Amphibian assemblages in zero-order basins

8. Zero-order basins supported amphibian species usually associated with riparian lotic and terrace habitats, as well as amphibians usually associated with terrestrial hillslope habitats.

9. Amphibian groups partitioned spatial habitats in zero-order basins. “Dry”, terrestrial-breeding species (ensatina, clouded and western red-backed salamanders) were captured twice as far from fluvial center as “wet”, riparian-associated species (Pacific giant, torrent and Dunn’s salamanders), and roughly half as far from (downslope of) ridgelines. Wet species occurred most commonly in valley areas and in areas close to fluvial center (within 5 m).

10. No single environmental gradient fully described amphibian species composition. The importance of different environmental parameters (e.g., geomorphic and landscape position, moisture, substrate, and overstory parameters) for different amphibian species suggested habitat partitioning by these taxa.

11. Zero-order basins supported: (*i*) a valley assemblage of torrent and Dunn's salamanders, associated with fluvial processes 0-2 m from center; (*ii*) a headmost assemblage of ensatina and clouded salamanders, associated with intermediate overstory structure and fluvial surfaces; and (*iii*) a less distinct slope assemblage, with western red-backed salamander, 2-5 m from center.

Synthetic findings

12. Both plant and amphibian species had their highest species diversity and most significant indicator values in zero-order basin inner gorges, areas within 5 m of valley center. There was weaker support for the distinctness of plant and amphibian assemblages in headmost areas and ridge geomorphic surfaces.

13. Although both plant and amphibian species compositions were strongly related to stability, geomorphic position, and substrate characteristics, individual amphibian species had stronger ties to discrete microhabitat elements such as

downed wood or large saturated substrates, defying simple categorization along continuous environmental gradients.

Management implications

14. Zero-order basins in this study supported two plant vegetation types and three amphibian species associated with lotic and splash zone riparian habitats. These taxa were most common in inner gorges, areas within 5 m of basin centers, including valley floors and lower slope surfaces, but also followed fluvial and substrate gradients into lower headmost areas. For management, these findings suggest that drainage-level management of riparian communities and aquatic functions should include zero-order basins.

15. Plant and amphibian species composition was strongly associated with environmental parameters, some of which were unaffected by most management activities (e.g., basin gradient and aspect), and others which were directly affected by management activities (e.g., overstory tree basal area, substrate composition). Modification of overstory and substrate characteristics within zero-order basins would be predicted to alter vegetation types, and could lead to loss of certain amphibian species, such as torrent salamander.

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APPENDICES

APPENDIX A: DEVELOPMENT OF *A PRIORI* THOUGHT MODELS FOR PLANT COMPOSITION IN ZERO-ORDER BASINS

Development of *a priori* models for the association of axis scores with environmental variables used the following logical steps: (*i*) consider environmental factors known to affect plant species directly (Daubenire 1974, Bazzaz 1996, Pabst and Spies 1998); (*ii*) create models based on direct measures where feasible, and use increasingly indirect measures as necessary (Figure A1); (*iii*) follow additional rules below.

Parameters selected from literature review were checked against observations of potentially important environmental variables made in zero-order basins in the field during preliminary surveys. Thought models favored variables facilitating establishment of plant assemblage boundaries in the field, including substrate variables and distance metrics. Less emphasis was placed on using parameters that did not vary significantly in the sample, like geology, stand age or management. Models represented competing hypotheses on the environmental drivers of plant assemblages in zero-order basins.

Models used less than five parameters to allow tractability and the ability to discern between different processes, and because the information-theoretic methodology tends to favor models with more parameters (Anderson et al. 2000). Total *a priori* model number was kept < 25 to facilitate interpretation. Models included both proximal (direct) and indirect parameters. Models attempted to use parameters available to managers in the field and amenable to delineation of community boundaries in the field. Model sets included single parameter models, to facilitate ranking of important drivers of plot position in species-space. Separate models were developed to test the effect of covariates. The importance of covariates was assessed through their performance against other models. Models did not consider interspecific or intraspecific effects. Models did not incorporate parameter interaction, because I believed the data set was not comprehensive enough to support these complex effects.

Using the above rules, I developed 20 models describing sample unit (plots averaged for each lateral zone) position in species-space, as a function of sets of environmental parameters. After development of *a priori* model sets, I performed correlation analyses on environmental variables within models. Where Spearman rank correlations between variables were greater than 0.6, correlated terms were removed, leaving those parameters most amenable to management and delineation of community boundaries in the field.

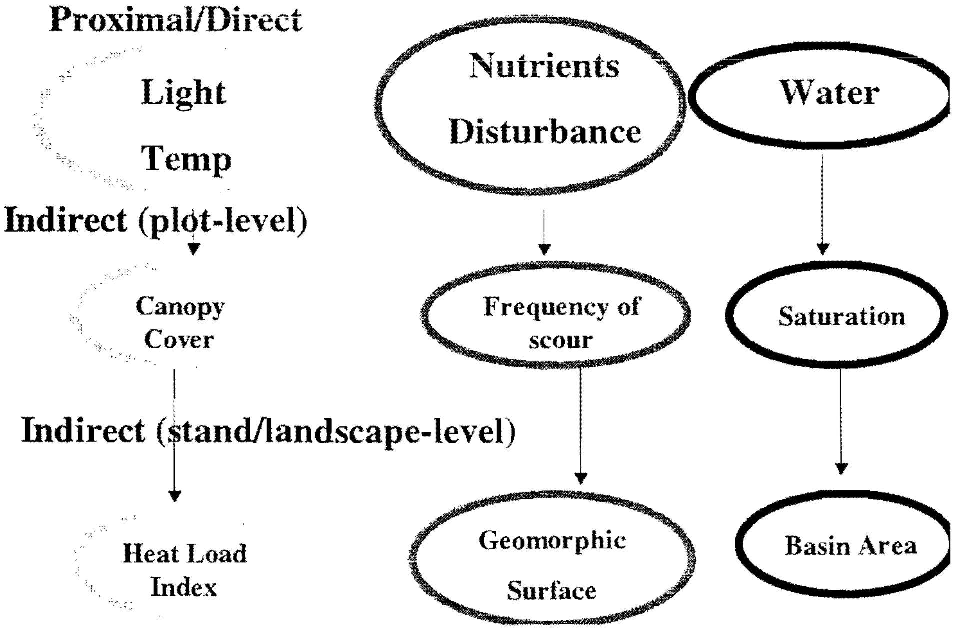

Figure A1. Schematic representation of hierarchy of direct and indirect factors affecting plant composition (after Bazzaz 1998).

APPENDIX B: *A PRIORI* AICC MODEL SETS FOR PLANT ORDINATION

Table B1. *A priori* set of ecological models used to describe three plant ordination axes. Codes for parameters used in AICc models are explained in Table B5. Parameters described in Table 2.3 (Chapter 2).

Model No.	Hypothesis	Model
AX0	Null model[1]	B_0
AX1	Covariate model[2]	$B_0 + B_1$ (YEAR)+B_2 (ELEV)+ B_3 (ROADS)+ B_4 (HARVEST)
AX2	Physical parameter covariate model[2]	$B_0 + B_1$ (BASIN)+B_2 (GEOSRF)+ B_3 (GEOL)+ B_4 (SOIL) + B5 (ELEV)
	Direct Factor Models	
AX3	Average surface moisture for lateral zone	$B_0 + B_1$ (MOISTR)
AX4	Stability model: proportion of stable plots in the lateral zone	B_0 + B1(STABLE)
	Indirect (Plot-level) Models	
AX5	Litter depth model	$B_0 + B_1$ (LITTER)
AX6	Average depth of plot surface for lateral zone	$B_0 + B_1$ (DEPTH)
AX7	Position model: corrected distance from ridge, distance from basin center	$B_0 + B_1$ (DISTRIDG)+B_2 (DISTC)
AX8	Overstory model: canopy cover and RD of trees rooted in geomorphic surface	$B_0 + B_1$ (CCTOT)+ B2 (RDIN)
	Indirect (Landscape-level) Models	
AX9	Heat load index model	$B_0 + B_1$ (HEATNDX)
AX10	Gradient model: gradient of entire basin	$B_0 + B_1$ (GRADE)
AX11	Geomorphic surface model	$B_0 + B_1$ (GEOSRF)
AX12	Basin area model: Flow area contributing to pour point	B0 + B1 (AREA)
	Multiple drivers models	
AX13	Surface moisture, overstory and stability model	$B_0 + B_1$ (MOISTR)+ B_2 (CCTOT)+ B_3 (STABLE)
AX14	Macromodel: geomorphic surface, basin area, slope of entire basin, heat load index	$B_0 + B_1$ (GEOSRF)+ B_2 (AREA)+B_3(GRADE)+ B4 (HEATNDX)
AX15	Geomorphic surface, average surface moisture, canopy cover, heat load index	$B_0 + B_1$ (GEOSRF)+ B_2 (MOISTR) + B_3(CCTOT)+ B4 (HEATNDX)
AX16	Microclimate model: depth, canopy cover, heat load index for basin, RD of "in" trees	$B_0 + B_1$ (DPTH)+B2(CC)+ B3 (HEATNDX) + B4 (RDIN)
AX17	W. hemlock model: surface moisture, litter depth, relative density of hemlock	B_0 + B1 (MOISTR) + B2 (LITTER) + B3 (RDTSHE)

Table B1. (continued)

Model No.	Hypothesis	Model
AX18	Riparian model: Surface moisture, freq of scour, RD of hardwoods	B_0 + B1 (MOISTR) + B2 (SCOUR)+ B3 (RDHW)
AX19	Delineation model: Distance from ridge, distance from basin center, trees in-surface, litter depth	B_0 + B_1 (DISTRIDG) + B_2 (DISTC)+B_3(RDIN)+ B_4 (LITTER)
AX20	**Full Rich Model**	B0 + B1(MOISTR)+B2 (DISTRIDG) + B3 (DISTC) + B4 (STABLE) +B5 (GRADE) +B6 (HEATNDX)+ B7 (AREA) + B8 (RDTSHE) +B9 (CCTOT) B10 (RDHW) + B14 (YEAR)

[1] Included in model set to determine if any of the measured parameters had utility in describing plant composition (axis scores).

[2] Covariates included measured parameters which may have influenced response (ordination axis scores) but which were unrelated to the hypotheses being tested.

Table B2. Results of model ranking for a set of 20 *a priori* models describing Axis 1 ordination score as a function of selected environmental parameters. "***w***" is model weighting. Model AX0 = null model. Models with ΔQAICc ≤ 2 shown in **bold**. Codes for parameters used in AICc models are explained in Table B5. Model parameters described in Table 2.3 (Chapter 2).

Rank	Model #	Model	AICc	ΔAICc	*w*	Cumulative weights
1	**AX15**	**GEOSRF MOISTR CCTOT HEATNDX**	**367**	**0**	**0.999**	**0.999**
2	AX14	GEOSRF AREA GRADE HEATNDX	390	23.368	0.0001	>0.999
3	AX11	GEOSRF	391	24.314	<0.0001	
4	AX2	GEOSRF GEOL SOILTYP DISTOCN	399	32.141		
5	AX20	MOISTR DISTRIDG DISTC STABLE GRADE HEATNDX AREA RDTSHE CCTOT RDHW YEAR	406	39.153		
6	AX19	DISTRIDG DISTC RDIN LITTER	435	67.955		
7	AX13	MOISTR CCTOT STABLE	441	74.331		
8	AX4	STABLE	455	88.667		
9	AX7	DISTRIDG DISTC	464	96.895		
10	AX16	DEPTH CCTOT HEATNDX RDIN	477	110.721		
11	AX17	MOISTR LITTER RDTSHE	479	112.695		
12	AX3	MOISTR	481	114.106		
13	AX18	MOISTR SCOUR RDHW	486	119.186		
14	AX8	CCTOT RDIN	494	126.995		
15	AX9	HEATNDX	498	130.944		
16	AX6	DEPTH	500	132.998		
17	AX5	LITTER	505	137.978		
18	AX10	GRADE	505	138.077		
19	AX0		506	139.138		
20	AX1	YEAR ROADS HARVEST	511	143.962		
21	AX12	AREA	511	144.066		

Table B3. Results of model ranking for a set of 20 *a priori* models describing Axis 2 ordination score as a function of selected environmental parameters. "***w***" is model weighting. Model AX0 = null model. Models with ΔQAICc < 2 shown in **bold**. Codes for parameters used in AICc models are explained in Table B5. Model parameters described in Table 2.3 (Chapter 2).

Rank	Model no.	Model	AICc	ΔAICc	*w*	Cumulative weights
1	**AX9**	**HEATNDX**	**463**	**0.000**	**0.497**	**0.497**
2	**AX7**	**DISTRIDG DISTC**	**463**	**0.214**	**0.447**	**0.944**
3	AX11	GEOSRF	469	6.337	0.021	0.965
4	AX0		470	7.156	0.014	0.979
5	AX6	DEPTH	471	8.086	0.009	0.988
6	AX4	STABLE	473	10.053	0.003	0.991
7	AX15	GEOSRF MOISTR CCTOT HEATNDX	473	10.412	0.003	0.994
8	AX3	MOISTR	475	11.880	0.001	0.995
9	AX14	GEOSRF AREA GRADE HEATNDX	475	12.018	0.001	0.997
10	AX12	AREA	475	12.113	0.001	0.998
11	AX5	LITTER	475	12.326	0.001	0.999
12	AX19	DISTRIDG DISTC RDIN LITTER	475	12.575	0.001	>0.999
13	AX10	GRADE	478	14.956	<0.001	
14	AX18	MOISTR SCOUR RDHW	483	20.652		
15	AX1	YEAR ROADS HARVEST	484	20.736		
16	AX2	GEOSRF GEOL SOILTYP DISTOCN	484	20.807		
17	AX16	DEPTH CCTOT HEATNDX RDIN	487	24.488		
18	AX13	MOISTR CCTOT STABLE	488	25.585		
19	AX17	MOISTR LITTER RDTSHE	490	26.829		
20	AX8	CCTOT RDIN	492	29.086		
21	AX20	MOISTR DISTRIDG DISTC STABLE GRADE	498	35.033		

Table B4. Results of model ranking for a set of 20 *a priori* models describing Axis 3 ordination score as a function of selected environmental parameters. "*w*" is model weighting. Model AX0 = null model. Models with ΔQAICc < 2 shown in **bold**. Codes for parameters used in AICc models are explained in Table B5. Model parameters described in Table 2.3 (Chapter 2).

Rank	**Model no.**	Model	AICc	**ΔAICc**	***w***	**Cumulative weights**
1	**AX10**	**GRADE**	**387**	**0.000**	**0.775**	**0.775**
2	AX1	YEAR ROADS HARVEST	391	3.634	0.126	0.901
3	AX2	GEOSRF GEOL SOILTYP DISTOCN	393	5.487	0.050	0.951
4	AX14	GEOSRF AREA SPDGRE HEATNDX	394	6.910	0.024	0.975
5	AX3	MOISTR	396	8.760	0.010	0.985
6	AX17	MOISTR LITTER RDTSHE	397	9.860	0.006	0.990
7	AX18	MOISTR SCOUR RDHW	397	9.970	0.005	0.996
8	AX9	HEATNDX	400	12.947	0.001	0.997
9	AX5	LITTER	400	13.268	0.001	0.998
10	AX0		401	13.692	0.001	0.999
11	AX11	GEOSRF	402	14.777	<0.001	>0.999
12	AX4	STABLE	402	14.793		
13	AX12	AREA	405	17.542		
14	AX15	GEOSRF MOISTR CCTOT HEATNDX	405	18.166		
15	AX13	MOISTR CCTOT STABLE	406	19.140		
16	AX6	DEPTH	411	23.468		
17	AX7	DISTRIDGDISTC	414	26.668		
18	AX20	MOISTR DISTRIDG DISTC STABLE SPDGRE HEATNDX AREA RDTSHE CCTOT RDHW YEAR	417	29.790		
19	AX8	CCTOT RDIN	421	33.764		
20	AX19	DISTRIDG DISTC RDIN LITTER	424	36.526		
21	AX16	DEPTH CCTOT HEATNDX RDIN	429	42.220		

Table B5. Codes for parameters used in AICc models describing ordination axis scores as a function of environmental parameters. Model parameters described in Table 2.3 (Chapter 2)

Model code	Parameter
Plot/ basin-scale parameters	
AREA	Basin area
DEPTH	Basin depth
GRADE	Basin gradient
CCTOT	Canopy cover
CCCON	Conifer canopy cover
DEPOSIT	Deposition
DISTC	Distance from basin center
GEOSRF	Geomorphic surface
CCHW	Hardwood canopy cover
HEATNDX	Heat load index
BA70	Large overstory
LRGSUB	Large substrate
LITTER	Litter depth
ORGANICS	Organic depth
ORGSUB	Organic substrate
HEIGHT	Plot height
RD	Relative density
RDHW	Relative density of hardwood
RDTSHE	Relative density of hemlock
RDIN	Relative density within geomorphic surface
DISTRIDG	Ridge distance
SATUR	Saturation
SCOUR	Scour
STABLE	Stability
MOISTR	Surface moisture
Covariates	
AGE	Stand age
DISTOCN	Ocean distance
ELEV	Elevation
GEOL	Geology class
HARVEST	Disturbance due to harvest
ROADS	Disturbance due to roads
SOILTYP	Soil class
YEAR	Year of survey

APPENDIX C: PLANT SPECIES COVERS AND VEGETATION TYPES

Table C1. Herb, shrub and tree seedling areal covers (95% CI). Species ordered by maximum indicator values for 1 of 7 vegetation types. Maximum indicator value (Dufrene and Legendre 1997), value significance (p-values), areal coverage for each geomorphic/lateral zone, and average cover for the sample is presented for each species. Proportion (percent) of units assigned to each vegetation type shown (*in italics*) for each geomorphic/lateral zone, and for entire sample (*Veg. type %*).

Veg. type Species	MAX IV	p	0 m	1 m	5 m	Slope	Headmost	Nose	*Veg. type %* Species means
Mitella			*6.1*	*1.59*	*0*	*0*	*0*	*0*	*7.69*
Mitella ovalis	56.2	0.001	4.82 (3.59,6.05)	5.14 (3.46,6.81)	0.71 (0.23,1.19)	0.07 (-0.03,0.17)	0.11 (-0.09,0.31)	0	1.81 (1.39, 2.23)
Mimulus dentatus	43.4	0.001	1.79 (1.01,2.57)	1.1 (0.44,1.76)	0.34 (-0.15,0.82)	0.04 (-0.04,0.12)	0	0	0.55 (0.35, 0.74)
Tolmiea menziesii	41.7	0.001	2.48 (1.35,3.62)	2.71 (1.3,4.12)	0.58 (-0.06,1.23)	0.12 (-0.12,0.36)	0.29 (-0.05,0.64)	0.04 (-0.04,0.12)	1.04 (0.7, 1.38)
Rubus spectabilis	31.5	0.001	2.42 (1.06,3.78)	2.75 (1.02,4.48)	0.95 (0.16,1.74)	1.09 (-0.05,2.22)	0.42 (0,0.84)	0.21 (-0.11,0.54)	1.31 (0.87, 1.75)
Chrysosplenium glechomaefolium	21.3	0.001	1.37 (-0.09,2.82)	0.9 (-0.06,1.86)	0.32 (-0.32,0.95)	0	0.04 (-0.04,0.12)	0	0.44 (0.13, 0.75)
Ribes bracteosum	21.1	0.001	2.16 (0.84,3.48)	2.27 (0.81,3.72)	1.08 (-0.02,2.19)	0	0.01 (-0.01,0.02)	0.08 (-0.08,0.24)	0.94 (0.55, 1.32)
Mitella caulescens	15.5	0.002	0.11 (-0.01,0.24)	0.19 (-0.07,0.45)	0.04 (-0.04,0.12)	0	0	0	0.06 (0.01, 0.11)
Lysichiton americanum	12.7	0.003	0.17 (-0.03,0.38)	0.2 (-0.15,0.55)	0	0	0	0	0.06 (0, 0.13)
Athyrium filix-femina	20.7	0.004	1.92 (1.14,2.71)	3.82 (2.38,5.25)	1.75 (0.68,2.82)	0.66 (0.15,1.17)	0.64 (0.19,1.09)	0.28 (-0.12,0.67)	1.51 (1.15, 1.88)
Cardamine oligosperma	11.4	0.004	0.17 (-0.05,0.4)	0.1 (-0.04,0.24)	0.06 (-0.06,0.18)	0	0.17 (-0.16,0.49)	0	0.08 (0.01, 0.15)
Viola glabella	15.7	0.01	0.57 (0.19,0.94)	0.52 (-0.23,1.27)	0.21 (-0.03,0.45)	0.13 (-0.06,0.33)	0.51 (-0.01,1.03)	0.08 (-0.08,0.24)	0.34 (0.17, 0.51)
Dryopteris arguta	10.9	0.01	0.09 (-0.02,0.2)	0.38 (-0.27,1.02)	0.3 (-0.01,0.6)	0	0	0	0.13 (0.01, 0.25)
Saxifraga mertensiana	6.9	0.013	0.03 (-0.03,0.1)	0.01 (-0.01,0.02)	0	0	0	0	0.01 (0, 0.02)
Streptopus amplexifolius	8.8	0.054	1.13 (0.47,1.78)	1.62 (0.81,2.42)	0.03 (-0.03,0.08)	0.12 (-0.12,0.36)	0	0.12 (-0.12,0.36)	0.5 (0.31, 0.69)
Claytonia sibirica	13	0.083	0.96 (0.53,1.39)	1.07 (0.41,1.74)	0.68 (0.29,1.06)	0.72 (0.29,1.16)	1.15 (0.12,2.19)	0.65 (-0.09,1.39)	0.87 (0.61, 1.13)
Thuja plicata	3.2	0.141	0.2 (-0.2,0.6)	0	0	0	0.08 (-0.08,0.24)	0	0.05 (-0.02, 0.12)
Oplopanax horridum	3.1	0.169	0.12 (-0.12,0.36)	0	0.05 (-0.05,0.16)	0	0	0	0.03 (-0.01, 0.07)
Boykinia elata	6	0.179	0.61 (0.19,1.03)	0.87 (-0.01,1.76)	0.14 (-0.08,0.35)	0	0.43 (-0.25,1.11)	0	0.34 (0.14, 0.54)

Table C1. (continued)

Veg. type	**MAX**								***Veg. type %***
Species	**IV**	**p**	**0 m**	**1 m**	**5 m**	**Slope**	**Headmost**	**Nose**	Species means
Stellaria crispa	4.9	0.181	0.12 (0.01,0.23)	0.1 (-0.02,0.22)	0.05 (-0.03,0.13)	0.04 (-0.04,0.12)	0.19 (-0.13,0.52)	0.05 (-0.05,0.16)	0.09 (0.03, 0.16)
Galium triflorum	9.8	0.188	0.91 (0.52,1.31)	0.7 (0.34,1.05)	0.6 (0.24,0.97)	1.46 (0.7,2.23)	0.68 (0.32,1.05)	0.52 (0.16,0.87)	0.81 (0.63, 1)
Polystichum kruckebergii	4.5	0.302	0.06 (0,0.12)	0.09 (0.01,0.17)	0.21 (0.03,0.39)	0.04 (0,0.09)	0.02 (-0.01,0.06)	0.01 (-0.01,0.02)	0.07 (0.04, 0.11)
Galium oreganum	2.6	0.431	0.05 (-0.05,0.16)	0.06 (-0.03,0.14)	0.08 (-0.08,0.24)	0.04 (-0.04,0.12)	0.12 (-0.03,0.28)	0.08 (-0.08,0.24)	0.07 (0.02, 0.12)
Saxifraga occidentalis	1.9	0.495	0.02 (-0.01,0.06)	0.01 (-0.01,0.02)	0	0	0	0	0.01 (0, 0.01)
Ranunculus uncinatus	2.6	0.57	0.12 (0.01,0.24)	0.07 (-0.01,0.16)	0.03 (-0.02,0.09)	0.16 (-0.03,0.35)	0.17 (-0.16,0.49)	0.04 (-0.04,0.12)	0.1 (0.03, 0.17)
Mimulus guttatus	2.5	+	0.26 (0.02,0.5)	0.09 (0,0.19)	0.35 (-0.12,0.82)	0	0	0	0.12 (0.03, 0.21)
Blechnum			***0.53***	***4.51***	***0.8***	***0.53***	***0.27***	***0***	***6.64***
Blechnum spicant	67.8	0.001	3 (2.07,3.94)	7.13 (5.02,9.24)	2.28 (1.16,3.39)	1.6 (0.49,2.7)	2.23 (-0.54,5.01)	0	2.71 (2.03, 3.38)
Tiarella trifoliata var. trifoliata	34.4	0.001	0.96 (0.54,1.37)	1.6 (0.72,2.47)	0.21 (0.07,0.35)	0.48 (0.01,0.94)	0.35 (0.11,0.59)	0.22 (0.01,0.44)	0.64 (0.45, 0.83)
Achlys triphylla	7.6	0.106	0.31 (-0.22,0.85)	0.53 (-0.15,1.21)	0.61 (0.15,1.06)	0.73 (0.1,1.36)	0.4 (0,0.79)	0.29 (-0.01,0.6)	0.48 (0.27, 0.69)
Mitella petandra	4.3	0.162	0.25 (0.03,0.47)	0.1 (-0.06,0.26)	0.01 (-0.01,0.03)	0.08 (-0.08,0.24)	0	0	0.07 (0.02, 0.13)
Marah oreganus	3	0.206	0.03 (-0.03,0.1)	0.08 (-0.08,0.24)	0	0	0	0	0.02 (-0.01, 0.05)
Equisetum telmatiea	2.6	0.257	0.05 (-0.03,0.13)	0.03 (-0.03,0.08)	0	0	0	0	0.01 (0, 0.03)
Tiarella trifoliata var. unifoliata	3.9	0.303	0.18 (0.03,0.33)	0.06 (-0.01,0.12)	0.07 (-0.02,0.17)	0.16 (-0.06,0.38)	0.01 (-0.01,0.03)	0.1 (-0.07,0.26)	0.1 (0.04, 0.15)
Panicum dichotomiflorum	2.6	0.306	0.08 (-0.08,0.24)	0	0	0	0.14 (-0.14,0.42)	0	0.04 (-0.02, 0.09)
Festuca occidentalis	3.5	0.342	0.1 (-0.05,0.25)	0.05 (-0.02,0.11)	0.18 (-0.14,0.5)	0.08 (-0.08,0.24)	0.21 (-0.12,0.54)	0.17 (-0.02,0.37)	0.13 (0.04, 0.22)
Luzula parviflora	4	0.484	0.15 (0.03,0.27)	0.27 (0.04,0.5)	0.33 (0.01,0.64)	0.13 (-0.03,0.29)	0.27 (0.09,0.45)	0.04 (-0.02,0.1)	0.2 (0.12, 0.28)
Oxalis			***7.16***	***9.02***	***7.43***	***3.18***	***5.04***	***1.59***	***33.42***
Oxalis oregana	31.8	0.001	14.17 (11.66,16.69)	24.23 (20.67,27.78)	21.74 (18.3,25.2)	17.5 (14.13,20.87)	18.12 (13.6,22.7)	7.32 (4.62,10.02)	17.18 (15.7, 18.65)
Dicentra formosa	9.2	0.073	0.17 (0.01,0.33)	0.02 (-0.01,0.04)	1.21 (0.04,2.37)	0.57 (0.09,1.06)	0.22 (0.04,0.41)	0.12 (-0.12,0.36)	0.38 (0.17, 0.6)
Stachys mexicana	11.2	0.103	0.88 (0.47,1.3)	1.19 (0.74,1.64)	1.33 (0.62,2.04)	1.06 (0.43,1.69)	1.27 (0.27,2.26)	0.34 (0,0.69)	1.01 (0.76, 1.27)
Adiantum pedatum	10	+	1.6 (0.95,2.26)	2.38 (1.19,3.57)	2.07 (0.88,3.25)	1.49 (0.54,2.44)	0.83 (0.22,1.44)	0.15 (0.01,0.29)	1.42 (1.07, 1.78)
Hydrophyllum tenuipes	3.8	0.204	0.26 (-0.11,0.64)	0.11 (-0.06,0.27)	0.21 (-0.04,0.45)	0.24 (-0.24,0.71)	0	0	0.14 (0.03, 0.25)
Osmorhiza chilensis	3.2	0.206	0.02 (-0.02,0.07)	0.01 (-0.01,0.04)	0.04 (-0.04,0.12)	0	0.01 (-0.01,0.04)	0	0.01 (0, 0.03)
Carex hedersonii	4.1	0.219	0.23 (-0.01,0.48)	0.17 (-0.02,0.35)	0.09 (-0.07,0.24)	0.02 (-0.02,0.05)	0.13 (-0.04,0.31)	0.02 (-0.02,0.07)	0.11 (0.05, 0.17)

Table C1. (continued)

Veg. type	**MAX**								***Veg. type %***
Species	**IV**	**p**	**0 m**	**1 m**	**5 m**	**Slope**	**Headmost**	**Nose**	Species means
Galium aparine	3.2	0.422	0.12 (0,0.23)	0.19 (-0.02,0.41)	0.09 (-0.04,0.22)	0.24 (-0.11,0.59)	0.24 (-0.09,0.57)	0	0.15 (0.06, 0.24)
Asarum caudatum	2.7	0.456	0.18 (-0.07,0.43)	0.27 (-0.11,0.65)	0.05 (-0.02,0.11)	0	0.13 (-0.11,0.37)	0	0.1 (0.02, 0.19)
Acer macrophyllum	1.5	0.52	0	0	0.26 (-0.26,0.79)	0	0.01 (0,0.02)	0	0.05 (-0.04, 0.13)
Nemophila parviflora	2.6	0.529	0.08 (-0.08,0.24)	0.03 (-0.01,0.06)	0.07 (-0.01,0.14)	0.16 (0,0.31)	0.14 (0,0.28)	0	0.08 (0.03, 0.12)
Elymus glaucus	1.6	0.539	0.02 (-0.02,0.07)	0.01 (-0.01,0.02)	0	0	0	0	0 (0, 0.01)
Cardamine occidentalis	1.6	0.585	0.1 (-0.1,0.29)	0.03 (-0.03,0.08)	0	0	0	0	0.02 (-0.01, 0.05)
Holcus lanatus	1.6	0.629	0.05 (-0.05,0.14)	0.07 (-0.07,0.2)	0	0	0	0	0.02 (-0.01, 0.04)
Vancouveri hexandra	4.6	0.657	0.45 (0.13,0.76)	1.13 (0.34,1.93)	0.87 (0.31,1.44)	0.51 (0.14,0.88)	0.32 (0.03,0.62)	0.35 (0,0.7)	0.61 (0.41, 0.8)
Equisetum arvense	1.6	0.659	0.05 (-0.01,0.1)	0.03 (-0.03,0.08)	0	0	0	0	0.01 (0, 0.02)
Polypodium hesperium	0.9	0.846	0.02 (-0.02,0.06)	0.03 (-0.03,0.08)	0	0	0.02 (-0.02,0.07)	0	0.01 (0, 0.03)
Tsuga heterophylla	4.4	0.943	1.32 (0.72,1.91)	0.69 (0.18,1.2)	1.16 (0.32,2)	0.63 (0.09,1.18)	0.59 (0.19,1)	0.61 (-0.27,1.49)	0.84 (0.57, 1.1)
Polystichum			**0**	**0.53**	**5.04**	**6.9**	**4.77**	**3.98**	**21.22**
Polystichum munitum	36.9	0.001	8.05 (6.12,9.98)	14.98 (12.33,17.64)	28.19 (23.72,32.67)	28.53 (23.33,33.73)	22.86 (18.26,27.47)	16.88 (12.1,21.66)	19.91 (18.1, 21.71)
Alnus rubra	1.4	0.774	0	0.07 (-0.05,0.19)	0.05 (-0.05,0.16)	0	0.4 (-0.17,0.98)	0	0.09 (-0.01, 0.18)
Listera caurina	1.7	0.89	0.01 (-0.01,0.03)	0.05 (-0.02,0.13)	0.04 (-0.02,0.1)	0.01 (-0.01,0.03)	0.06 (-0.02,0.14)	0.15 (-0.01,0.31)	0.05 (0.02, 0.09)
Coptis laciniata	1.1	0.923	0	0.06 (-0.04,0.17)	0.03 (-0.03,0.08)	0.16 (-0.16,0.48)	0.04 (-0.04,0.11)	0.13 (-0.1,0.37)	0.07 (0, 0.14)
Gaultheria			**2.12**	**0.8**	**1.59**	**1.59**	**1.86**	**1.86**	**9.82**
Gaultheria shallon	29.3	0.001	1 (0.29,1.7)	1.05 (0.39,1.71)	1.19 (0.27,2.11)	1.17 (0.11,2.23)	1.61 (0.66,2.57)	2.94 (1.13,4.74)	1.49 (1.05, 1.93)
Holodiscus discolor	15.9	0.003	0.21 (-0.07,0.48)	0.17 (-0.06,0.39)	1.11 (0.09,2.13)	0.81 (-0.16,1.78)	0.42 (-0.21,1.04)	0.36 (-0.11,0.82)	0.51 (0.24, 0.78)
Acer circinatum	17.3	0.004	1.4 (0.49,2.31)	0.7 (0.27,1.14)	1.5 (0.75,2.24)	0.73 (0.19,1.27)	1.28 (0.35,2.21)	1 (0.11,1.89)	1.1 (0.79, 1.41)
Whipplea modesta	15.5	0.006	0.05 (-0.02,0.11)	0.02 (-0.01,0.05)	0.12 (-0.04,0.29)	0.63 (-0.34,1.59)	0.1 (-0.03,0.24)	0.31 (0.06,0.57)	0.21 (0.04, 0.37)
Rubus parviflorus	6.6	0.055	0.24 (0.02,0.46)	0.42 (-0.42,1.27)	0.03 (-0.03,0.1)	0.24 (-0.24,0.71)	0.91 (-0.48,2.29)	0	0.31 (0.03, 0.58)
Pentagramma triangularis	5.4	0.055	0	0	0.01 (-0.01,0.02)	0.02 (-0.02,0.07)	0	0	0.01 (0, 0.01)
Smilacina racemosa	5.8	0.061	0.02 (-0.02,0.06)	0	0	0.08 (-0.08,0.24)	0.08 (-0.05,0.21)	0.6 (-0.06,1.25)	0.13 (0.01, 0.24)
Corylus cornuta	6	0.068	0.24 (-0.1,0.58)	0	0.2 (-0.09,0.5)	0.68 (-0.59,1.95)	0.19 (-0.08,0.45)	0	0.22 (-0.01, 0.44)
Sambucus racemosa	4.9	0.115	0.04 (-0.02,0.1)	0.24 (-0.24,0.71)	0	0	0.32 (-0.32,0.97)	0	0.1 (-0.03, 0.23)

Table C1. (continued)

Veg. type Species	MAX IV	p	0 m	1 m	5 m	Slope	Headmost	Nose	*Veg. type %.* Species means
Bromus carinatus	10.5	0.118	1.02 (0.56,1.47)	1.38 (0.69,2.07)	0.77 (0.22,1.33)	1.1 (0.3,1.91)	0.92 (0.21,1.62)	0.2 (-0.05,0.46)	0.9 (0.65, 1.14)
Hieracium albiflorum	3.6	0.128	0	0	0	0.02 (-0.02,0.05)	0.11 (-0.11,0.33)	0.06 (-0.03,0.14)	0.03 (-0.01, 0.07)
Toxicodendron diversilobum	3.5	0.136	0.02 (-0.02,0.06)	0.19 (-0.18,0.56)	0.08 (-0.08,0.24)	0	0	0	0.05 (-0.02, 0.11)
Castanopsis chrysophylla	3.5	0.17	0.01 (-0.01,0.04)	0	0.03 (-0.03,0.08)	0.04 (-0.04,0.12)	0	0	0.01 (0, 0.03)
Circaea alpina	5.8	0.229	0.25 (0.02,0.48)	0.33 (0.03,0.64)	0.27 (-0.02,0.57)	0.24 (-0.24,0.71)	0.36 (-0.17,0.89)	0	0.24 (0.1, 0.38)
Carex deweyana	8	0.231	0.7 (0.37,1.03)	0.97 (0.44,1.5)	0.64 (0.18,1.1)	1.18 (-0.15,2.5)	1.19 (0.08,2.31)	0	0.78 (0.47, 1.09)
Rosa gymnocarpa	3.2	0.234	0	0	0	0.07 (-0.04,0.18)	0.35 (-0.18,0.88)	0.13 (-0.1,0.37)	0.09 (0, 0.19)
Trientalis latifolia	4.9	0.254	0	0.01 (-0.01,0.03)	0	0.3 (-0.02,0.62)	0.47 (0.18,0.75)	0.31 (0.08,0.53)	0.18 (0.1, 0.26)
Lathyrus polyphyllus	2.4	0.329	0	0	0	0	0.01 (-0.01,0.04)	0.04 (-0.04,0.11)	0.01 (0, 0.02)
Actea rubra	2.3	0.364	0	0	0	0.02 (-0.02,0.05)	0	0.04 (-0.04,0.12)	0.01 (0, 0.02)
Tellima grandiflora	3.4	0.409	0.19 (-0.01,0.38)	0.08 (-0.03,0.19)	0.16 (-0.04,0.36)	0.04 (-0.03,0.1)	0.01 (0,0.02)	0.04 (-0.04,0.12)	0.09 (0.03, 0.14)
Prunella vulgaris	2	0.51	0	0.06 (-0.05,0.17)	0.05 (-0.05,0.14)	0	0	0	0.02 (-0.01, 0.04)
Vaccinium parvifolium	7.2	0.515	1.03 (0.6,1.46)	1.35 (0.62,2.08)	1.65 (0.73,2.57)	1.31 (-0.01,2.63)	1.56 (0.48,2.65)	0.33 (0.03,0.63)	1.2 (0.85, 1.55)
Thalictrum occidentale	2.7	0.546	0.12 (-0.04,0.27)	0.28 (0,0.56)	0.09 (-0.04,0.21)	0.32 (-0.07,0.7)	0.01 (-0.01,0.02)	0	0.13 (0.05, 0.22)
Festuca idahoensis	1.7	0.575	0	0	0	0.04 (-0.04,0.12)	0	0.04 (-0.04,0.12)	0.01 (-0.01, 0.03)
Synthyris reniformis	2	0.619	0.01 (-0.01,0.04)	0	0.21 (0,0.43)	0.08 (-0.08,0.24)	0.07 (-0.02,0.16)	0.1 (-0.05,0.26)	0.08 (0.03, 0.13)
Hierochloe occidentalis	1.1	0.754	0	0	0	0	0.09 (-0.09,0.27)	0.24 (-0.24,0.71)	0.05 (-0.03, 0.14)
Anemone deltoidea	2.3	0.769	0.01 (-0.01,0.02)	0.11 (-0.1,0.32)	0.07 (-0.04,0.18)	0.32 (-0.04,0.68)	0.1 (0,0.2)	0.12 (-0.06,0.3)	0.12 (0.04, 0.2)
Epilobium angustifolium	1.4	0.774	0.02 (-0.01,0.05)	0.01 (-0.01,0.02)	0.02 (-0.02,0.06)	0	0	0	0.01 (0, 0.02)
Arabidopsis thaliana	1.2	0.865	0	0	0	0	0.07 (-0.07,0.21)	0	0.01 (0, 0.03)
Adenocaulon bicolor	2.7	0.892	0.15 (-0.01,0.31)	0.43 (0.14,0.72)	0.24 (-0.05,0.53)	0.4 (-0.1,0.9)	0.45 (0.05,0.85)	0.08 (-0.01,0.17)	0.29 (0.16, 0.42)
Berberis			***0.53***	***0.27***	***1.86***	***3.98***	***3.71***	***6.9***	***17.25***
Berberis nervosa	56.1	0.001	0.54 (0.1,0.97)	1.08 (0.2,1.96)	3.1 (1.68,4.53)	7.46 (5.28,9.65)	6.07 (3.87,8.27)	11.38 (8.4,14.36)	4.94 (4.09, 5.78)
Pteridium aquilinum	6	0.081	0.08 (-0.08,0.24)	0.06 (-0.06,0.18)	0.02 (-0.02,0.05)	0.11 (-0.06,0.28)	0.12 (-0.05,0.29)	0.42 (0.06,0.79)	0.13 (0.06, 0.21)
Disporum hookeri	9	0.216	0.29 (0.07,0.5)	0.81 (0.33,1.29)	1.43 (0.68,2.18)	1.02 (0.52,1.52)	1.12 (0.6,1.64)	0.68 (0.1,1.25)	0.89 (0.67, 1.11)
Corallorhiza maculata	3.1	0.222	0 (0,0.01)	0	0.03 (-0.03,0.08)	0	0.08 (-0.08,0.24)	0.02 (-0.02,0.05)	0.02 (-0.01, 0.05)
Chimaphila umbellata	3.1	0.24	0	0	0	0.12 (-0.12,0.36)	0 (0,0.01)	0.04 (-0.04,0.12)	0.03 (0, 0.07)

Table C1. (continued)

Veg. type	**MAX**								***Veg. type %***
Species means	**IV**	**p**	**0 m**	**1 m**	**5 m**	**Slope**	**Headmost**	**Nose**	Species means
Corallorhiza striata	3.3	0.245	0	0.05 (-0.05,0.16)	0.01 (-0.01,0.03)	0	0	0.1 (-0.02,0.21)	0.03 (0, 0.05)
Trillium ovatum	6.3	0.395	0.08 (0.01,0.14)	0.2 (-0.05,0.45)	1.09 (0.51,1.67)	0.69 (0.26,1.12)	0.28 (0.05,0.51)	0.5 (0.13,0.86)	0.47 (0.32, 0.62)
Campanula scouleri	2.1	0.471	0 (0,0.01)	0	0.02 (-0.01,0.05)	0.01 (-0.01,0.02)	0.04 (-0.04,0.12)	0	0.01 (0, 0.03)
Chimaphila menziesii	2.1	0.488	0	0	0.05 (-0.05,0.16)	0.11 (-0.06,0.27)	0	0.04 (-0.01,0.09)	0.01 (-0.01, 0.04)
Rhamnus purshiana	1.4	0.597	0	0	0	0.16 (-0.16,0.48)	0.01 (-0.01,0.02)	0	0.03 (-0.02, 0.08)
Luzula comosa	1.3	0.87	0.02 (-0.02,0.05)	0.03 (-0.03,0.08)	0.08 (-0.04,0.2)	0.2 (-0.09,0.48)	0	0.22 (-0.1,0.55)	0.09 (0.02, 0.16)
Vaccinium			***0.27***	***0***	***0***	***0.53***	***0.8***	***2.39***	***3.99***
Vaccinium ovatum	62.9	0.001	0.68 (0.18,1.17)	0.45 (0.05,0.85)	0.11 (-0.03,0.24)	0.61 (0.03,1.19)	1.44 (0.08,2.8)	4.59 (1.2,7.98)	1.31 (0.68, 1.94)
Rhododendron macrophyllum	28	0.001	0.17 (-0.05,0.38)	0.09 (-0.04,0.22)	0.4 (0.03,0.78)	1.78 (0.54,3.01)	1.9 (0.44,3.36)	1.21 (0.36,2.05)	0.92 (0.57, 1.27)
Pyrola picta	18.5	0.001	0	0.02 (-0.02,0.06)	0.01 (-0.01,0.03)	0.04 (-0.04,0.12)	0.01 (-0.01,0.02)	0.28 (-0.03,0.58)	0.06 (0.01, 0.11)
Umbellularia californica	11.6	0.014	0.03 (-0.03,0.08)	0.03 (-0.02,0.09)	0.08 (-0.04,0.2)	0.39 (0,0.78)	0.69 (-0.44,1.83)	0.36 (0.06,0.65)	0.26 (0.06, 0.46)
Monotropa uniflora	6	0.045	0.02 (-0.02,0.05)	0	0	0	0	0.02 (-0.02,0.05)	0.01 (0, 0.01)
Rubus nivalis	6	0.049	0	0	0	0.04 (-0.04,0.12)	0.16 (-0.16,0.48)	0.04 (-0.04,0.12)	0.04 (-0.02, 0.1)
Montia parvifolia	5.1	0.069	0.1 (-0.1,0.3)	0	0.03 (-0.03,0.08)	0.04 (-0.04,0.12)	0	0.08 (-0.08,0.24)	0.04 (0, 0.09)
Sanicula crassicaulis	4.7	0.105	0	0	0.02 (-0.02,0.05)	0	0	0.02 (-0.02,0.05)	0.01 (0, 0.01)
Polypodium glycyrrhiza	3.4	0.188	0.02 (-0.02,0.06)	0.01 (-0.01,0.03)	0.01 (-0.01,0.03)	0	0	0.02 (-0.02,0.05)	0.01 (0, 0.02)
Viola sempervirens	6.3	0.249	0.04 (-0.01,0.08)	0.11 (-0.06,0.27)	0.24 (0.04,0.44)	0.72 (0.28,1.17)	0.36 (0.1,0.62)	0.79 (0.4,1.18)	0.38 (0.26, 0.49)
Rubus ursinus	4.2	0.325	0.02 (-0.01,0.05)	0.15 (-0.05,0.35)	0.04 (-0.03,0.12)	0.14 (0.01,0.27)	0.07 (-0.02,0.16)	0.04 (-0.04,0.12)	0.08 (0.03, 0.12)
Rubus laciniatus	2.8	0.427	0.08 (-0.08,0.24)	0.3 (-0.19,0.8)	0.11 (-0.06,0.27)	0.08 (-0.02,0.18)	0.03 (-0.02,0.09)	0.2 (-0.13,0.52)	0.13 (0.03, 0.24)
Disporum smithii	1.8	0.827	0.02 (-0.01,0.06)	0.08 (-0.03,0.19)	0.1 (0.01,0.19)	0.12 (-0.06,0.3)	0.09 (-0.04,0.21)	0.08 (-0.08,0.24)	0.08 (0.03, 0.13)

[+] Re-assigned from *Gaultheria* vegetation type, based on field observations (therefore no Monte Carlo test performed).

APPENDIX D: PLANT SPECIES CODES

Table D1: List of species codes for species used in direct ordination of plant species in environment-space.

Species	Code	Species	Code
Acer circinatum	ACCI	Equisetum telmatiea	EQTE
Acer macrophyllum	ACMA	Festuca idahoensis	FEID
Achlys triphylla	ACTR	Festuca occidentalis	FEOC
Actea rubra	ACRU	Galium aparine	GAAP
Adenocaulon bicolor	ADBI	Galium oreganum	GAOR
Adiantum pedatum	ADPE	Galium triflorum	GATR
Alnus rubra	ALRU	Gaultheria shallon	GASH
Anemone deltoidea	ANDE	Hieracium albiflorum	HIAL
Arabidopsis thaliana	ARTH	Hierochloe occidentalis	HIOC
Asarum caudatum	ASCA3	Holcus lanatus	HOLA
Athyrium filix-femina	ATFI	Holodiscus discolor	HODI
Berberis nervosa	BENE	Hydrophyllum tenuipes	HYTE
Blechnum spicant	BLSP	Lathyrus polyphyllus	LAPO
Boykinia occidentalis	BOEL	Listera caurina	LICA3
Bromus carinatus	BRCA	Luzula comosa	LUCO
Campanula scouleri	CASC2	Luzula parviflora	LUPA
Cardamine occidentalis	CAOC	Lysichiton americanum	LYAM
Cardamine oligosperma	CAOL	Marah oreganus	MAOR
Carex deweyana	CADE	Mimulus dentatus	MIDE
Carex hedersonii	CAHE	Mimulus guttatus	MIGU
Castanopsis chrysophylla	CACH	Mitella caulescens	MICA3
Chimaphila menziesii	CHME	Mitella ovalis	MIOV
Chimaphila umbellata	CHUM	Mitella petandra	MIPE
Chrysosplenium glechomaefolium	CHGL	Monotropa uniflora	MOUN2
Circaea alpina	CIAL	Montia parvifolia	MOPA
Claytonia sibirica	CLSI	Nemophila parviflora	NEPA
Coptis laciniata	COLA	Oplopanax horridum	OPHO
Corallorhiza maculata	COMA3	Osmorhiza chilensis	OSCH
Corallorhiza striata	COST2	Oxalis oregana	OXOR
Corylus cornuta	COCO2	Panicum dichotomiflorum	PADI
Dicentra formosa	DIFO	Pentagramma triangularis	PETR
Disporum hookeri	DIHO	Polypodium glycyrrhiza	POGL4
Disporum smithii	DISM	Polypodium hesperium	POHE2
Dryopteris arguta	DRAR	Polystichum kruckebergii	POKR
Elymus glaucus	ELGL	Polystichum munitum	POMU
Epilobium angustifolium	EPAN	Prunella vulgaris	PRVU
Equisetum arvense	EQAR		

Table D1: (continued)

Species	Code	Species	Code
Pteridium aquilinum	PTAQ	Pteridium aquilinum	PTAQ
Pyrola picta	PYPI	Pyrola picta	PYPI
Ranunculus uncinatus	RAUN2	Ranunculus uncinatus	RAUN2
Rhamnus purshiana	RHPU	Rhamnus purshiana	RHPU
Rhododendron macrophyllum	RHMA	Rhododendron macrophyllum	RHMA
Galium oreganum	GAOR	Sanicula crassicaulis	SACR
Galium triflorum	GATR	Saxifraga mertensiana	SAME3
Gaultheria shallon	GASH	Saxifraga occidentalis	SAOC3
Hieracium albiflorum	HIAL	Smilacina racemosa	SMRA
Hierochloe occidentalis	HIOC	Stachys mexicana	STME2
Holcus lanatus	HOLA	Stellaria crispa	STCR
Holodiscus discolor	HODI	Streptopus amplexifolius	STAM
Hydrophyllum tenuipes	HYTE	Synthyris reniformis	SYRE
Lathyrus polyphyllus	LAPO	Tellima grandiflora	TEGR
Listera caurina	LICA3	Thalictrum occidentale	THOC
Luzula comosa	LUCO	Thuja plicata	THPL
Luzula parviflora	LUPA	Tiarella trifoliata var. trifoliata	TITR
Lysichiton americanum	LYAM	Tiarella trifoliata var. unifoliata	TIUN
Marah oreganus	MAOR	Tolmiea menziesii	TOME
Mimulus dentatus	MIDE	Toxicodendron diversilobum	TODI
Mimulus guttatus	MIGU	Trientalis latifolia	TRLA2
Mitella caulescens	MICA3	Trillium ovatum	TROV
Mitella ovalis	MIOV	Tsuga heterophylla	TSHE
Mitella petandra	MIPE	Umbellularia californica	UMCA
Monotropa uniflora	MOUN2	Vaccinium ovatum	VAOV2
Montia parvifolia	MOPA	Vaccinium parvifolium	VAPA
Nemophila parviflora	NEPA	Vancouveri hexandra	VAHE
Oplopanax horridum	OPHO	Viola glabella	VIGL
Osmorhiza chilensis	OSCH	Viola sempervirens	VISE
Oxalis oregana	OXOR	Whipplea modesta	WHMO
Panicum dichotomiflorum	PADI		
Pentagramma triangularis	PETR		
Polypodium glycyrrhiza	POGL4		
Polypodium hesperium	POHE2		
Polystichum kruckebergii	POKR		
Polystichum munitum	POMU		
Prunella vulgaris	PRVU		

APPENDIX E: AMPHIBIAN QAICC MODEL SETS

Table E1. *A priori* model set describing southern torrent salamander captures as a function of environmental variables. "k" represents parameter number (including intercept, not shown), "*w*" is model weighting. Model RV0 = null model. Model parameters described in Table 3.2. Models with ΔQAICc $\leq$ 2 shown in **bold**.

Model Rank	Model no.	Ecological model	k	QAICc	ΔQAICc	*w*	Cum *w*
1	**RV18**	**GRADE HEATNDX DISTRIDG SATUR**	**5**	**7.264**	**0.000**	**0.844**	**0.844**
2	RV1	SATUR	2	12.314	5.050	0.068	0.912
3	RV6	SATUR LRGSUB	3	14.368	7.104	0.024	0.936
4	RV13	SATUR LRGSUB SHRUBS RDIN	5	14.89	7.626	0.019	0.954
5	RV11	SATUR LRGSUB RDHW	4	15.405	8.140	0.014	0.969
6	RV8	SATUR LRGSUB LN(BA70)	4	15.983	8.719	0.011	0.980
7	RV14	SATUR LRGSUB CCTOT FERNS LN(BA70)	6	16.283	9.019	0.009	0.989
8	RV17	SATUR LRGSUB DISTRIDG AREA	5	16.833	9.569	0.007	0.996
9	RV9	SATUR LRGSUB LM3HA LN(BA70)	5	18.126	10.862	0.004	>0.999
10	RV10	MOISTR LRGSUB LITTER RDTSHE	5	74.102	66.838	<0.001	
11	RV7	MOISTR SCOUR DEPOSIT	4	79.276	72.012		
12	RV15	MOISTR LRGSUB DISTRIDG CCTOT RDIN	6	82.922	75.658		
13	RV12	MOISTR LRGSUB SCOUR LN(M3HA) LN(BA70)	6	83.522	76.258		
14	RV19	DISTRIDG AREA RDIN	4	107.383	100.119		
15	RV4	LITTER	2	125.486	118.221		
16	RV20	DISTRIDG SCOUR DEPTH LN(BA70) AREA	6	141.492	134.228		
17	RV5	SCOUR DEPOSIT	3	151.245	143.981		
18	RVN2	DAY RH TEMPF	4	166.418	159.154		
19	RV16	DISTRIDG GRADE HEATNDX DEPTH AREA	6	166.509	159.245		
20	RVN1	DAY RH TEMPF ELEV DISTOCN	6	168.057	160.793		
21	RVN6	TEMPF	2	171.164	163.899		
22	RV3	DISTRIDG	2	171.361	164.097		
23	RVN3	DAY	2	172.276	165.012		
24	RV2	LRGSUB	2	176.303	169.039		
25	RVN5	RH	2	177.567	170.303		
26	RV0		1	183.454	176.190		
27	RVN4	AGE	2	183.801	176.537		

Note: Global model was over-parameterized, and was not used in model ranking.

Table E2. *A priori m*odel set describing Dunn's salamander captures as a function of environmental variables. "k" represents parameter number (including intercept, not shown), "*w*" is model weighting. Model PD0 = null model. Model parameters described in Table 3.2. Models with ΔQAICc $\leq$ 2 shown in **bold**.

Model Rank	Model no.	Ecological model	k	QAICc	ΔQAICc	*w*	Cum *w*
1	**PD11**	**SHRUBS CCTOT SATUR LRGSUB**	**5**	**112.43**	**0.000**	**0.903**	**0.903**
2	PD8	SATUR LRGSUB CCTOT LN(BA70)	5	118.24	5.806	0.050	0.953
3	PD21	LN(DISTRIDG) SATUR LN(BA70) AREA	5	120.08	7.644	0.020	0.973
4	PD6	SATUR DEPOSIT	3	121.99	9.555	0.008	0.980
5	PD10	SATUR LRGSUB LN(BA70) LN(M3HA)	5	123.05	10.621	0.004	0.985
6	PD1	SATUR	2	123.44	11.002	0.004	0.988
7	PD13	SATUR LRGSUB LN(DISTRIDG) DEPOSIT LN(BA70)	6	123.77	11.340	0.003	0.992
8	PD7	SATUR LRGSUB	3	123.87	11.432	0.003	0.994
9	PD22	SATUR LRGSUB LN(DISTRIDG) CCTOT RDHW	6	124.39	11.951	0.002	0.997
10	PD9	SATUR LRGSUB FERNS CCTOT LN(M3HA)	6	124.67	12.234	0.002	0.999
11	PD14	SATUR LRGSUB DEPOSIT RDHW	5	125.73	13.301	0.001	>0.999
12	PD23	SATUR LRGSUB LN(DISTRIDG) DEPOSIT LN(M3HA) LN(BA70) AREA GRADE HEATNDX RDTSHE CCTOT DEPTH SHRUBS RDHW DAY RH TEMPF ELEV DISTOCN	20	132.06	19.623	<0.001	
13	PD5	SCOUR DEPOSIT	3	135.76	23.329		
14	PD15	LITTER LN(BA70) RDTSHE	4	139.56	27.131		
15	PD16	DEPOSIT LN(BA70) RDIN	4	140.31	27.877		
16	PD12	LRGSUB DEPOSIT LITTER RDIN	5	141.35	28.920		
17	PD4	LITTER	2	147.25	34.819		
18	PD18	LN(DISTRIDG) SCOUR GRADE HEATNDX	5	149.57	37.136		
19	PD20	LN(DISTRIDG) GRADE LRGSUB LN(BA70)	5	162.12	49.691		
20	PD2	LRGSUB	2	166.64	54.205		
21	PD3	LN(DISTRIDG)	2	166.68	54.244		
22	PD17	LN(DISTRIDG) GRADE HEATNDX DEPTH AREA	6	170.80	58.364		
23	PD19	LN(DISTRIDG) GRADE HEATNDX DEPTH AREA	6	170.80	58.364		
24	PDN1	DAY RH TEMPF ELEV DISTOCN	6	171.78	59.346		
25	PD0		1	175.07	62.637		
26	PDN5	TEMPF	2	175.19	62.753		
27	PDN3	DAY	2	175.39	62.954		
28	PDN4	RH	2	175.68	63.248		
29	PDN2	DAY RH TEMPF	4	178.15	65.714		

Table E3. *A priori m*odel set describing western red-backed salamander captures as a function of environmental variables. "k" represents parameter number (including intercept, not shown), "*w*" is model weighting. Model PV0 = null model. Model parameters described in Table 3.2. Models with ΔQAICc $\leq$ 2 shown in **bold**.

Model rank	Model no.	Ecological model	k	QAICc	ΔQAICc	w	Cum w
1	**PV7**	**SATUR LRGSUB**	**3**	**202.669**	**0.000**	**0.337**	**0.337**
2	**PV19**	**GRADE AREA HEATNDX DISTC LN(DISTRIDG)**	**6**	**203.377**	**0.708**	**0.237**	**0.574**
3	**PV15**	**LRGSUB SATUR RDHW CCTOT**	**5**	**204.398**	**1.729**	**0.142**	**0.716**
4	PV18	LRGSUB DISTC GRADE LN(BA70)	5	204.913	2.244	0.110	0.826
5	PV14	SATUR LRGSUB LN(M3HA) LN(RD)	5	205.56	2.892	0.079	0.905
6	PV23	SATUR LN(DISTRIDG) DISTC LRGSUB CCTOT	6	207.986	5.317	0.024	0.929
7	PV24	SATUR LRGSUB LN(DISTRIDG) LN(M3HA) LN(BA70) AREA GRADE HEATNDX RDTSHE CCTOT LN(RD) DISTC RDHW DEPOSIT DAY RH TEMPF ELEV DISTOCN	20	209.065	6.397	0.014	0.943
8	PV9	MOISTR ORGSUB CCTOT RDTSHE	5	209.191	6.523	0.013	0.956
9	PVN3	DAY	2	209.595	6.926	0.011	0.966
10	PV21	GEOMSRF ORGSUB CCTOT LN(BA70)	6	209.922	7.253	0.009	0.975
11	PV16	MOISTR ORGSUB CCTOT LITTER	5	210.276	7.607	0.008	0.983
12	PVN2	DAY RH TEMPF	4	211.633	8.964	0.004	0.987
13	PV2	SATUR	2	212.034	9.365	0.003	0.990
14	PV8	ORGSUB CCTOT LN(BA70) LITTER	5	212.749	10.080	0.002	0.992
15	PV3	ORGSUB LITTER	3	212.781	10.112	0.002	0.994
16	PV11	ORGSUB SCOUR CCTOT	4	213.269	10.601	0.002	0.996
17	PV6	ORGSUB LRD	3	214.161	11.492	0.001	0.997
18	PV1	MOISTR	2	214.416	11.747	0.001	0.998
19	PVN1	DAY RH TEMPF ELEV DISTOCN	6	215.301	12.632	0.001	0.998
20	PVN5	TEMPF	2	215.448	12.779	0.001	0.999
21	PV10	SATUR SHRUBS CCTOT RD	5	217.225	14.556	<0.001	>0.999
22	PVN4	RH	2	217.262	14.593		
23	PV0		1	217.598	14.929		
24	PV17	GEOMSRF	3	218.449	15.781		
25	PV13	LITTER LN(BA70)	3	218.514	15.845		
26	PV12	STABLE LN(BA70)	3	219.085	16.416		
27	PV5	LN(RD) CCTOT	3	220.131	17.462		
28	PV4	LN(DISTRIDG) DISTC	3	220.913	18.245		
29	PV22	GEOMSRF MOISTR LN(M3HA) CCTOT	6	221.106	18.437		
30	PV20	LN(DISTRIDG) SCOUR DEPOSIT	4	222.911	20.242		

Table E4. *A priori* model set describing clouded salamander captures as a function of environmental variables. "k" represents parameter number (including intercept, not shown), "***w***" is model weighting. Model AF0 = null model. Model parameters described in Table 3.2. Models with ΔQAICc ≤ 2 shown in **bold**.

Model rank	Model no.	Ecological models	k	QAICc	ΔQAICc	w	Cum w
1	**AF16**	**GEOSRF**	**3**	**208.93**	**0.000**	**0.310**	**0.310**
2	**AF19**	**GEOSRF SATUR LN(BA70) WOODFREQ LRGSUB**	**7**	**209.769**	**0.840**	**0.204**	**0.513**
3	**AF17**	**GEOSRF AREA GRADE HEATNDX**	**6**	**210.74**	**1.811**	**0.125**	**0.639**
4	AF22	STABLE LN(BA70)	3	211.312	2.383	0.094	0.733
5	AF23	GEOSRF GRADE LN(M3HA) LN(BA70) AREA	7	212.181	3.251	0.061	0.794
6	AF4	STABLE	2	213.216	4.286	0.036	0.830
7	AF7	CWDM3HA LN(BA70)	3	213.351	4.422	0.034	0.864
8	AF10	LRGSUB LN(M3HA) LN(BA70) SNAGSHA	5	213.908	4.978	0.026	0.890
9	AF3	LRGSUB	2	214.199	5.269	0.022	0.912
10	AF8	ORGSUB LN(M3HA) LN(BA70) RDIN	5	215.545	6.616	0.011	0.923
11	AF15	LRGSUB WOODFREQ LN(BA70) FERNS LITTER	6	216.145	7.215	0.008	0.932
12	AF6	WOODFREQ LRGSUB	3	216.145	7.215	0.008	0.940
13	AF12	ORGSUB LN(M3HA) LN(BA70) SNAGSHA LITTER	6	216.385	7.455	0.007	0.948
14	AF0		1	216.761	7.831	0.006	0.954
15	AF14	LN(M3HA) ORGSUB LITTER RDTSHE	5	216.882	7.952	0.006	0.960
16	AF18	DISTRIDG DISTC GRADE HEATNDX AREA	6	216.937	8.007	0.006	0.965
17	AF9	LRGSUB LN(M3HA) LITTER	4	217.087	8.158	0.005	0.970
18	AF21	DISTRIDG DISTC STABLE LN(M3HA) GRADE	6	217.448	8.518	0.004	0.975
19	AF5	CWDM3HA	2	217.746	8.816	0.004	0.979
20	AF2	SATUR	2	217.966	9.036	0.003	0.982
21	AFN4	RH	2	218.051	9.121	0.003	0.985
22	AFN5	TEMPF	2	218.666	9.736	0.002	0.988
23	AF11	LN(M3HA) LN(BA70) CCTOT SHRUBS FERNS	6	218.694	9.764	0.002	0.990
24	AFN3	DAY	2	218.704	9.774	0.002	0.992
25	AF24	DISTRIDG DISTC CCTOT LRGSUB LN(M3HA)	6	218.71	9.780	0.002	0.995
26	AF1	WOODFREQ	2	218.802	9.872	0.002	0.997

Table E4. (continued)

Model rank	Model no.	Ecological models	k	QAICc	ΔQAICc	w	Cum w
27	AF13	SATUR LRGSUB WOODFREQ RDHW	5	218.946	10.017	0.002	0.999
28	AFN2	DAY RH TEMPF	4	220.559	11.629	0.001	>0.999
29	AFN1	DAY RH TEMPF ELEV DISTOCN	6	223.717	14.788	<0.001	
30	AF25	GEOSRF SATUR LRGSUB LN(BA70) CWDM3HA AREA DISTOCN GRADE HEATNDX RDTSHE DISTRIDG CCTOT DISTC SNAGSHA FERNS SHRUBS RH TEMPF DAY ELEV RDHW	23	234.893	25.963		

Table E5. *A priori* model set describing ensatina captures as a function of environmental variables. "k" represents parameter number (including intercept, not shown), "*w*" is model weighting. Model EE0 = null model. Model parameters described in Table 3.2. Models with ΔQAICc $\leq$ 2 shown in **bold**.

Model rank	Model no.	Ecological model	k	QAICc	ΔQAICc	*w*	Cum *w*
1	**EE4**	**RDIN CCTOT**	**3**	**180.503**	**0.000**	**0.194**	**0.194**
2	**EE10**	**RDTSHE CCTOT LITTER**	**4**	**180.864**	**0.361**	**0.162**	**0.356**
3	**EE21**	**RDIN CCTOT LITTER STABLE**	**5**	**181.297**	**0.794**	**0.130**	**0.486**
4	**EE11**	**LRGSUB RDHW SATUR**	**4**	**181.312**	**0.810**	**0.129**	**0.616**
5	**EE7**	**CCTOT LITTER ORGSUB**	**4**	**182.005**	**1.502**	**0.092**	**0.707**
6	**EE20**	**CCTOT ORGSUB DISTC GRADE**	**5**	**182.472**	**1.969**	**0.072**	**0.780**
7	EE2	ORGSUB	2	183.562	3.059	0.042	0.822
8	EE6	ORGSUB LITTER	3	183.805	3.303	0.037	0.859
9	EE9	ORGSUB LITTER DISTC CCTOT	5	183.964	3.462	0.034	0.893
10	EE8	ORGSUB LITTER CCTOT LN(M3HA)	5	184.084	3.581	0.032	0.926
11	EE17	DISTC STABLE GRADE	4	184.213	3.710	0.030	0.956
12	EE16	DISTC ORGSUB LN(M3HA) CCTOT GRADE	6	184.66	4.157	0.024	0.980
13	EE3	SATUR	2	187.554	7.051	0.006	0.986
14	EE12	GEOSRF GRADE HEATNDX	4	188.263	7.760	0.004	0.990
15	EE18	LITTER LN(BA70)	3	190.094	9.591	0.002	0.992
16	EE0		1	190.23	9.727	0.002	0.993
17	EE1	LITTER	2	191.049	10.546	0.001	0.994
18	EE22	DISTRIDG DISTC CCTOT LITTER	5	191.072	10.570	0.001	0.995
19	EE15	DISTRIDG DISTC GRADE HEATNDX AREA	6	191.386	10.883	0.001	0.996
20	EE19	DISTC DEPTH AREA CCTOT	5	191.936	11.433	0.001	0.996
21	EEN5	TEMPF	2	191.952	11.449	0.001	0.997
22	EEN3	DAY	2	191.989	11.486	0.001	0.998
23	EE14	GEOSRF	2	192.064	11.561	0.001	0.998
24	EEN4	RH	2	192.208	11.706	0.001	0.999
25	EE23	ORGSUB LN(M3HA) AREA GRADE HEATNDX RDTSHE RDHW DISTRIDG CCTOT DFC SATUR DAY RH TEMPF ELEV DISTOCN LN(BA70) DEPTH	19	193.004	12.501	<0.000	>0.999
26	EE5	DISTRIDG DISTC	3	193.792	13.289		
27	EEN1	DAY RH TEMPF ELEV DISTOCN	6	194.126	13.623		
28	EEN2	DAY RH TEMPF	4	194.387	13.885		
29	EE13	GEOSRF DEPTH HEATNDX AREA	5	196.788	16.285		