Vegetation–environment relationships in zero-order basins in coastal Oregon

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Abstract: Zero-order basins, where hillslope topography converges to form drainages, are common in steep, forested landscapes but we know little about their ecological structure. We used indirect gradient analysis to characterize gradients in plant species composition and cluster analysis to characterize groups of plant species associated with specific geomorphic areas. We sampled vegetation within 63 randomly selected zero-order basins in the southern Coast Range of Oregon and collected data on herb, shrub, and overstory tree cover, as well as environmental conditions. Zero-order basin overstories were similar in tree composition to both first-order riparian and upland plant assemblages, but were intermediate in tree density. Shrubs in zero-order basins included both species associated with dry upland conditions and species associated with riparian conditions. Results suggest that understory plant species composition in zero-order basins follows gradients in geomorphic and overstory conditions. Furthermore, it appears that zero-order basins have distinctive geomorphology and fluvial regimes. These distinctive features appear to support both plant species associated with riparian conditions and species associated with upland conditions. Zero-order basins represent the farthest upstream extension of riparian plant species into upland areas, increasing plant species diversity in steep, forested landscapes.

Résumé : Les bassins d'ordre zéro où convergent les versants pour former le drainage sont communs dans les paysages forestiers escarpés mais nous savons peu de choses à propos de leur structure écologique. Les auteurs ont utilisé l'analyse indirecte de gradient pour caractériser les gradients dans la composition en espèces végétales et l'analyse en composantes principales pour caractériser les groupes d'espèces végétales associés à des zones géomorphologiques spécifiques. Ils ont échantillonné la végétation dans 63 bassins d'ordre zéro sélectionnés au hasard dans la partie sud de la chaîne côtière de l'Oregon, en collectant des données sur les plantes herbacées, les arbustes et le couvert arbustif ainsi que sur les conditions environnementales. L'étage dominant dans les bassins d'ordre zéro avait une composition arbustive similaire à la fois aux assemblages de premier ordre de plantes ripariennes et de plantes des hautes terres, mais la densité des arbres était intermédiaire. Les arbustes dans les bassins d'ordre zéro comprenaient des espèces présentes dans les conditions plus sèches des hautes terres et des espèces présentes dans les zones ripariennes. Les résultats suggèrent que la composition en espèces végétales de sous-bois dans les bassins d'ordre zéro suit les gradients des conditions géomorphologiques et de l'étage dominant. En outre, il semble que ces bassins d'ordre zéro aient des régimes géomorphologiques et fluviaux distinctifs en supportant à la fois les espèces végétales associées aux conditions ripariennes et les espèces associées aux conditions des hautes terres. Les bassins d'ordre zéro constituent l'extension la plus profonde des plantes ripariennes vers les zones des hautes terres, augmentant ainsi la diversité des espèces végétales dans les paysages forestiers escarpés.

[Traduit par la Rédaction]

Introduction

Headwater drainages, the initiation points for streams, make up a significant proportion of forested landscapes in mountainous areas of western North America (Hack and Goodlett 1960; Benda 1990; USDA Forest Service and USDI Bureau of Land Management 1994) and other regions (Kikuchi and Miura 1993; Tsukamoto et al. 1982). In portions of the central Coast Range of Oregon, stream drainage density is 2.9 km of streams/km^2, and 76% of these are first- and second-order (Strahler 1964) stream systems (USDI Bureau of Land Management 2000). Headwater systems play an important role in the transport of materials down-gradient to higher order systems (Benda 1990; May and Gresswell 2002) and influence downstream water quality (Beschta et al. 1987). 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 steep forested areas; however, these landscape features have received relatively little ecological study.

Zero-order basins are the uppermost portions of headwater systems, terminating at the start of first-order conditions. Zero-order basins have been studied for their unique physical characteristics, including their disturbance regime (Reneau and Dietrich 1990; May and Gresswell 2002) and moisture relations (Montgomery and Dietrich 1989). Zero-order basins have been defined as hillslope features where flow lines

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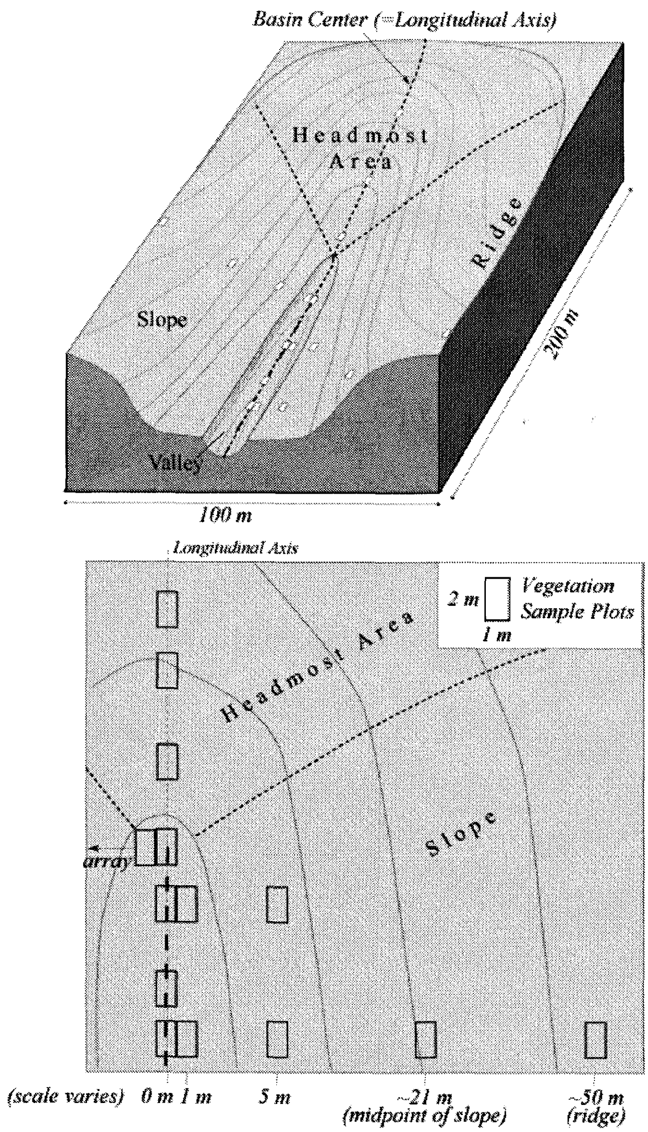
Fig. 1. Schematic of geomorphic surfaces and plant sampling plots within zero-order basin. Distances are not corrected for slope. Each "array" consisted of three 2 m^2 plots spaced at 0, 1, and 5 m from the fluvial center of the basin. Additionally, two 2 m^2 plots were placed at the midpoint between fluvial center and ridgeline (opposite sides), two plots were placed at opposite ridgelines, and three plots were placed in the headmost area (spaced evenly).



converge on a hollow (Tsukamoto et al. 1982; Dietrich et al. 1987), which include intermittent scour areas and extend from ridgelines down to the initiation of first-order streams (Fig. 1). Although the geomorphology of zero-order basins has been investigated, few studies have described vegetation in the uppermost portions of headwater basins (Waters et al. 2002). It is unclear whether the distribution of plant species in zero-order basins follows the physical patterns within these landforms, as described in first-order and larger headwater basins (Kovalchik and Chitwood 1990; Gregory et al. 1991; Pabst and Spies 1998, 1999). It is unknown which, if any, physical patterns best explain vegetation distribution in these basins. It is also unknown whether the plant assemblages (groups of species occupying a distinct geomorphic unit) in these basins are distinct from assemblages in surrounding hillslopes and larger order riparian systems. This type of information is needed by managers seeking to develop strategies to maintain plant diversity in forested watersheds.

This study provides base-line information on the vascular-plant composition of unmanaged zero-order basins. We sought specifically to (*i*) characterize geomorphology, overstory tree, and shrub composition; (*ii*) identify and describe the dominant gradients in plant species composition in terms of physical environment; and (*iii*) identify groups of plants associated with different geomorphic features and environmental conditions.

In this paper, the nomenclature follows Hitchcock and Cronquist (1973).

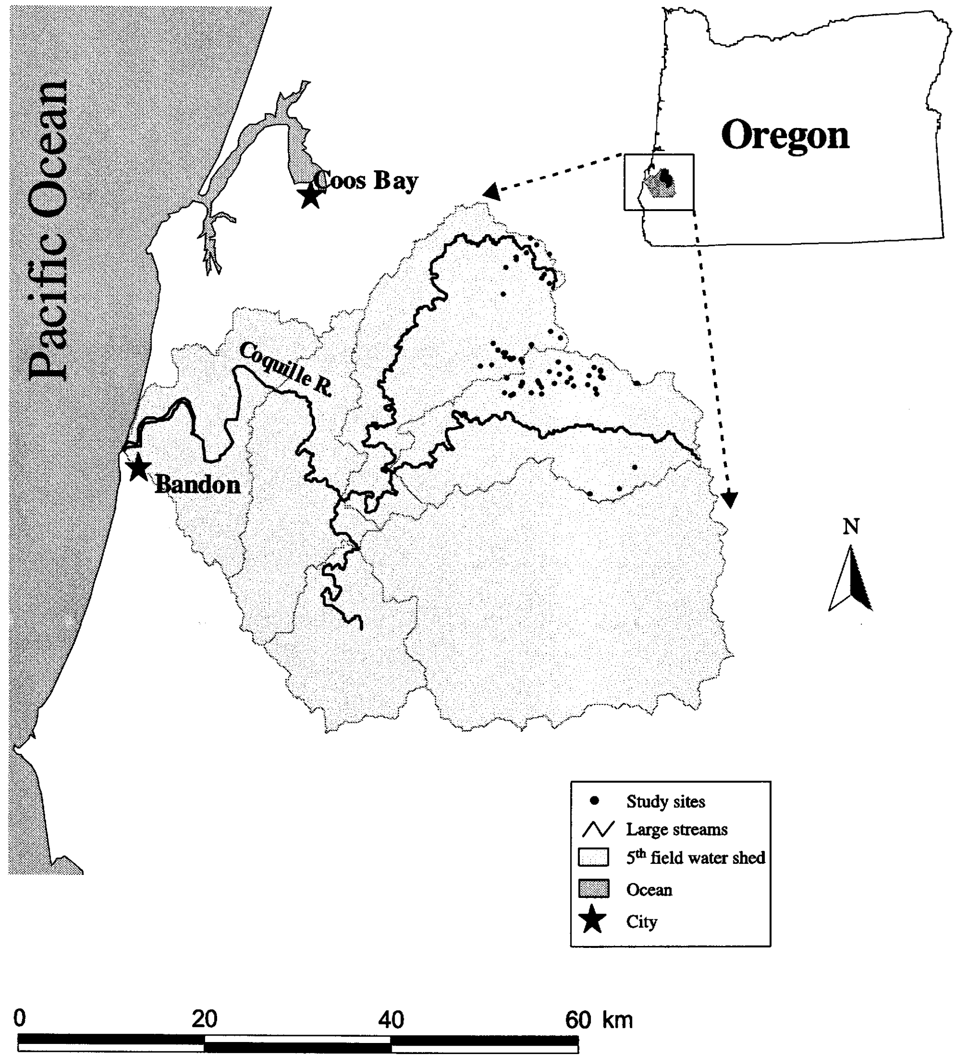
Methods

Study area

This study used the same study area and study sites as a companion study that was completed to provide baseline information on the amphibian composition of unmanaged zero-order basins (Sheridan and Olson 2003). The criteria for choosing the study area were the presence of large areas of unmanaged forest, the relatively high density of first-order systems, and the need 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 in the central Oregon Coast Range (Fig. 2). The area encompassed approximately 850 km^2 of the headwaters of the Coquille River Basin (Zone 10, 4767N to 4798N UTM, 418E to 445E UTM). This region is underlain by uplifted sea floor sediment and basalt, with geologic formations composed of sandstone and sandy siltstone (USDI Bureau of Land Management 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 Bureau of Land Management 2000). Most precipitation occurs as rainfall, ranging from 1397 to more than 3810 mm annually (Oregon State University 1982).

The study area falls within the western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) zone (Franklin and Dyrness 1973). Stands in the study area are dominated by Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and include western hemlock, western redcedar (*Thuja plicata* Donn.), and grand fir (*Abies grandis* (Dougl.) Forbes). Hardwoods make up <10% of stand densities and include bigleaf maple (*Acer macrophyllum* Pursh), chinquapin (*Castanopsis chrysophylla* Dougl.), and California bay (*Umbellularia californica* Hook & Arn.). Common shrub species include evergreen huckleberry (*Vaccinium ovatum* Pursh) and salal (*Gaultheria shallon* Pursh). Herbaceous species include sword fern (*Polystichum munitum* (Kaulf.) Presl) and oxalis (*Oxalis oregana* Nutt.). Second-order and larger riparian areas in the study area support hardwoods, including red alder (*Alnus rubra* Bong.),

Fig. 2. Location of 63 study sites within the study area.



and mesic conifers such as western redcedar. Common riparian shrubs in these systems include salmonberry (*Rubus spectabilis* Pursh) and stink currant (*Ribes bracteosum* Dougl.); common riparian herbs include maidenhair fern (*Adiantum pedatum* L.) and deer fern (*Blechnum spicant* L.).

Historically, fire and landslides were the most important disturbance processes affecting vegetation patterns in the study area (USDI Bureau of Land Management 2000). Unmanaged portions of the study area include stands approximately 250 and 450 years old that originated after stand-replacing fires in the periods from 1534 to 1590 and from 1735 to 1798, respectively (USDI Bureau of Land Management 2000). Zero-order basins are the principal initiation points for landslides in the steep, deeply dissected mountainous landscapes of the Pacific Northwest (Dietrich et al. 1987). Study site selection was not stratified by fire- or landslide-disturbance history, and the sample thus has a range of time periods since natural disturbance; partial natural failure occurred in several basins less than 2 years prior to survey. 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 Bureau of Land Management 2000), and, at smaller spatial scales, substrate characteristics and fluvial processes. Anthropogenic influences on disturbance regimes in study sites were minimized by selecting zero-order basins in stands that had regenerated after fires and aged more than 200 years, with minimal evidence of overstory cutting or road effects ("unmanaged", hereafter).

Study site and survey plot establishment

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 (Clarke and Burnett 2003)), and first-order systems. Sites were not considered if they were disturbed by management activities, too time-consuming to access (>0.8 km from a transportation corridor), cliff areas, or did not terminate at the start of a first-order channel (Dietrich et al. 1987). From this initial set of 222 zero-order basins, 63 were randomly selected for study, stratified into two aspect classes, and stratified into two map-estimated basin-slope classes. Aspect classes represented arbitrary divisions into a south- and west-facing class (120°–300°) and a north- and east-facing class (301°–119°), to ensure a range of basin aspects in the sample. Slope classes (<39°, ≥39°) represented rough break points in initial, map-estimated basin slopes; these breaks were roughly comparable to geomorphic changes observed in the field. Sample zero-order basins had a field-verified mean slope of 20° and averaged about 1 ha in size.

In the field, we delineated the extent of each zero-order basin as the area extending downslope from the ridgeline to the point where fluvial scour became clearly more continuous than discontinuous (estimated visually over a length of 15 m), often at the junction with another zero-order basin. Within delineated zero-order basins, we established a longitudinal axis along and parallel to the most fluvially active portion of the basin (Fig. 1). We considered this longitudinal axis to be the basin center. Measurements of distance from ridge to sampling plot were measured along this axis; lateral distances from center were measured perpendicular to this axis (Fig. 1, detail area).

Studies have framed the importance of physical drivers in headwater areas in two different but closely related (nested) ways. Geomorphic surfaces (Gregory et al. 1991; Pabst and Spies 1998) and lateral zones (Pabst and Spies 1999; Nierenberg and Hibbs 2000) have both been used to explain patterns of species composition in first-order and larger headwater riparian drainage basins; we hypothesized that similar processes would be important in zero-order basins. We delineated four geomorphic surfaces within zero-order basins: valleys, headmost areas, slopes, and ridges (Fig. 1), and we stratified plant and environmental sampling by them. Valleys were defined as convergent areas (collecting surface flow), downslope of the first evidence of scour and deposition, but above sustained scour. Headmost areas were defined as convergent surfaces above the first evidence of scour and deposition, extending upslope to a topographic break. We defined slope surfaces as planar surfaces (where surface flow lines would be parallel) extending laterally from valley margins upslope to ridges. Ridges were defined as the convex surfaces connecting slope surfaces in one zero-order basin to slope surfaces in adjoining basins. For several analyses, valleys and the lower portions of slope surfaces were further stratified into lateral distance zones, to characterize changes in plant composition and environmental variables at finer spatial scales; 1 m wide lateral zones were centered on points 0, 1, and 5 m from the basin center (slope distance).

We established 17 plots for sampling plant cover and environmental variables within the six geomorphic–lateral zones in each zero-order basin in the sample (Fig. 1). Seven plots were established randomly along the longitudinal axis, four in the valley zone and three in the headmost zone, each a minimum of 10 m apart (slope distance). Lateral plots were placed 1 and 5 m from basin center, perpendicular to three of the valley (0 m) plots (Fig. 1). Additional sampling points were established perpendicular to the uppermost and lowermost valley plots, exactly halfway between basin center and ridgelines in the slope zone (an average of 24 m (95% CI: 21.8, 26.6) from basin center), 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 (Fig. 1). For the sampling frame, flexible rubber tubing was staked to an approximate 1 m × 2 m rectangle and formed to fit within constraints of the geomorphic surface. The sampling area for an individual plot was, therefore, always 2 m^2 (not slope-corrected), although sampling shape was slightly variable.

Data collection

Data on plant cover were collected from July to September of three years (1999, 2000, 2001). Within plots, we measured herb and shrub cover, overstory tree cover and density, and plot-scale environmental variables. Percent cover was visually estimated for each herb (forb and graminoid), shrub, and seedling tree species in each plot. Canopy cover and density metrics for overstory trees and shrubs more than 2 m tall were estimated separately.

We measured 33 environmental variables (Table 1), which we hypothesized might be important in structuring plant assemblages in zero-order basins. At the plot scale, data were collected for four variables describing plot position and gradient, five variables for surface moisture and stability (lack of disturbance), four variables for substrate composition, and eight variables for overstory conditions. Binary variables for the presence or absence of saturation, scour, deposition, and stability in individual plots became proportions when averaged for geomorphic or lateral zones. No corrections were made for seasonal differences in fluvial variables, beyond randomization of basin selection. Overstory basal area was measured using variable-radius sampling in one randomly selected plot per geomorphic surface. Estimates of basal area collected on sloped ground were corrected to horizontal using a relaskop, by multiplying slope by the secant of slope angle, or by tilting a wedge prism to approximate slope angle (Sheridan 2002). Relative density was calculated similarly to Curtis (1982), using English units and visual estimates of tree diameter calibrated by measuring 1 of 50 trees. At the zero-order basin scale, data were collected 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 adjacent harvest or (very limited) within-basin tree salvage. Year of survey was included as a covariate to determine whether differences in seasonal (phenology) or water status affected plant-cover data.

Data analysis

We calculated means and confidence intervals for gradient, litter depth, and frequency of fluvial disturbance (evidence of scour or deposition) for each of the four geomorphic surfaces. Means and confidence intervals were also calculated for basal area for each overstory tree species, as well as basal area and canopy cover for all tallied trees. Differences in the relative density of overstory trees between geomorphic surfaces were quantified with a repeated measures mixed linear model that related relative density to geomorphic surface (PROC MIXED procedure in SAS/STAT; SAS Institute Inc. 1999). This repeated measures model addressed spatial autocorrelation observed between geomorphic surfaces within individual zero-order basins ($r < 0.52$). Only species rooted in the geomorphic surface being measured were used for calculation of relative density.

Table 1. Environmental variables collected at the plot or zero-order basin scale and covariates.

Environmental variable	Units	Description
Geomorphic position		
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)
Ridge distance	m	Ridgeline to plot slope distance, divided by distance from ridgeline to initiation of scour
Surface gradient	Deg.	Slope of geomorphic surface, calculated using a clinometer sited across length of surface
Fluvial		
Deposition	0, 1	Presence or absence of deposition (material mobilized into the plot by fluvial or hillslope disturbance)
Saturation	0, 1	Presence or absence of field-estimated "saturated" conditions in plot (surface moisture ≥ 5)
Scour	0, 1	Presence or absence of scour (removal of above ground vegetation and litter)
Stability	0, 1	Presence or absence of stable conditions (no scour or deposition) in plot
Surface moisture	1–7	Integer index of plot moisture, modeled on categories developed by Crisafulli (1999). Values range from 1 (dry) to 7 (flowing)
Substrate		
Large substrate	%	Visual estimate of percent of plot surface obscured by gravel, cobble, boulders, or bedrock (substrates > 5 mm)
Litter depth	cm	Depth of undecomposed organic matter (litter), averaged from 5 points/plot
Organic depth	cm	Depth of decomposed organic matter (organic matter other than litter), averaged from 5 points/plot
Organic substrate	%	Visual estimate of percent of plot surface obscured by litter, organic material, bark, or fallen wood
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 large overstory trees (>70.0 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 of hardwood	0–100	Relative density (similar to Curtis (1982)), calculated using only hardwood species in variable-radius overstory plots
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 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
Zero-order basin scale		
Basin area	ha	Area potentially contributing surface flow to the point of initiation of scour and deposition in a zero-order basin. Generated in ArcInfo®, using flow direction and accumulation algorithms and a 10-m digital elevation model. Point of initiation of scour and deposition identified in the field used as "pour point"
Basin depth	m	Difference in elevation between the midpoint of the geomorphic surface and the surrounding ridgeline
Basin gradient	Deg.	Slope of zero-order basin, calculated as the difference in elevation along the basin length
Geomorphic surface	Cat.	Three categories: valley, headmost area, and slope
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

Table 1 (*concluded*).

Environmental variable	Units	Description
Covariates		
Disturbance due to harvest	0–4	Four categories: 0 (no discernible human influence) through 3 (removal affecting basal area measurement)
Disturbance due to roads	0–4	Four categories: 0 (no disturbance) through 3 (roads potentially affecting drainage and stability)
Elevation	m	Height above sea level of the highest point (ridgeline) in a zero-order basin (measured using an altimeter)
Geology class	Cat.	Three classes: Flournoy, Tyee, and Flournoy–Tyee boundary
Ocean distance	km	Distance from the basin to the ocean, derived from ArcInfo® GIS coverages of the study area
Soil class	Cat.	Three classes, based on soil map units, defined in the Soil Survey of Coos County, Ore. (USDA Soil Conservation Service 1989): A (38F, 58F, 44E), B (46D, 46E, 46F), and C (44D, 44E)
Stand age	Years	Time since last stand-replacing event for forested areas in the zero-order basin, derived from ArcInfo® GIS coverages of the study area
Year of survey	Cat.	Categorical variable for year of survey (1999, 2000, and 2001)

Tall shrubs represent an important biotic control over both herb composition and tree regeneration in Coast Range riparian areas (Hibbs and Giordano 1996; Pabst and Spies 1998). We hypothesized that shrubs might also play an important role in structuring plant assemblages in zero-order basins. We, therefore, analyzed shrub species independently, in addition to including them in forest floor plant analyses. For the independent analysis of shrub characteristics, we estimated shrub cover means and confidence intervals for each shrub species in each of four geomorphic surface zones. We defined shrubs as woody species >0.5 m tall and <15 m tall.

We performed two broad types of vegetation analysis for herbs and shrubs in zero-order basins. Diversity metrics and gradient analyses were used to describe the composition of plant assemblages associated with different geomorphic–lateral zones; the relationships between assemblage composition and environmental variables were also modeled. To simplify plant species complexity in these basins, we classified plots into vegetation types and characterized the differences in environmental conditions in plots assigned to different vegetation types. These analyses are described below.

Diversity and gradient analyses

We estimated plant species richness and diversity using two indices (N0, N1: Hill 1973). N0 was calculated as species richness, N1 was calculated as exp(–Shannon's Index). For this analysis, species cover was averaged for each of six geomorphic–lateral zones: 0, 1, and 5 m from basin center (in valley and lower slope surfaces), as well as headmost, slope, and ridge zones. Because subsample size was different for each zone type, and subsample size may have affected diversity estimates, the number of plots in each zone was standardized by randomly deleting plots a single time to provide exactly two plots per geomorphic–lateral zone per zero-order basin.

We used indirect gradient analysis to characterize gradients in plant species composition and to determine the environmental variables important in structuring plant assemblages in zero-order basins. For this and all subsequent analyses, species cover and environmental variables were averaged for each geomorphic–lateral zone in a basin; each geomorphic–lateral zone became one experimental unit ("unit", hereafter). Nonmetric multidimensional scaling (NMS) (Mather 1976) with PC-ORD software (McCune and Mefford 1999) was used as the ordination method. Species encountered in <10% of the units were not considered in the analysis. A Sorensen 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. We selected the smallest number of dimensions that maintained interpretable levels of "stress", a measure of dissimilarity between the original space and the reduced ordination space. Stress levels were compared with randomized data with 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. All subsequent analyses used this rotation, and correlations refer to this rotation. Interpretation of ordination axes was facilitated by overlaying geomorphic–lateral zone membership on ordination points and by calculating Kendall's rank correlations between axis scores and both plant species covers and environmental parameter values.

Plant species classifications: vegetation types

In addition to describing the continuous changes in plant species composition between different geomorphic–lateral zones in zero-order basins, we identified vegetation types as groups of units with similar plant composition. Vegetation types were developed to increase knowledge about plant species patterns in these basins and to provide managers with a heuristic tool to recognize ecologically relevant geomorphic areas in the field. Hierarchical cluster analysis was used to group units with similar species composition, using relative Euclidian distance and Ward's linkage method in PC-ORD (McCune and Mefford 1999). The total number of vegetation types was restricted to seven, based on ease of interpretation,

Table 2. Characteristics of the 63 zero-order basins measured within the study area.

Parameter	Mean (range)
Distance from ocean (km)	43.3 (35.9, 55.3)
Ridge elevation (m)	599.4 (227.1, 807.9)
Zero-order basin size (ha)[a]	1.1 (0.1, 7.2)
Zero-order basin gradient (deg.)	20.2 (3.5, 41.2)
Total length of zero-order basin (m)	274.4 (85.5, 783.0)
Distance from ridge to initiation of scour/deposition (m)	165.5 (64, 630)
Distance from ridge to start of channelization (m)	193.5 (48, 637)
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)

[a]Measured using flow accumulation algorithms; field-verified initiation of scour used as end point.

amount of information retained by the clustering process, and comparability to the number of distinct groups observed in the field. Indicator species analysis (Dufrene and Legendre 1999) was used to quantify the strength of association between individual species and vegetation types. The statistical significance of the indicator value of each species for its most closely associated vegetation type was tested using a Monte Carlo method with 2000 iterations (PC-ORD; McCune and Mefford 1999). Vegetation types were named using the genus name of the species with the highest indicator value for that type. We described vegetation types by calculating the percentage of units assigned to each type and by calculating the percent cover by different types in the sample as a whole. Means for key environmental variables were calculated for units assigned to each of the seven vegetation types, to provide a description of environmental conditions where individual vegetation types were encountered.

Results

Geomorphic, overstory, and shrub characteristics of zero-order basins

There were an average of 11.5 initiation points of first-order streams per square kilometre in hillslope areas in the study area, and first-order systems originated from an average of 1.6 zero-order basins, which suggests a density of approximately 18 zero-order basins per square kilometre in the study area. Areas contributing to the initiation point of scour and deposition in zero-order basins averaged 1.1 ha in size (Table 2), and entire zero-order basins made up <1% of the landscape in the study area. Zero-order basins in the study area had an average density of 4.1 km/km^2 (95% CI: –0.8, 9.0). First-order basins (inclusive of zero-order basins) averaged a density of 5.6 km/km^2 (95% CI: 1.2, 10.0) in the study area. Zero-order basins in the study area were steeper and narrower than larger riparian drainages observed downstream. Headmost and slope surfaces dominated basins. Valley floors were <5 m wide and accounted for <2% of zero-order basin surface area. Slope surfaces averaged more than 50 m in length (Table 2). Fluvial disturbance occurred in convergent surfaces, predominantly in valleys (71.4% supported fluvial disturbance) and also in headmost areas (11.1% with fluvial disturbance).

Douglas-fir and western hemlock had the highest overall basal area, with ridge and slope geomorphic surfaces having the highest basal areas within basins (Table 3). Basal area cover by hardwood species was low (Table 3); bigleaf maple had the highest hardwood basal area. Red alder, a common riparian species in larger order riparian corridors, had low basal area in zero-order basins. Overstory relative densities were significantly different between geomorphic surfaces ($F_{[3,62]} = 116.4$; $p < 0.0001$). Considering only trees rooted in the geomorphic surface being measured, the relative density of valley areas was 4.5 (95% CI: 2.5, 6.5), more than 35 units (95% CI: 30.3, 40.6) lower than headmost areas. Headmost areas had relative densities of 40 (95% CI: 35.3, 44.6), 11 units (95% CI: 5.1, 17.1) lower than slope areas. Slope and ridge areas had similar relative densities, 51 (95% CI: 45.7, 56.4) and 46 (95% CI: 41.5, 51.5), respectively. Shrub species had total cover >13% (95% CI: 12.5, 15.1) in zero-order basins and were dominated by dry-site, evergreen species (Table 4). Only Oregon grape (*Berberis nervosa* Pursh) had a basin mean cover >3% (95% CI: 3.3, 4.5). *Rubus spectabilis*, often dense in Oregon Coast Range riparian systems, averaged <2% (95% CI: 1.0, 1.8) cover in zero-order basins, with its highest cover in valley floors. *Ribes bracteosum* had the highest cover of any shrub in valley surfaces (Table 4) and was frequently associated with seepy depositional surfaces. Total shrub cover followed a gradient from lowest cover in valley surfaces to highest shrub cover along ridges.

Forest floor plants: diversity and compositional gradients

We analyzed cover data on 138 forest floor species, including 111 herb (forb and graminoids), 21 shrub, and six seedling tree species, collected in 1113 plots. Species richness (N0) ranged from 71 to 84, with the 5-m lateral zone having highest richness. Species diversity, as measured by N1, ranged from 14 to 24. N1 was highest in the 0- and 1-m lateral zones, with lower diversities in upslope zones.

Indirect gradient analysis using nonmetric multidimensional scaling identified several distinct patterns in plant species composition (Fig. 3). 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. Axis 1 position was positively correlated with stability, cover of organic substrate, depth of litter layers, and density and cover by overstory conifers (Table 5). Measures indicating fluvial and hillslope disturbance, such as large substrate cover, frequency of scour and deposition, and surface moisture, were negatively correlated with scores on axis 1. Variables operating at larger spatial scales (e.g., gradient, elevation, and distance to ocean) were not strongly correlated with axis 1 scores, but did show weak correlations with axis 3 scores. Correlations between environmental variables and axis 2 and axis 3 scores were generally weak and uninformative. Gradients in plant species composition along axis 1 were also clearly related to the geomorphic–lateral zone (Fig. 3). Along axis 1,

Table 3. Basal area (BA: m^2/ha) of overstory trees in geomorphic surfaces within zero-order basins, collected in variable-radius plots (95% CI, N = 63).

	Geomorphic surface				
Tree species	Valley	Headmost	Slope	Ridge	Basin means
Douglas-fir	26.0 (22.6, 29.5)	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	13.3 (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 redcedar	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)
Bigleaf 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)
Chinquapin	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)
BA for all trees[a] (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 DBH (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)
Canopy cover (%)	73.2 (69.5, 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)

Note: Basal area (m^2/ha) for all trees, basal area for trees >70 cm DBH (m^2/ha), and canopy cover (%), with 95% CI, presented above. Results are ordered by decreasing basin mean basal area.

[a]Species with BA <1.0 m^2/ha are not shown. These species include vine-maple (*Acer circinatum* Pursh.), madrone (*Arbutus menziesii* Pursh), incense cedar (*Calocedrus decurrens* (Torr.) Florin.), tanoak (*Lithocarpus densiflorus* (Hook. & Arn.) Rehder), Scouler's willow (*Salix scouleriana* Barratt.), and yew (*Taxus brevifolia* Nutt.).

Table 4. Percent cover of shrub species (95% CI) in four geomorphic surface zones in zero-order basins. (N = 63).

Shrub species	Valley	Headmost	Slope	Ridge	Basin mean
Berberis nervosa	0.3 (0, 0.6)	4.4 (3.1, 5.7)	4.1 (3.1, 5.0)	11.4 (8.6, 14.1)	3.9 (3.3, 4.5)
Rubus spectabilis	2.8 (1.6, 4.1)	0.4 (0.0, 0.7)	1.3 (0.7, 1.9)	0.2 (–0.1, 0.5)	1.4 (1.0, 1.8)
Gaultheria shallon	0.5 (0.3, 0.8)	1.6 (0.8, 2.4)	1.2 (0.7, 1.8)	3.0 (1.2, 4.8)	1.3 (1.0, 1.7)
Vaccinium parvifolium	1.3 (0.8, 1.8)	1.4 (0.7, 2.1)	1.5 (0.8, 2.1)	0.4 (0.0, 0.7)	1.3 (1.0, 1.6)
Ribes bracteosum	3.0 (1.8, 4.2)	0.3 (–0.1, 0.6)	0.9 (0.4, 1.4)	0.1 (0.0, 0.2)	1.3 (0.9, 1.7)
Acer circinatum	0.8 (0.4, 1.3)	1.6 (0.7, 2.5)	1.1 (0.7, 1.5)	1.0 (0.1, 1.9)	1.1 (0.8, 1.4)
Vaccinium ovatum	0.6 (0.2, 1.0)	1.2 (0.4, 2.1)	0.4 (0.1, 0.7)	4.2 (1.6, 6.7)	1.1 (0.7, 1.5)
Shrub species total[a]	10.7 (8.4, 13.0)	14.6 (11.8, 17.4)	13.0 (11.0, 15.0)	22.4 (17.9, 26.9)	13.8 (12.5, 15.1)

Note: Species arranged in order of decreasing total cover. Basin means were calculated using four subsamples, leading to slightly different values than in Table A1 (Appendix A), calculated using six subsamples.

[a]Species with total cover <1% are not shown. These species include *Corylus cornuta, Holodiscus discolor, Oemleria cerasiformis, Oplopanax horridum, Rhamnus purshiana, Rhododendron macrophyllum, Rosa gymnocarpa, Rubus laciniatus, Rubus leucodermis, Rubus nivalis, Rubus parviflorus, Rubus ursinus, Sambucus racemosa, Toxicodendron diversilobum,* and *Symphoricarpos albus.*

slope and ridge zones were associated with drier and more stable portions of ordination space, 0- and 1-m zones were associated with wetter and more disturbed ordination spaces, and 5-m and headmost zones were intermediate in ordination space. Axis 2 represented a complex gradient in species composition, weakly related to basin depth (r = 0.166) and basin area and heat load index (r = –0.232 and –0.228). Axis 3 represented a gradient in species composition associated with stand-level characteristics, including canopy cover of conifers (r = 0.427), relative density of hardwoods (r = –0.471), and basin gradient (r = –0.416). Groups of units did not show strong patterning on either axis 2 or axis 3, and these axes did little to separate units associated with different geomorphic–lateral zones.

Individual plant species were strongly associated with different portions of the ordination space. On axis 1, cover of *B. nervosa* was positively correlated with axis position (r = 0.55); plots with high *B. nervosa* cover, thus, also had high stability and low surface moisture. Cover by species associated with riparian and seep habitats such as oval-leaved mitrewort (*Mitella ovalis* Greene) was negatively correlated with axis 1 position (r = –0.61) and was thus associated with geomorphic–lateral zones with low stability and high surface moisture. Axis 2 differentiated between mesic associates such as *O. oregana* (r = 0.39) and species associated with dry habitats such as *B. nervosa* (r = –0.41). Axis 3 differentiated dry species associated with high conifer cover such as Pacific rhododendron (*Rhododendron macrophyllum* G. Donn) (r = 0.24) and *B. nervosa* (r = 0.25) from mesic species associated with open, steeper areas such as *Polystichum munitum* (r = –0.41) and western springbeauty (*Claytonia siberica* (L.) Howell) (r = –0.34).

Vegetation types in zero-order basins

Classification of units into groups (vegetation types) simplified plant compositional variability in zero-order basins and provided a more concrete description of plant communities in zero-order basins than ordination. Seven vegetation types were identified in zero-order basins, each consisting of groups of units with similar plant species composition (Appendix A) and similar environmental conditions (Fig. 4). This classification resulted in retention of >40% of the infor-

Table 5. Kendall's rank correlation coefficients (r) and summed coefficients of determination (R^2) between environmental variables and axis scores from an ordination of units in plant species space.

Environmental variable	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 overstory	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

Note: Variables ordered by summed R^2 values for the three ordination axes. Only variables with correlations significant at $p \leq 0.001$ for at least one axis are shown. ns, nonsignificance.

mation in the original data. Some of the species associated with each vegetation type were strong indicators for that type; other species were generalists, only slightly more common in their assigned type (Appendix A). The vegetation type descriptions below integrate classification and indicator species analysis results, averages of environmental variables for units in each type, and field observations.

The *Mitella* vegetation type, named for *Mitella ovalis* (the species with the highest indicator value for this group), consisted mainly of units from valley geomorphic surfaces and the slopes immediately adjacent to them, including seep and splash zone areas (Fig. 4). The *Mitella* vegetation type supported relatively high species richness; indicator species analysis identified 25 species associated with this type (Appendix A), but only 13 of these species had maximum indicator values significantly higher than random expectation ($p < 0.05$; "indicator species", hereafter).

The *Blechnum* vegetation type also included species often associated with splash zones and lower slope surfaces. Areas with this vegetation type had the highest average deposition and "moist" surface moisture, consisting principally of units in the 1-m lateral zone (Fig. 4). The *Blechnum* type was relatively simple, with 10 associated species and only two indicator species.

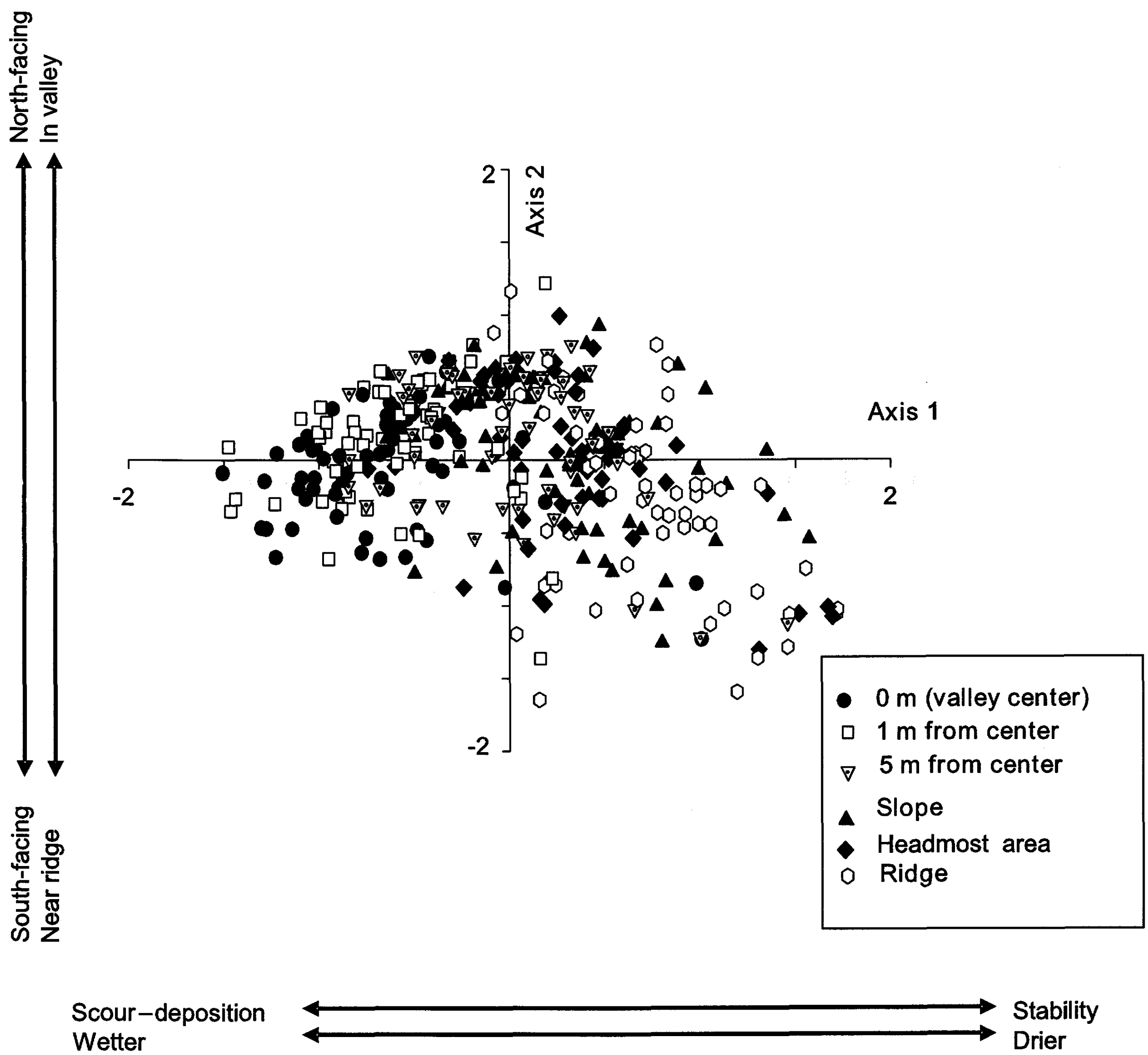
Units classed as the *Oxalis* vegetation type had conditions comparable to those of riparian terrace communities, including moderately stable moist surfaces and relatively high hardwood density (Fig. 4). *Oxalis* was the most common vegetation type in the sample, accounting for more than 33% of all units. *Oxalis oregana* was the only indicator species, suggesting that the other 18 species associated with this type were widely distributed.

The *Gaultheria* vegetation type had a slightly bimodal distribution, frequent both in valley center units and in units from drier headmost and ridge areas. This may have been due to associations between salal (the principal indicator species in the type) and fallen wood, which frequently spanned valley centers. Units with this vegetation type had the highest average density of hardwoods and occurred predominantly on relatively stable surfaces (Fig. 4). The *Gaultheria* vegetation type had high species richness including 30 associated species, but only four were indicators for the *Gaultheria* type.

The *Polystichum* vegetation type was primarily associated with midslope units (Appendix A) and was the second most common vegetation type in zero-order basins. Units with this vegetation type occurred in zones with low deposition of alluvial or colluvial material, low surface moisture, and relatively high stability and overstory relative density (Fig. 4). Only four species were associated with this vegetation type, and *P. munitum* was the only indicator species.

The *Vaccinium* and *Berberis* vegetation types were distinct from other vegetation types but were only weakly distinct from each other. The *Berberis* vegetation type included

Fig. 3. Nonmetric multidimensional scaling ordination of units in plant species space, for three ordination axes. Only axis 1 and axis 2 are depicted (n = 375; data from three zones were lost and are not presented). Units (points) represent plots averaged for each geomorphic–lateral zone in each basin. Geomorphic–lateral zone membership overlain on units. Directional arrows indicate important environmental gradients identified through correlation analysis and mixed linear model results. Coefficients of determination between the three axes and the original 45-dimensional space were 0.439, 0.188, and 0.180 for axes 1, 2, and 3, respectively.



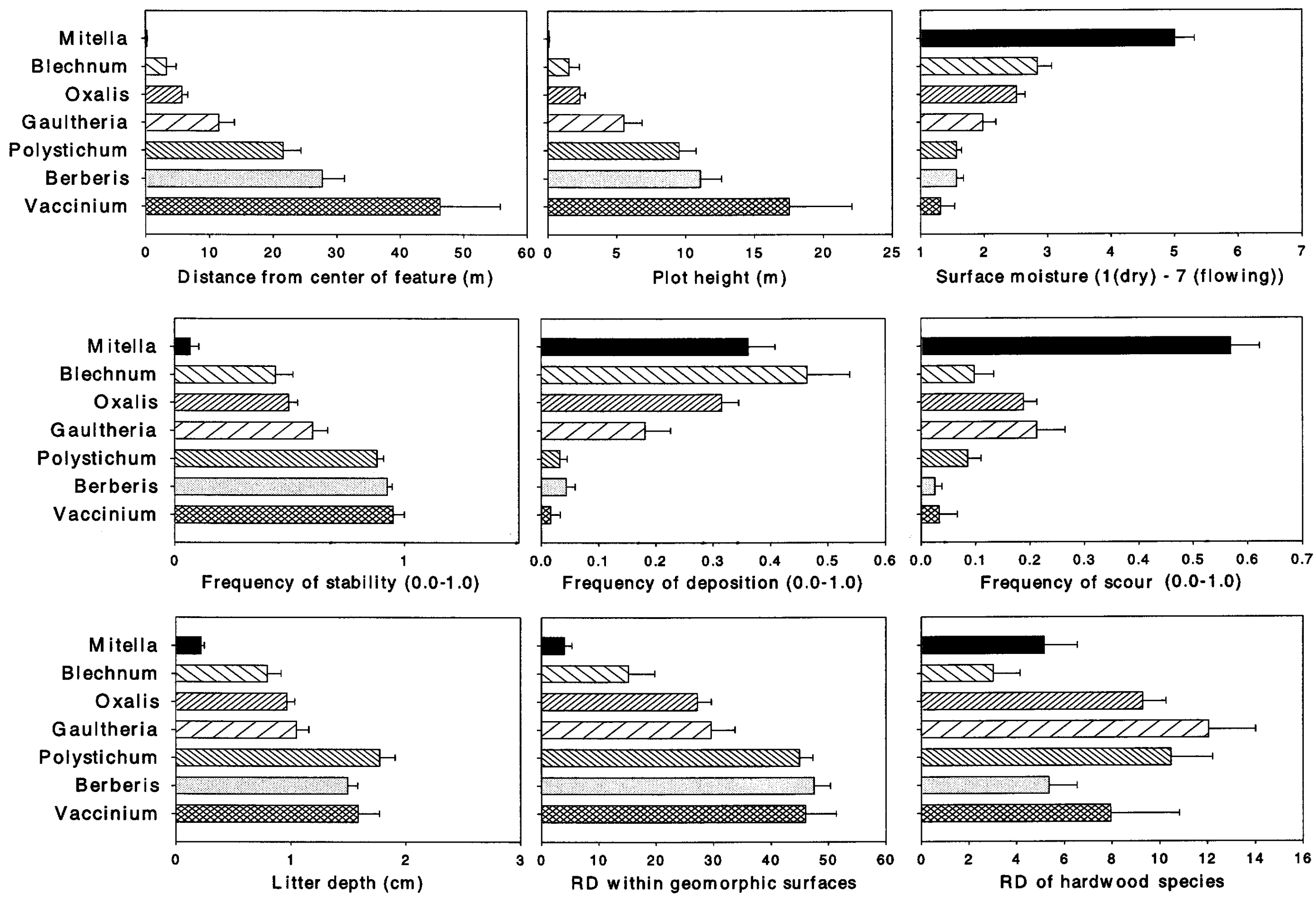
mainly upper slope and ridge units, where conditions were relatively dry and litter depth and stability were high. The *Vaccinium* vegetation type occurred in even drier areas, representing units on the forested ridges along basin margins, characterized by very stable surfaces and deep litter (Fig. 4). Thirteen species had their highest cover and frequency in the *Vaccinium* vegetation type, and this type supported the second-highest number of indicator species (Appendix A).

Discussion

Zero-order basins play a key role in providing and transporting coarse substrate and wood (Benda 1990; May and Gresswell 2002), as well as plant propagules (Guariguata 1990), to larger order systems and in supporting distinct amphibian faunas (Sheridan 2002; Sheridan and Olson 2003). Results from this study suggest that zero-order basins are also characterized by distinctive patterns of geomorphology and fluvial processes. These distinctive physical templates produce vegetation patterns intermediate between riparian and upland assemblages. Zero-order basins thus represent the final upstream extension of riparian plant species into upland areas and the increasing diversity of plant species in steep, forested landscapes.

Zero-order basin overstories were similar in tree composition to both first-order riparian and upland assemblages, but were intermediate in tree density. The top three coniferous species and the top hardwood species in terms of basal area in zero-order basins were the same as those identified in mature upland areas in the Oregon Coast Range (Spies 1991) and first-order riparian systems in the southern Coast Range (Pabst and Spies 1999). Zero-order basins supported higher densities of conifer species and lower densities of hardwoods, particularly red alder, than larger order riparian systems

Fig. 4. Averages of nine environmental variables ($\bar{x}$ + 1 SE) for seven vegetation types. Vegetation types are ordered by increasing distance from basin center. RD is relative density (defined in Table 1). Environmental variables here presented best display the differences between vegetation types.



(Nierenberg and Hibbs 2000; Pabst and Spies 1999). Tree relative densities on valley and headmost surfaces (convergent surfaces) were significantly lower than on surrounding slopes and ridges. A similar change in overstory tree composition and structure, from planar slopes (dominated by coniferous forest) to convergent valleys (supporting open deciduous broadleaf forest), was found by Kikuchi and Miura (1993) for zero-order basins in Japan. In our study, zero-order basins had shrub cover comparable to that of upland areas (Spies and Franklin 1991) and lower than that of headwater riparian areas (Hibbs and Giordano 1996; Pabst and Spies 1998). Zero-order basins supported both shrub species associated with dry upland conditions, such as *B. nervosa*, and those associated with riparian conditions, such as *Rubus spectabilis* and *Ribes bracteosum*.

Our study is consistent with other work documenting the importance of geomorphic gradients and the relatively high species diversity of "inner gorges", hillslope-constrained portions of headwater systems close to basin center (Pabst and Spies 1999; Olson et al. 2000). In our study, strong correlations were found between axis scores and variables related to position within the basin (Table 5). Along these geomorphic gradients, valley and lower slope surfaces within 5 m of basin center made the greatest contribution to plant richness (N0) and plant diversity (N1).

The vegetation types we identified characterized specific groups of species associated with distinct portions of geomorphic gradients in zero-order basins and the strength of these associations. Vegetation types associated with proximity to fluvial centers (e.g., *Mitella, Blechnum* types) included hydrophytes, splash-zone species, and species capable of surviving higher disturbance levels or capable of recolonizing quickly; 13 of the 28 identified indicator species were associated with the wettest vegetation type (*Mitella*). Vegetation types consisting of drier, more upslope units had weaker associations and consisted of more generalist species (e.g., *P. munitum, G. shallon*).

Vegetation types facilitated comparison of plant groups in zero-order basins to groups described in larger riparian systems (Pabst and Spies 1998), as well as the microenvironments associated with these plant groups. Variation in species composition within zero-order basins may be explained by the presence or absence of particular riparian or upland microhabitat types. Microsites created by fluvial scour and deposition increase riparian diversity (Gregory et al. 1991). Zero-order basins supported fewer distinct types of scour and deposition microsites, compared with larger riparian systems. Zero-order basins lacked significant gravel bars, floodplains, or naturally open, disturbed microhabitats, and also lacked the species groups associated with these microhabitats, including the

Glyceria, Petasites, Urtica, and *Rubus ursinus* groups identified by Pabst and Spies (1998). Individual riparian plant species associated with floodplain and gravel bar habitats (e.g., water parsley (*Oenanthes sarmentosa* J.S. Presl) and coltsfoot (*Petasites frigidus* (L.) Fries)) were absent from zero-order basins, although they were present in the study area. Species associated with seep microhabitats (golden saxifrage (*Chrysosplenium glechomaefolium* Nutt.) and yellow skunk cabbage (*Lysichitum americanum* Hulten & St. John)) and splash zone microhabitats (pig-a-back-plant (*Tolmiea menziesii* (Pursh) Torrey & A. Gray) and stream violet (*Viola glabella* Nutt.)) formed two natural groups (*Chrysosplenium, Tolmiea*) in the larger riparian systems studied by Pabst and Spies (1998), but were subsumed in one broad, wet vegetation type (*Mitella*) in zero-order basins. Zero-order basins supported a broader range of dry vegetation types than larger riparian systems, including *Berberis* and *Vaccinium* vegetation types. These dry vegetation types would be expected to occur in upland areas of the Oregon Coast Range.

Because of their frequency, geomorphology, and landscape position, zero-order basins may play a key role in maintaining beta diversity in upland forested hillslopes. Zero-order basins averaged more than 4 km/km^2 in the study area and contributed significantly to the size of first-order systems. Hillslopes near ridgelines are topographically the driest portions of landscapes, yet zero-order basins in this landscape position support plant species shown by Pabst and Spies (1998) to be associated with Oregon Coast Range headwater riparian communities (e.g., *Mitella ovalis, Chrysosplenium glechomaefolium*, and devilsclub (*Oplopanax horridum* Miq.)). The juxtaposition of these riparian species with species associated with extremely dry conditions greatly increases plant species diversity in hillslopes as a whole.

Conclusions and management implications

Individual plant species respond to variation in light and moisture levels at small spatial scales (Grime 1979). The distinct gradients in light, moisture, and substrate composition in riparian (Pabst and Spies 1998) and landslide (Pabst and Spies 2001) areas can affect composition of plant assemblages associated with these habitat features. Results from this study suggest that geomorphic processes in zero-order basins also produce a variety of light levels and fluvially influenced microhabitats at small scales, which may lead to distinctive vegetation communities intermediate between those of wetter larger riparian systems and drier upland hillslopes. Although specific species documented in this study might be absent from vegetation types in zero-order basins outside this study area, the range of adaptations and certain key species (e.g., oval-leaved mitrewort, *Blechnum spicants* (L.) Smith) in vegetation types may be comparable to zero-order basins in much of the Oregon Coast Range. These intermediate community types could be used in rapid assessment and mapping (Spies and Barnes 1985). For example, the limits of zero-order basin fluvial vegetation types could be used by managers as one measure of the extent of riparian influence on biotic components of headwater basins.

Managers have lacked basic information about the ecology of zero-order basin ecosystems. This study suggests a role for these basins in providing important refugia or microsites at the landscape scale and provides a base line of plant assemblages and plant–environment relationships against which to compare management effects in these basins. The effect of management activities on plants and other taxa in zero-order basins has not been investigated. Potential influences on these environments from forest management include landslides that remove soil down to bedrock, debris flows, soil compaction, and invasion by non-native species that could enter sites from roadsides and nearby clearcuts. Until studies of the effects of these influences are conducted, it will not be possible to predict the consequences of forest management in these areas with any degree of certainty.

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Appendix A

Appendix appears on the following page.

Table A1. Herb, shrub, and tree seedling area covers.

Veg. type and species	0 m	1 m	5 m	Slope	Headmost	Ridge	Basin mean (%)
Mitella	***6.1***	***1.59***	***0***	***0***	***0***	***0***	***7.69***
*Mitella ovalis***	●●●●	●●●●	●●	●	●	0	1.8 (1.4, 2.2)
*Mimulus dentatus***	●●●	●●●	●	●	0	0	0.6 (0.4, 0.7)
*Tolmiea menziesii***	●●●●	●●●●	●●	●	●	●	1.0 (0.7, 1.4)
*Rubus spectabilis***	●●●●	●●●●	●●	●●●	●	●	1.3 (0.9, 1.8)
*Chrysosplenium glechomaefolium***	●●●	●●	●	0	●	0	0.4 (0.1, 0.8)
*Ribes bracteosum***	●●●●	●●●●	●●●	0	●	●	0.9 (0.6, 1.3)
*Athyrium filix-femina***	●●●	●●●●	●●●	●●	●●	●	1.5 (1.1, 1.9)
*Viola glabella**	●●	●	●	●	●	●	0.3 (0.2, 0.5)
*Mitella caulescens**	●	●	0	0	0	0	0.1 (0.0, 0.1)
Claytonia sibirica	●●	●●●	●●	●●	●●●	●●	0.9 (0.6, 1.1)
*Lysichiton americanum***	●	●	0	0	0	0	0.1 (0.0, 0.1)
*Cardamine oligosperma***	●	●	●	0	●	0	0.1 (0.0, 0.2)
*Dryopteris arguta**	●	●	●	0	0	0	0.1 (0.0, 0.3)
Galium triflorum	●●	●●	●●	●●●	●●	●	0.8 (0.6, 1.0)
Streptopus amplexifolius	●●●	●●●	●	●	0	●	0.5 (0.3, 0.7)
*Saxifraga mertensiana**	●	●	0	0	0	0	0.0 (0.0, 0.0)
Boykinia elata	●●	●●	●	0	●	0	0.3 (0.1, 0.5)
Stellaria crispa	●	●	●	●	●	●	0.1 (0.0, 0.2)
Polystichum kruckebergii	●	●	●	●	●	●	0.1 (0.0, 0.1)
Thuja plicata	●	0	0	0	●	0	0.1 (0.0, 0.1)
Oplopanax horridum	●	0	●	0	0	0	0.0 (0.0, 0.0)
Galium oreganum	●	●	●	●	●	●	0.1 (0.0, 0.1)
Ranunculus uncinatus	●	●	●	●	●	●	0.1 (0.03, 0.17)
Mimulus guttatus	●	●	●	0	0	0	0.12 (0.03, 0.21)
Saxifraga occidentalis	●	●	0	0	0	0	0.0 (0.0, 0.01)
Blechnum	***0.53***	***4.51***	***0.8***	***0.53***	***0.27***	***0***	***6.64***
*Blechnum spicant***	●●●●	▲	●●●●	●●●	●●●●	0	2.7 (2.0, 3.4)
Tiarella trifoliata var. *trifoliata***	●●	●●●	●	●	●	●	0.6 (0.5, 0.8)
Achlys triphylla	●	●	●●	●●	●	●	0.5 (0.3, 0.7)
Mitella petandra	●	●	●	●	0	0	0.1 (0.0, 0.1)
Luzula parviflora	●	●	●	●	●	●	0.2 (0.1, 0.3)
Tiarella trifoliata var. *unifoliata*	●	●	●	●	●	●	0.1 (0.0, 0.2)
Festuca occidentalis	●	●	●	●	●	●	0.1 (0.0, 0.2)
Marah oreganus	●	●	0	0	0	0	0.0 (0.0, 0.1)
Equisetum telmatiea	●	●	0	0	0	0	0.0 (0.0, 0.0)
Panicum dichotomiflorum	●	0	0	0	●	0	0.0 (0.0, 0.1)
Oxalis	***7.16***	***9.02***	***7.43***	***3.18***	***5.04***	***1.59***	***33.42***
*Oxalis oregana***	▲▲	▲▲▲▲	▲▲▲▲	▲▲▲	▲▲▲	▲	17.2 (15.7, 18.7)
Stachys mexicana	●●	●●●	●●●	●●●	●●●	●	1.0 (0.8, 1.3)
Adiantum pedatum	●●●	●●●●	●●●●	●●●	●●	●	1.4 (1.1, 1.8)
Dicentra formosa	●	●	●●●	●●	●	●	0.4 (0.2, 0.6)
Vancouveria hexandra	●	●●●	●●	●	●	●	0.6 (0.4, 0.8)
Tsuga heterophylla	●●●	●●	●●●	●●	●●	●●	0.8 (0.6, 1.1)
Carex hedersonii	●	●	●	●	●	●	0.1 (0.1, 0.2)
Hydrophyllum tenuipes	●	●	●	●	0	0	0.1 (0.0, 0.3)
Osmorhiza chilensis	●	●	●	0	●	0	0.0 (0.0, 0.0)
Galium aparine	●	●	●	●	●	0	0.2 (0.1, 0.2)
Asarum caudatum	●	●	●	0	●	0	0.1 (0.0, 0.2)
Nemophila parviflora	●	●	●	●	●	0	0.1 (0.0, 0.1)

Table A1 (*continued*).

Veg. type and species	0 m	1 m	5 m	Slope	Headmost	Ridge	Basin mean (%)
Elymus glaucus	●	●	0	0	0	0	0 (0, 0.0)
Cardamine occidentalis	●	●	0	0	0	0	0.0 (0.0, 0.1)
Holcus lanatus	●	●	0	0	0	0	0.0 (0.0, 0.0)
Acer macrophyllum	0	0	●	0	●	0	0.1 (0.0, 0.1)
Equisetum arvense	●	●	0	0	0	0	0.0 (0, 0.0)
Polypodium hesperium	●	●	0	0	●	0	0.0 (0.0, 0.0)
Gaultheria	***2.12***	***0.8***	***1.59***	***1.59***	***1.86***	***1.86***	***9.82***
*Gaultheria shallon***	●●	●●●	●●●	●●●	●●●	●●●●	1.5 (1.1, 1.9)
*Acer circinatum***	●●●	●●	●●●	●●	●●●	●●	1.1 (0.8, 1.4)
*Holodiscus discolor***	●	●	●●●	●●	●	●	0.5 (0.2, 0.8)
*Whipplea modesta***	●	●	●	●●	●	●	0.2 (0.0, 0.4)
Bromus carinatus	●●	●●●	●●	●●●	●●	●	0.9 (0.7,1.1)
Carex deweyana	●●	●●	●●	●●●	●●●	0	0.8 (0.5, 1.1)
Vaccinium parvifolium	●●	●●●	●●●	●●●	●●●	●	1.2 (0.9, 1.6)
Rubus parviflorus	●	●	●	●	●●	0	0.3 (0.0, 0.6)
Corylus cornuta	●	0	●	●●	●	0	0.2 (0.0, 0.4)
Circaea alpina	●	●	●	●	●	0	0.2 (0.1, 0.4)
Smilacina racemosa	●	0	0	●	●	●●	0.1 (0.0, 0.2)
Pentagramma triangularis	0	0	●	●	0	0	0.0 (0, 0.0)
Trientalis latifolia	0	●	0	●	●	●	0.2 (0.1, 0.3)
Sambucus racemosa	●	●	0	0	●	0	0.1 (0.0, 0.2)
Hieracium albiflorum	0	0	0	●	●	●	0.0 (0.0, 0.1)
Toxicodendron diversilobum	●	●	●	0	0	0	0.1 (0.0, 0.1)
Castanopsis chrysophylla	●	0	●	●	0	0	0.0 (0.0, 0.0)
Tellima grandiflora	●	●	●	●	●	●	0.1 (0.0, 0.1)
Rosa gymnocarpa	0	0	0	●	●	●	0.1 (0, 0.2)
Adenocaulon bicolor	●	●	●	●	●	●	0.3 (0.2, 0.4)
Thalictrum occidentale	●	●	●	●	●	0	0.1 (0.1, 0.2)
Lathyrus polyphyllus	0	0	0	0	●	●	0.0 (0.0, 0.0)
Anemone deltoidea	●	●	●	●	●	●	0.1 (0.0, 0.2)
Actaea rubra	0	0	0	●	0	●	0.0 (0.0, 0.0)
Synthyris reniformis	●	0	●	●	●	●	0.1 (0.0, 0.1)
Prunella vulgaris	0	●	●	0	0	0	0.0 (0.0, 0.0)
Festuca idahoensis	0	0	0	●	0	●	0.0 (0.0, 0.0)
Epilobium angustifolium	●	●	●	0	0	0	0.0 (0.0, 0.0)
Arabidopsis thaliana	0	0	0	0	●	0	0.0 (0.0, 0.0)
Hierochloe occidentalis	0	0	0	0	●	●	0.1 (0.0, 0.1)
Polystichum	***0***	***0.53***	***5.04***	***6.9***	***4.77***	***3.98***	***21.22***
*Polystichum munitum***	▲	▲▲	▲▲▲▲▲	▲▲▲▲▲	▲▲▲▲	▲▲▲	19.9 (18.1, 21.7)
Listera caurina	●	●	●	●	●	●	0.1 (0.0, 0.1)
Alnus rubra	0	●	●	0	●	0	0.1 (0.0, 0.2)
Coptis laciniata	0	●	●	●	●	●	0.1 (0, 0.1)
Berberis	***0.53***	***0.27***	***1.86***	***3.98***	***3.71***	***6.9***	***17.25***
*Berberis nervosa***	●	●●●	●●●●	▲	▲	▲▲	4.9 (4.1, 5.8)
Disporum hookeri	●	●●	●●●	●●	●●●	●●	0.9 (0.7, 1.1)
Trillium ovatum	●	●	●●●	●●	●	●	0.5 (0.3, 0.6)
Pteridium aquilinum	●	●	●	●	●	●	0.1 (0.1, 0.2)
Corallorhiza striata	0	●	●	0	0	●	0.0 (0.0, 0.1)
Chimaphila umbellata	0	0	0	●	●	●	0.0 (0.0, 0.1)
Corallorhiza maculata	●	0	●	0	●	●	0.0 (0.0, 0.1)

Table A1 (*concluded*).

Veg. type and species	0 m	1 m	5 m	Slope	Headmost	Ridge	Basin mean (%)
Campanula scouleri	●	0	●	●	●	0	0.0 (0.0, 0.0)
Chimaphila menziesii	0	0	●	●	0	●	0.0 (0.0, 0.0)
Rhamnus purshiana	0	0	0	●	●	0	0.0 (0.0, 0.1)
Luzula comosa	●	●	●	●	0	●	0.1 (0.0, 0.2)
Vaccinium	***0.27***	***0***	***0***	***0.53***	***0.8***	***2.39***	***3.99***
*Vaccinium ovatum***	●●	●	●	●●	●●●	●●●●	1.3 (0.7, 1.9)
*Rhododendron macrophyllum***	●	●●	●	●●●	●●●	●●●	0.9 (0.6, 1.3)
*Pyrola picta***	0	●	●	●	●	●	0.1 (0.0, 0.1)
*Umbellularia californica**	●	●	●	●	●●	●	0.3 (0.1, 0.5)
Viola sempervirens	●	●	●	●●	●	●●	0.4 (0.3, 0.5)
Monotropa uniflora	●	0	0	0	0	●	0.0 (0.0, 0.0)
*Rubus nivalis**	0	0	0	●	●	●	0.0 (0.0, 0.1)
Montia parvifolia	●	0	●	●	0	●	0.0 (0.0, 0.1)
Sanicula crassicaulis	0	0	●	0	0	●	0.0 (0.0, 0.0)
Rubus ursinus	●	●	●	●	●	●	0.1 (0.0, 0.1)
Polypodium glycyrrhiza	●	●	●	0	0	●	0.0 (0.0, 0.02)
Rubus laciniatus	●	●	●	●	●	●	0.1 (0.0, 0.2)
Disporum smithii	●	●	●	●	●	●	0.1 (0.0, 0.1)

Note: Species ordered by maximum indicator values for one of seven vegetation types. Vegetation types were named using the genus name of the species with the highest indicator value for that type. Species with maximum indicator values (Dufrene and Legendre 1997) significantly higher than random expectation are shown for $p \le 0.01$ (**) and $p \le 0.05$(*). The percentage of units assigned to each vegetation type is shown (in bold italics) for each geomorphic–lateral zone and for the entire sample (Basin mean, in bold italics). Cover classes for each species are provided for each geomorphic–lateral zone. Cover classes include: absent, 0; >0–0.5%, ●; 0.6–1.0%, ●●; 1.1–2.0%, ●●●; 2.1–5.0%, ●●●●; 5.1–10.0%, ▲; 10.1–15.0%, ▲▲; 15.1–20.0%, ▲▲▲; 20.1–25.0%, ▲▲▲▲; and 25.1–30.0%, ▲▲▲▲▲. Species average cover for the full sample (95% CI) is also presented.