

assessed with data from stands in the age gradient, whereas variation from relative differences in moisture condition among old-growth stands was assessed with data from stands in the moisture gradient.

These analyses, and others conducted by Spies and Franklin (this volume), resulted in the construction of complex environmental gradients along which each stand could be assigned a quantitative value. We included these scores in our analyses to provide a means of identifying amphibian habitat relationships occurring along broad environmental gradients.

Amphibian Sampling

We sampled amphibians with pitfall traps in each stand after the onset of fall rains in 1984 and 1985. We installed 36 pitfall traps in each stand in a 6 x 6 square array with traps spaced 15 m apart. To prevent bias from the depletion of individuals in the immediate area of sampling, we moved each grid at least 50 m within the stand in 1985. We sampled all stands for 30 to 34 days each fall (with the exception of one stand that we sampled for only 24 days in 1984), and we checked the traps about once a week. All salvageable specimens were collected, preserved, and deposited in the University of Washington Burke Museum in Seattle.

Vegetation Sampling

We sampled vegetation at nine points within each grid, such that each vegetation point was uniquely associated with four traps. We sampled live vegetation and dead woody debris in two concentric circles around each vegetation point. We visually estimated the cover of vegetation and woody debris in the herb and shrub layers within a 5.6-m radius (100 m²), and estimated physiographic midstory, and canopy variables within a 15-m radius (707 m²). A list and description of the variables collected on each pitfall grid, the combined variables we constructed, and additional physiographic variables and environmental gradients that were used are included in appendix table 4.

Data Analyses

Because samples from 1984 and 1985 are not independent, we used the mean value for vertebrate and vegetation data from both years in all analyses. We calculated abundance indices for amphibian species as captures per 100 trap-nights for each stand. Data from time-constrained searches conducted in these stands in the spring of 1984 (Aubry and others 1988) were included only in species richness and presence/absence data sets.

Community-habitat relationships—Several species did not occur throughout the geographic range encompassed in our study; we therefore calculated species richness as the number of species captured in a stand divided by the number of species known to occur in the geographic area of the stand. The Shannon diversity index (H') was used to characterize species diversity for each stand. Note that, although our knowledge about the geographic distributions of birds and mammals in the Pacific Northwest is virtually complete, this is not true for amphibians. New distribution records have recently been reported for the Larch Mountain salamander (Aubry and others 1987), Van Dyke's salamander (Aubry and others 1987), Cope's giant salamander (Jones and Aubry 1984), tailed frog (Welsh 1985), and clouded salamander (Jones and Raphael 1989), among others.

We examined community patterns of amphibian abundances with detrended correspondence analysis (DCA) using the computer program DECORANA (Hill 1979a), and we identified stand clusters with TWINSPAN (Hill 1979b). We identified environmental gradients associated with each DCA axis with Spearman rank correlations and used direct gradient analysis (Gauch 1982) to further elucidate community-habitat relationships.

Species-habitat relationships—We used nonparametric analysis of variance (Kruskal-Wallis test) on log-transformed abundance values to examine differences in amphibian abundances among age-classes within the age gradient, and among moisture-classes within the old-growth moisture gradient. Because the study sites were preferentially selected to sample the full range of variation occurring within each age- and moisture-class (Carey and Spies, this volume), the variances in our data would be expected to exceed those resulting from random sampling. We therefore used an alpha level of $P \leq 0.1$ for all tests of significance. Because sampled stands were not selected randomly, we used these analyses to evaluate ecologically meaningful patterns in the data, rather than to conduct rigorous hypothesis testing. We identified significant pairwise differences using the Tukey Studentized Range test ($P \leq 0.05$).

We converted count variables in the vegetation data-set to densities, and transformed each vegetation variable with log, square-root, square, reciprocal, and arcsine transformations. We examined the resulting distributions for normality and performed all subsequent analyses on the transformed variables that best approximated univariate normality. We examined the relationships between abundances of individual species and physiographic and vegetative variables with Spearman rank correlations of transformed variables.

We used presence/absence data to further examine species-habitat relationships. We conducted stepwise and canonical discriminant function analyses (DFA) of stands in which a species was present versus those in which it was absent to identify habitat variables that may determine whether a species occurs in a stand. Because stands were not selected randomly, we used DFA only as an exploratory tool, and not as a method for deriving a predictive model. We used a subset of 33 uncorrelated habitat variables in all discriminant analyses (appendix table 4).

Results

We captured 1516 amphibians of 13 species (table 1). We selected seven species for inclusion in community- and species scale analyses of habitat relationships: ensatina, western redback salamander, northwestern salamander, roughskin newt, tailed frog, red-legged frog, and Cascades frog. The last five species have aquatic larval stages. Because juveniles of these species disperse seasonally from ponds and creeks, we do not know if such individuals captured in our pitfall traps were resident or simply moving through the stand to preferred habitats. For this reason, we only used data from adult captures of these species for our analyses (see table 1).

Other species were excluded because their abundances or percentage occurrence in sampled stands were too low (long-toed salamander and Pacific giant salamander), because they did not occur in all of the geographic areas sampled (Larch Mountain salamander and Olympic salamander), or because they are not effectively sampled with pitfall traps (western toad and Pacific treefrog). Data on Pacific giant salamanders and Olympic salamanders were only used in calculations of species richness.

Community-Habitat Relationships

We found no significant differences in species richness or species diversity among stand classes within either the age gradient or the old-growth moisture-gradient. Our data, however, do suggest trends of increasing species richness and diversity with stand age, and with drier conditions in old-growth stands (fig. 1). Species richness and diversity were also less variable in old growth than in younger stands, suggesting that old-growth stands may be more stable in community composition. Species richness appears to be influenced more by elevation than by stand age. We found significant negative correlations ($P < 0.05$) between species richness and elevation for both the age gradient (fig. 2) and the old-growth moisture gradient (fig. 3).

Age gradient-Ordination of abundance data for amphibian communities occurring in stands within the age gradient resulted in two non-overlapping clusters of stands with distinct community composition (fig. 4). The first DCA axis (X axis)

Table 1-Amphibians captured in pitfall traps in the southern Washington Cascade Range in 1984 and 1985

Species	Total captures ^a	Percentage of stands
Salamanders:		
Woodland salamanders-		
Ensatina	800	85
Western redback salamander	162	28
Larch Mountain salamander		2
Mole salamanders-		
Northwestern salamander	135	52
Long-toed salamander	5	2
Newts-		
Roughskin newt	87	46
Giant and Olympic Salamanders		
Pacific giant salamander	12	11
Olympic salamander	14	9
Frogs and toads:		
True frogs-		
Red-legged frog	69	48
Cascades frog	11	17
Tailed frogs-		
Tailed frog	203	67
Treefrogs-		
Pacific treefrog	5	4
True toads-		
Western toad	12	13
Total captures	1516	100

^a Only adults are reported for the long-toed salamander (snout-vent length (SVL) >45 mm); northwestern salamander (SVL >70 mm); roughskin newt (SVL >40 mm); red-legged, Cascades, and tailed frogs (SVL >35 mm).

represents a gradient of increasing moisture and elevation; the second DCA axis (Y axis) is negatively associated with slope and temperature and positively associated with stand age. Most of the separation of clusters occurs along DCA 2. Stands in cluster 1 are located near the origin of DCA 1, whereas stands in cluster 2 occur along the entire length of this axis.

Ensatinas were abundant in most stands, but all other species occurred in high numbers in only one of the two clusters. Cluster 1 consists of stands with abundant pond-breeding frogs and salamanders (red-legged and Cascades frogs, northwestern salamanders, and roughskin newts) and few tailed frogs (a stream-breeding species) and western redback salamanders (a woodland salamander that breeds on land).

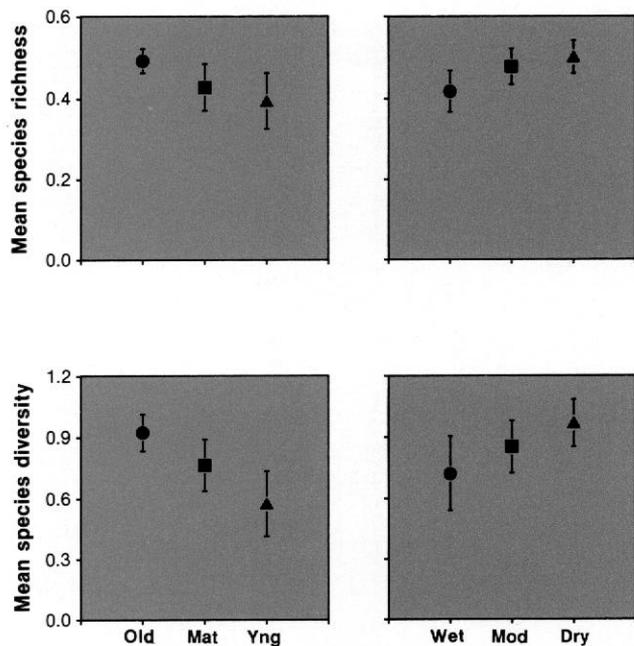


Figure 1—Mean species richness (upper graphs) and diversity (lower graphs) for the age gradient and old-growth moisture gradient. Vertical bars represent standard errors of the mean. Stand age-class: Old = old growth, Mat = mature, Yng = young. Old-growth moisture condition: Wet = wet old growth, Mod = moderate old growth, Dry = dry old growth.

Cluster 1 primarily consists of mature and old-growth stands that are relatively flat and cool; only one young stand occurred in this cluster.

The wettest and highest elevation stands occur in cluster 2, which is characterized by low numbers of the pond-breeding species and abundant tailed frogs, western redback salamanders, and ensatinas. The stands in this cluster are generally younger than those in cluster 1 and characterized by steeper slopes and warmer temperatures. They encompass the full range of variation in moisture and elevation that occurs in stands within the age gradient.

Old-growth moisture gradient—Ordination of the abundance data for only old-growth stands also resulted in two clusters of stands with distinct community composition (fig. 5). DCA 1 (X axis) represents a gradient of increasing elevation and moisture, whereas DCA 2 (Y axis) is weakly associated with a stand-development gradient that is primarily related to increasing basal area of western hemlock and other shade-tolerant species (Spies and Franklin, this volume).

Most of the stands occur in cluster 1 and all seven species are relatively abundant. Stands in cluster 2 were depauperate, by comparison, with low abundances of all species except tailed frogs and northwestern salamanders. Complete overlap

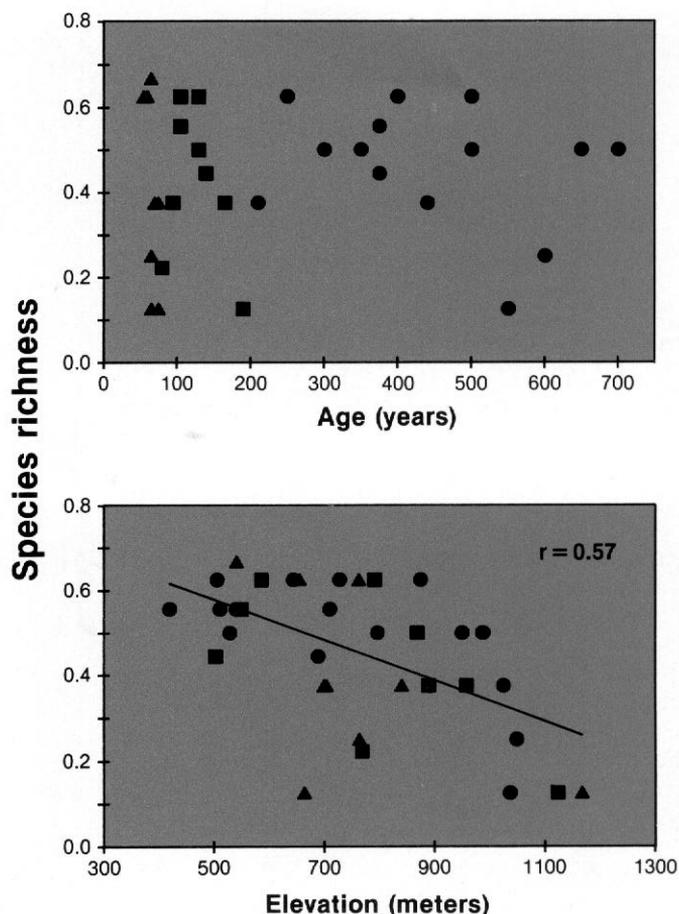


Figure 2—Gradient analyses of species richness vs. stand age (upper graph) and elevation (lower graph) for stands included in the age gradient. Age-class symbols: circle = old growth, square = mature, triangle = young.

of clusters 1 and 2 occurred along the stand-development gradient, but the clusters were fully distinguishable along the gradient of increasing elevation and moisture. Stands in cluster 2 consist of the wetter, higher elevation, old-growth stands.

Species-Habitat Relationships

Age gradient—Mean abundance values for the seven selected species and for all seven species combined within each age-class of the age gradient are shown in figure 6. Significant differences among age-classes were found only for the tailed frog, which was more abundant in mature stands than in young stands.

Although differences among age-classes for other species were not significant, patterns of association with age were evident. The ensatina and western redback salamander were most abundant in young stands. Western redback salamanders, in particular, occurred in very low numbers in mature

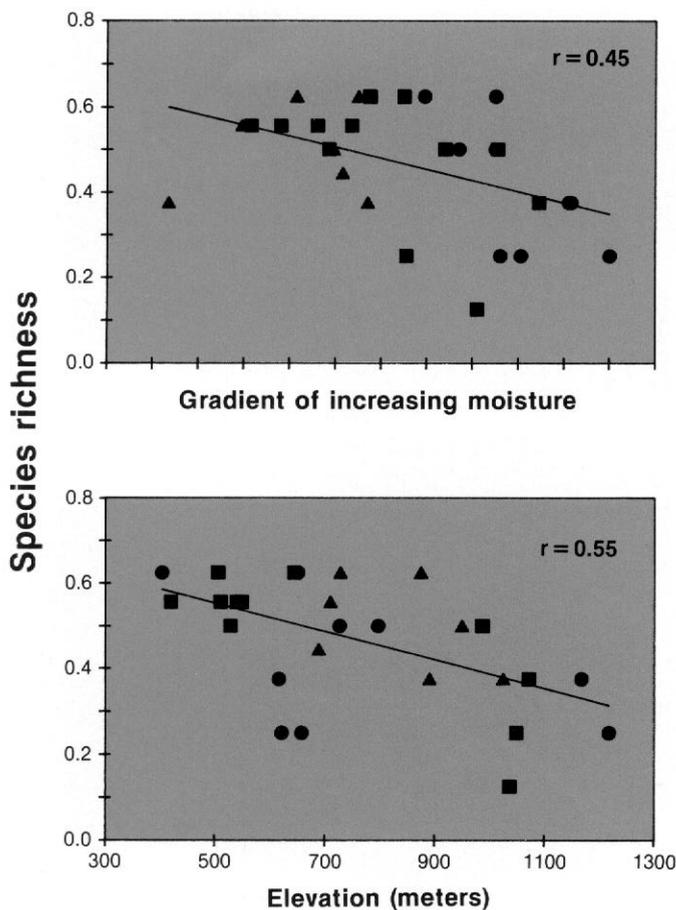


Figure 3—Gradient analyses of species richness vs. moisture condition (upper graph) and elevation (lower graph) for stands included in the old-growth moisture gradient. Moisture-condition symbols: circle = wet, square = moderate, triangle = dry.

and old-growth stands. The northwestern salamander, roughskin newt, and Cascades frog all reached their highest abundances in old growth. Tailed frogs and red-legged frogs were most abundant in mature stands and least abundant in young stands. Total combined abundances of all seven species was highest in young stands, although variation among stands in this age-class was high. Variation in total abundance among mature and old-growth stands, by contrast, was relatively low, which again suggests that older forests may provide more consistently suitable habitat for amphibians than do young forests.

Old-growth moisture gradient—Mean abundance values for amphibians among old-growth moisture-classes are depicted in figure 7. Abundances for the roughskin newt alone varied significantly among moisture-classes, but multiple-range tests failed to identify which moisture-classes differed significantly.

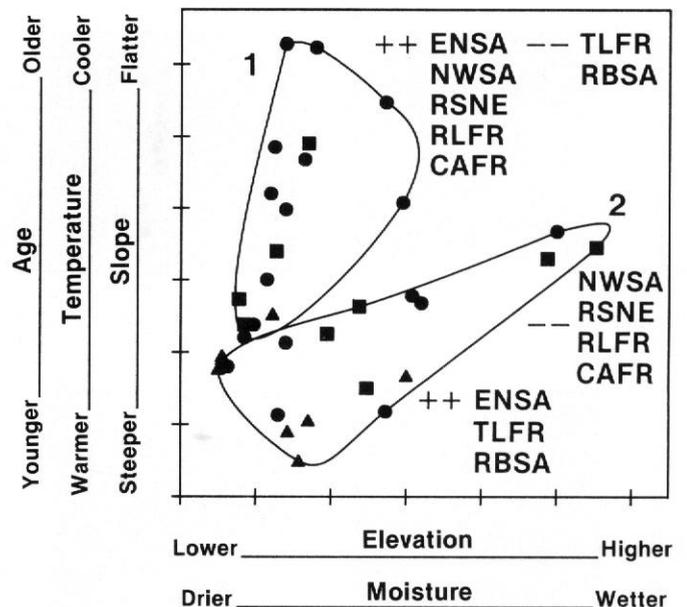


Figure 4—Ordination of species abundances for stands included in the age gradient. Axes represent associated environmental and physiographic gradients. Age-class symbols: circle = old growth, square = mature, triangle = young. Species abbreviations: ENSA = ensatina, RBSA = western redback salamander, NWSA = northwestern salamander, RSNE = roughskin newt, RLFR = red-legged frog, CAFR = Cascades frog, TLFR = tailed frog.

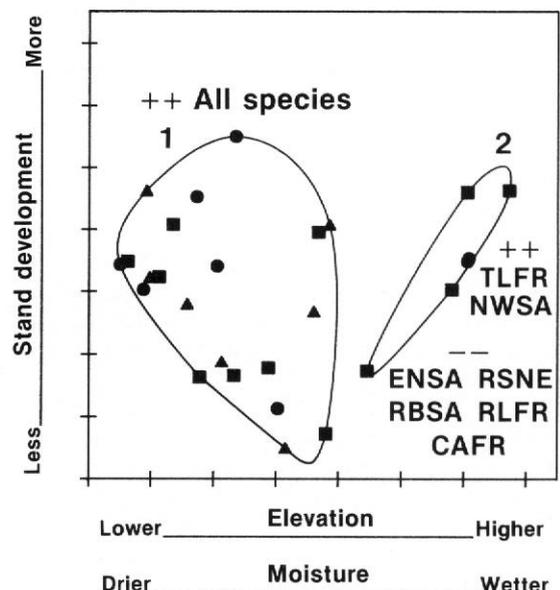


Figure 5—Ordination of species abundances for stands included in the old-growth moisture gradient. Axes represent associated environmental and physiographic gradients. Moisture-class symbols: circle = wet, square = moderate, triangle = dry. Species abbreviations: ENSA = ensatina, RBSA = western redback salamander, NWSA = northwestern salamander, RSNE = roughskin newt, RLFR = red-legged frog, CAFR = Cascades frog, TLFR = tailed frog.

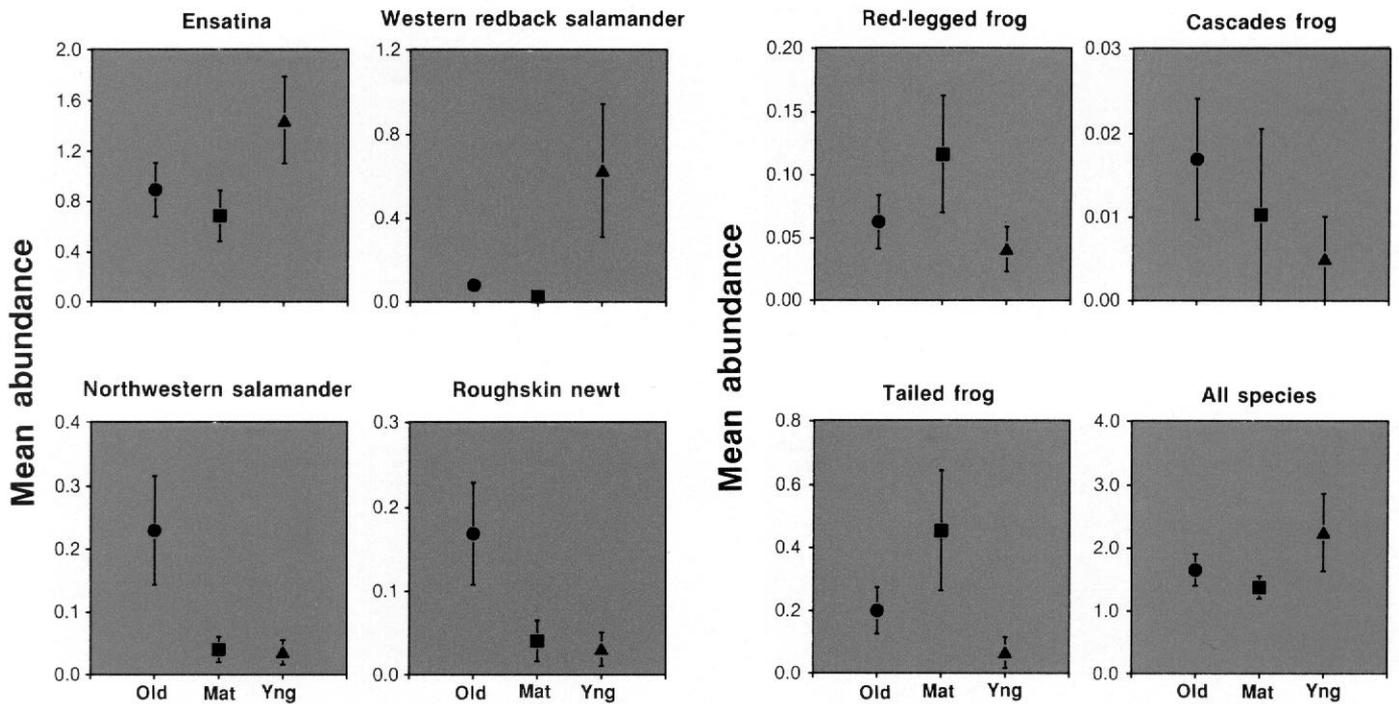


Figure 6—Mean abundance and standard error for seven selected amphibian species by age-class for stands included in the age gradient. Age-classes: Old = old growth, Mat = mature, Yng = young.

Wet old-growth stands appear to provide low-quality habitat for several species. The ensatina and roughskin newt were rarely found in wet stands, and mean abundance values for northwestern salamanders, and for all seven species combined, increased with drier conditions. Red-legged and Cascades frogs reached their highest abundances in stands with moderate moisture, whereas western redback salamanders and tailed frogs showed little association with moisture condition.

All stands—Significant correlations between species abundances and physiographic, vegetative, and structural habitat variables are listed in table 2. Several of the environmental variables associated with community organization (figs. 4, 5) and with abundance patterns across the age and moisture gradients (figs. 6-9) showed meaningful correlations. These included negative correlations with increasing elevation and moisture for the ensatina, roughskin newt, and red-legged frog; positive correlation with increasing elevation for the tailed frog; positive correlation with increasing temperature for the western redback salamander; negative correlation with increasing age for the ensatina; and negative correlation with increasing slope for the red-legged frog (table 2).

Table 2—Significant correlations ($P \leq 0.05$) between physiographic and vegetative variables and abundances of amphibian species in the southern Washington Cascade Range (variables are listed in order of decreasing importance, by column)

Species	Significant correlations		
Ensatina	MDTREE (+)	STUMPC (-)	CONIFL (-)
	WPDCA1 (-)	LMSNAGA (-)	LITTERD (-)
	ESHRUB (+)	WATER (-)	AGE (-)
	ELEV (-)	LMSNAGC (+)	CONIFVL (-)
	BRODLEAF (+)	LTSNAGC (+)	
	MTSNAGB (-)	MSHRUB (+)	
Western redback salamander	SNAGSB (-)	STUMPB (-)	WPDCA2 (+)
	CBTREE (-)	CDTREE (-)	
Northwestern salamander	LTSNAGA (+)	SSNAGA (-)	LMSNAGA (+)
Roughskin newt	ELEV (-)	WPDCA1 (-)	SHRUB (+)
	BRODLEAF (+)	SNAGSC (-)	MSNAGS (-)
	MDTREE (+)	STUMPC (-)	
Red-legged frog	ELEV (-)	TALUS (-)	SLOPE (-)
	OUTCROP (-)	BRODLEAF (+)	
	MDTREE (+)	WPDCA1 (-)	
Cascades frog	SSNAGC (+)		
Tailed frog	ESHRUB (-)	TALUS (+)	SNAGSB (-)
	ELEV (+)	FERN (-)	MSHRUB (-)
	MOSS (-)	BROADM (-)	DLOGSB (-)

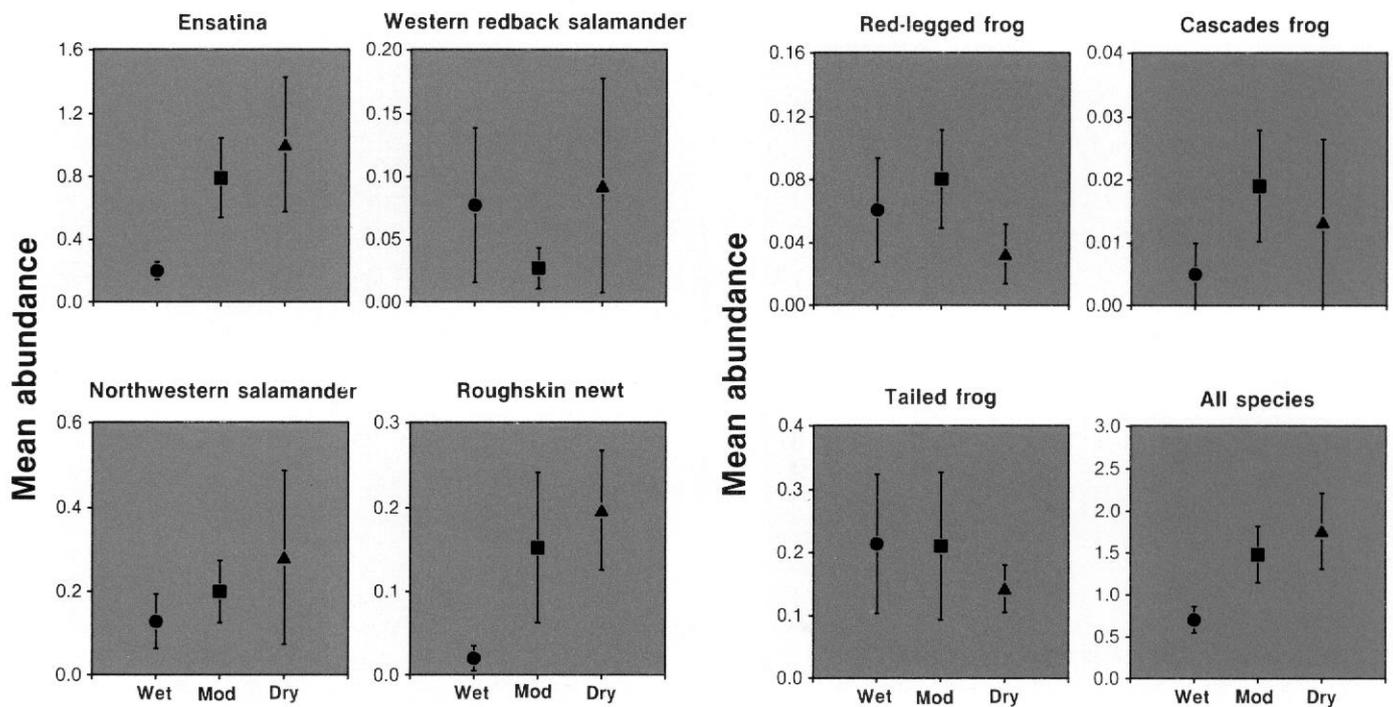


Figure 7—Mean abundance and standard error for seven selected amphibian species by moisture-class for stands included in the old-growth moisture gradient. Moisture classes: Wet = wet old growth, Mod = moderate old growth, Dry = dry old growth.

Correlations with vegetative and structural variables were difficult to interpret, especially for those variables that were positively correlated with abundance. Except for the northwestern salamander, which was positively correlated with only three different height- and diameter-classes of intact snags, most species were positively correlated with vegetative features of the shrub and canopy layers. Speculating about the habitat value of such features for amphibians occupying the forest floor is difficult.

Discriminant function analyses of presence/absence data revealed sets of variables for each species that differed somewhat from those generated with correlation analysis (table 3). Variables in the DFA models also generally supported the findings of detrended correspondence analysis of the composition of amphibian communities (figs. 4, 5). Ensatinas and red-legged frogs were typically absent from relatively wet stands. Ensatinas did not occur in stands containing surface water, however, whereas red-legged frogs were found in relatively flat stands where surface water was present. Tailed frogs occurred in relatively steep stands containing surface water. Both ensatinas and roughskin newts were absent from high-elevation stands. Northwestern salamanders occurred in stands containing surface water and a relatively deep litter layer. The red-legged frog was the only species of amphibian associated with high amounts of woody debris.

Discussion

Community-Habitat Relationships

A suite of environmental variables—of which stand age is but one minor factor—apparently determines the structure and composition of terrestrial amphibian communities in unmanaged Douglas-fir forests in the southern Washington Cascade Range. Young stands contained a relatively depauperate amphibian community compared to older stands, but young stands were also generally steeper and warmer. These conditions generally result in a lack of ponds and correspondingly poor habitat for the pond-breeding salamanders and frogs that represent the majority of species studied. Older stands with flatter slopes and cooler temperatures, which presumably favor formation of ponds, generally contained the most species (fig. 5). Species richness and diversity generally increased with stand age (fig. 1), but age appeared to have less influence on community composition than either elevation or moisture condition.

In our study sites, elevation and moisture condition were highly correlated; the highest elevation stands were also the wettest (see figs. 4, 5). Harsher climatic conditions at higher elevations in the Cascade Range (Franklin and Dyrness 1973) may account for lower species richness there, but very wet stands also appear to provide low-quality habitat for most amphibians. Ensatinas, which prefer moist habitats and are not tied to streams or ponds for reproduction, are rarely found

Table 3-Results of discriminant function analysis between stands in which a species was present versus those in which it was absent

Item	Ensatina (39:7) ^a	Western redback salamander (14:32)	North- western salamander (24:22)	roughskin newt (21:25)	Red- legged frog (22:24)	Cascades frog (9:37)	Tailed frog (31:15)
Variables ^b	WPDCAI MCTREE (+) CDTREE SSNAGS ELEV WATER CCTREE (+) DLOGS	CDTREE MCTREE (+) CBTREE CONIFERS LSNAGS SSNAGS	WATER (+) CANOPY CBTREE LITTERD (+) CONIFL BROADVL	ELEV SNAGSC ASPECT	WPDCAI CCTREE SLOPE WATER (+) DLOGS (+) TALUS	DLOGSA DLOGS CDTREE (+) FLITTER CCTREE (+) BRODLEAF (+) CBTREE (+)	ESHRUB SLOPE (+) CANOPY MCTREE (+) WATER (+)
R ²	0.63	0.45	0.36	0.47	0.51	0.42	0.57
Percentage correct ^c	90	69	51	60	72	68	75

^a Numbers in parentheses indicate the number of stands in which a species was present in proportion to the number of stands in which a species was absent.
^b Variables are listed in order of decreasing importance in the model. Variables that are associated with the Occurrence of a species are indicated with a plus (+).
^c The percentage correct classification was established through cross-validation.

in wet old-growth stands where soils may be saturated with water (see also Aubry and others 1988). Northwestern salamanders and roughskin newts also rarely occurred in wet old-growth stands (fig. 7), even though these species were most abundant in old-growth stands in the age gradient (fig. 6). Among stands in the old-growth moisture gradient, species richness was lowest in wet stands (figs. 1,5), and combined abundances for all species were substantially lower in wet old-growth stands than in either moderate or dry stands (fig. 7).

The structural and functional complexity that is characteristic of old-growth Douglas-fir forests has resulted from hundreds of years of stand development. This ecological complexity would not be expected to occur in younger forests (Franklin and others 1981). We consequently expected to find significantly lower amphibian species richness and abundances in young stands. The reason we did not is probably related to the pattern of input and loss of coarse woody debris in stands that have regenerated after catastrophic wildfires. Naturally regenerated young stands have a large carryover component of snags and logs (Spies and others 1988). Younger-aged unmanaged stands therefore have many of the ecological characteristics of old-growth forests. In unmanaged closed-canopy forests, these features provide habitat for amphibians that would not be expected to occur in forest stands that result from current timber-harvesting practices (Aubry and others 1988; Bury and Corn 1988a, b; Spies and Cline 1988). Unmanaged closed-canopy forests of similar physiography apparently support similar terrestrial amphibian communities, regardless of age. Whether these communities would also occur in managed forests is not a question that can be adequately addressed with our data.

Species-Habitat Relationships

Ensatina-Ensatinas were most often found in young stands in the age gradient (fig. 6), and in moderate and dry stands in the old-growth moisture gradient (fig. 7). Relatively dry to mesic conditions at low to mid-elevations appear to be the major environmental influences on abundance for this species (tables 2,3).

Previous studies of microhabitat use in the Cascade Range indicate a positive association between ensatina abundances and amounts of coarse woody debris, especially with moderately and well-decayed logs and snags (Aubry and others 1988, Bury and Corn 1988a). Our pitfall results also support this hypothesis. Ensatinas were least abundant in mature stands (fig. 6), which typically contain less coarse woody debris than do either old-growth or young stands (Spies and others 1988). This pattern was primarily because of high inheritance of coarse woody debris in young stands resulting from catastrophic fires. Lower amounts accumulate in mature stands as existing debris decays, but inputs remain low. By comparison, old-growth stands accumulate high amounts of debris as the large Douglas-firs die and inputs are high. Ensatina abundances were also positively correlated to the density of well-decayed stumps and snags >50 cm d.b.h. and at least 1.5-m tall (table 2). Such features provide favorable habitat for ensatinas as the bark sloughs to the ground in piles around the snag and forms multilayered, structurally complex cover (Aubry and others 1988). Well-decayed stumps and snags may also provide below-ground habitat within the decomposing root system.

The ensatina is not associated with old-growth stands, but some evidence indicates that this species is associated with the large amounts of coarse woody debris characteristic of

old-growth forests (Franklin and others 1981). Our results suggest that ensatinas may be adversely affected by timber harvesting because intensive forest management results in substantially less coarse woody debris than that encountered in unmanaged forests (Spies and Cline 1988). Provision for increased amounts of coarse woody debris in managed forests would be expected to benefit this species.

Western redback salamander-Western redback salamanders were most abundant in young stands. Young stands, however, were also relatively steep, warm, and dry (fig. 4), and analyses of habitat variables suggest that these factors are more important environmental influences for this species than is stand age. Abundance of western redback salamanders was positively correlated with a gradient of increasing temperature (table 2), yet neither analysis indicated a negative association with age.

Previous authors have reported that western redback salamanders are commonly found in talus slopes (Herrington 1988, Nussbaum and others 1983). Although this species favored steeper slopes, we found no evidence of an association with talus in the southern Washington Cascade Range. Our observations indicate that talus slopes are relatively rare in these forests. The drier conditions of steep slopes apparently are more important for this species than the presence of talus. Studies of cover-object use showed that western redback salamanders are most frequently found under moderately decayed logs >10 cm in diameter (Aubry and others 1988). The western redback salamander is also not strongly associated with old-growth stands, but the retention of coarse woody debris in managed forests would probably also create conditions favorable for this species.

Northwestern salamander-Northwestern salamanders were five times more abundant in old-growth than in younger stands (fig. 6). The northwestern salamander was also the only species of salamander present in relatively high numbers in both clusters of the old-growth ordination (fig. 5). Mean abundance increased with drier conditions in old growth, but variation in abundances in dry stands was extremely high (fig. 7). The age-gradient ordination indicated that this species and all other pond-breeding salamanders and frogs reached their highest abundances in relatively old, cool, flat stands that were not extremely wet or high in elevation (fig. 4). We found a strong correlation with all sizes of relatively intact snags (table 2), but how these structural features might provide habitat for northwestern salamanders is not clear.

Our results showed the northwestern salamander to be closely associated with old-growth Douglas-fir forests in the southern Washington Cascade Range during the late fall. Bury and Corn (1988a) previously found little evidence that northwestern salamanders were associated with old-growth

forests in the southern Washington Cascade Range, but differences in the timing of sampling probably explain our divergent results. Bury and Corn (1988a) ran their pitfall traps from May to November, and our traps were open from late September to November. Northwestern salamanders migrate seasonally to and from breeding ponds, and captures during the reproductive season may therefore simply reflect individual movement through the stand to and from breeding ponds rather than selection of the habitat in which they were captured. Suitable breeding ponds are essential habitat features for this species, but high-quality overwintering habitat may also be critical for population persistence. Our results indicate that old-growth forests are important habitats for northwestern salamanders during the nonbreeding season in southern Washington.

Regional comparisons by Bury and others (this volume a) showed that northwestern salamanders were associated with old-growth forests only in southern Washington, and that late-fall abundances in both the Oregon Cascade Range and the Oregon Coast Range were similar across the age gradient. Pitfall captures for northwestern salamanders were much lower in the Coast Range (38; Corn and Bury, this volume b) and the Oregon Cascade Range (38; Gilbert and Allwine, this volume c), than in the southern Washington Cascade Range (135; this study). Data on this species from the Oregon provinces, therefore, should be interpreted with caution. These results may, however, indicate a latitude effect whereby harsher climatic conditions in more northerly forests (Franklin and Dymess 1973) force north-western salamanders to seek overwintering sites in old-growth forests where climatic conditions are less extreme (Spies and Franklin 1988). Results from the Oregon Cascade Range provide additional support for this hypothesis. The northernmost 16 stands in the Oregon Cascades (in the vicinity of Mount Hood) accounted for 31 of 38 captures for this species in the Oregon Cascade Range. For these stands, northwestern salamanders occurred at significantly higher abundances in old-growth forests than in either mature or young forests (Gilbert and Allwine, this volume c).

Roughskin newt-Roughskin newts were four to five times more abundant in old growth than in younger stands (fig. 6). Unlike northwestern salamanders, however, this species was much less abundant in wet old-growth than in either moderate or dry stands (fig. 7). This difference was also evident in the old-growth ordination, where roughskin newts were found at lower abundances than northwestern salamanders in wetter stands at higher elevations (fig. 5). Ordination of stands in the age gradient showed that roughskin newts exhibited the same community associations as northwestern salamanders in stands where environmental conditions were relatively moderate (fig. 4). Unlike northwestern salamanders, however, roughskin newts were generally absent from high-elevation stands (table 3). Consequently, although the roughskin newt

is closely associated with old-growth forests during the nonbreeding season in southern Washington, it does not occupy wet sites at high elevations.

Just as for northwestern salamanders, marked variation was found in regional abundance patterns for roughskin newts (see Bury and others, this volume a). In the Oregon Cascade Range, roughskin newts were associated with young forests (Gilbert and Allwine, this volume c). In the Oregon Coast Range, by contrast, no strong patterns were found in the data although roughskin newts reached highest abundances in old-growth stands (Corn and Bury, this volume b). These results may also reflect a latitude effect where old-growth forests provide critical overwintering habitat only at northern latitudes.

Red-legged frog-Red-legged frogs were most abundant in mature stands within the age gradient (fig. 6) and in moderate old-growth stands within the old-growth moisture gradient (fig. 7). In terms of community association, red-legged frogs exhibited the same patterns as the other pond breeders, with the exception of the northwestern salamander, which alone occupies the higher, wetter old-growth stands (figs. 4, 7). This species was negatively associated with elevation, stand moisture condition, talus, and steep slopes, and was positively associated with cover by woody debris and the presence of water (tables 2, 3). The presence and abundance of this species apparently was largely determined by conditions favoring the formation of ponds in relatively moderate stand conditions. This species showed little association with stand age, but its presence was correlated with high levels of woody debris, which suggests that red-legged frogs may require this habitat feature for hiding cover.

Cascades frog-Captures for Cascades frogs were low, but their abundance increased with stand age (fig. 6). Of 13 Cascades frogs captured (11 in pitfalls and 2 in time-constrained searches), 10 (77 percent) were found in old-growth stands. Community-association patterns for Cascades frogs were the same as for red-legged frogs (figs. 4,5), as were their apparent preferences for old-growth stands of moderate moisture condition (fig. 7). Patterns of association with individual habitat variables revealed little interpretable information, probably because of low abundance values. Further work is needed on this species to evaluate its potential preference for old-growth forests.

Tailed frog-The tailed frog was significantly more abundant in mature stands than in young stands (fig. 6). Its patterns of community association were the same as those for western redback salamanders within the age gradient (fig. 4) and for northwestern salamanders within the old-growth moisture gradient (fig. 5). Habitat analyses indicated that tailed frogs were associated with steep slopes, high elevations, talus, and the presence of water (tables 2,3).

Western redback salamanders appear to be correlated with the drier environmental conditions found on steep slopes, but tailed frogs are more likely associated with the cool, clear creeks that also occur on steep slopes (Nussbaum and others 1983). Our results do not show the tailed frog to be associated with old-growth forests; however, young stands apparently provide relatively unsuitable habitat for this species in the southern Washington Cascades.

Recommendations for Further Research

- Intensive research is needed on the northwestern salamander and roughskin newt to elucidate the ecological basis of their association with old-growth forests in southern Washington. These studies should be conducted during both the breeding and nonbreeding seasons to evaluate the potential seasonality of habitat association patterns.
- Research should also be directed at evaluating the importance of coarse woody debris as habitat features for the ensatina, western redback salamander, and possibly the red-legged frog, to determine if amounts of coarse woody debris in managed forests will be sufficient to maintain viable populations of these species in Douglas-fir forests.
- Studies of the tailed frog should be undertaken in both unmanaged and managed young forests to investigate the low habitat quality of young stands.
- Extensive studies of amphibian communities in managed forests should be initiated immediately.
- Long-term research on terrestrial amphibians in unmanaged and managed Douglas-fir forests should be initiated to determine if patterns of association and habitat relationships vary over time, and to evaluate the extent to which amphibian populations may be affected by forest management over the long term.

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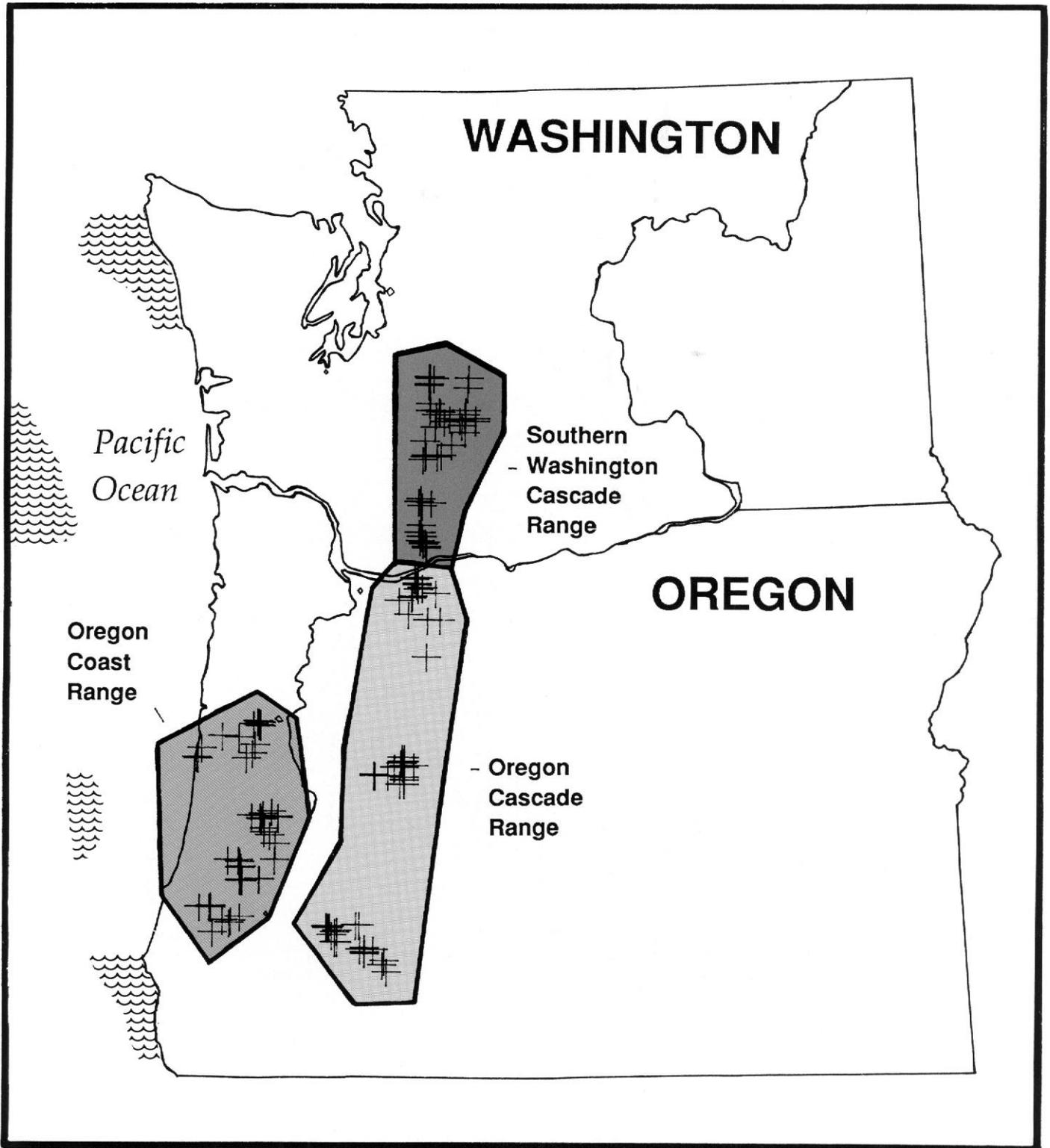
Appendix

Table 4-Physiographic and vegetative variables examined in the southern Washington Cascade Range (variables used in discriminant function analyses are indicated with a solid circle)

Variable	Description
Physiographic:	
. ELEV	Elevation
• AGE	Age
. ASPECT	Aspect
• SLOPE	Percentage slope
. WPDCA1	Moisture gradient
. WPDCA2	Temperature gradient
CDACHRN1	Age gradient
CDACHRN2	Coarse woody debris gradient
CDAOLDG1	Stand-development gradient
CDAOLDG2	Stand-development gradient
. TALUS	Percentage of stations with talus present
OUTCROP	Percentage of stations with outcrops present
INTSTREM	Percentage of stations with intermittent streams present
PERSTREM	Percentage of stations with perennial streams present
POOLS	Percentage of stations with pools or ponds present
. WATER	Percentage of stations with a source of water present
Percentage cover:	
GRASS	Grass
HERB	Herbaceous vegetation
• ROCK	Rocks
• SOIL	soil
MOSS	Moss
• LICHEN	Lichen
. FLITTER	Fine litter
FERN	Fern
. ESHRUB	Evergreen shrubs
DSHRUB	Deciduous shrubs
• BSHRUB	Berry-bearing shrubs
SHRUB	All shrubs
TALLCOVR	All shrubs and ferns
MSHRUB	Shrubs in the midcanopy
. MCTREE	Conifer trees in the midcanopy
MDTREE	Deciduous trees in the midcanopy
. MBTREE	Broadleaved evergreen trees in the midcanopy
MCANOPY	Midcanopy
. CDTREE	Deciduous trees in the canopy
• CBTREE	Broadleaved evergreen trees in the canopy
• CCTREE	Conifer trees in the canopy
• CANOPY	Canopy
. DLOGSA	Intact woody debris
DLOGSB	Moderately decayed woody debris
DLOGSC	Well-decayed woody debris
• DLOGS	Woody debris

Variable	Description
Live-tree density:	
CONIFS	Conifer trees, d.b.h. 1-10 cm
CONIFM	Conifer trees, d.b.h. 10-50 cm
. CONIFL	Conifer trees, d.b.h. 50-100 cm
• CONIFVL	Conifer trees d.b.h. >100 cm
. CONIFERS	All conifer trees
BROADS	Deciduous and broadleaved evergreen trees, d.b.h. 1-10 cm
BROADM	Deciduous and broadleaved evergreen trees, d.b.h. 10-50 cm
• BROADL	Deciduous and broadleaved evergreen trees, d.b.h. 50-100 cm
• BROADVL	Deciduous and broadleaved evergreen trees d.b.h. >100 cm
• BRODLEAF	All deciduous and broadleaved evergreen trees
Stump and snag density:	
STUMPA	Intact to slightly decayed stumps
STUMPB	Moderately decayed stumps
STUMPC	Well-decayed stumps
STUMPS	stumps
SSNAGA	Intact to slightly decayed snags, d.b.h. <10 cm, ht <1.5 m
SSNAGB	Moderately decayed snags, d.b.h. <10 cm, ht <1.5 m
SSNAGC	Well-decayed snags, d.b.h. <10 cm, ht <1.5 m
. SSNAGS	All snags, d.b.h. <10 cm, ht <1.5 m
MMSNAGA	Intact to slightly decayed snags, d.b.h. 10-50 cm, ht 1.5-15 m
MMSNAGB	Moderately decayed snags, d.b.h. 10-50 cm, 1.5-15 m
MMSNAGC	Well-decayed snags, d.b.h. 10-50 cm, ht 1.5-15 m
MTSNAGA	Intact to slightly decayed snags, d.b.h. 10-50 cm, ht >15 m
MTSNAGB	Moderately decayed snags, d.b.h. 10-50 cm, ht >15 m
MTSNAGC	Well-decayed snags, d.b.h. 10-50 cm, ht >15 m
. MSNAGS	All snags, d.b.h. 10-50 cm, ht >1.5 m
LMSNAGA	Intact to slightly decayed snags, d.b.h. 250 cm, ht 1.5-15 m
LMSNAGB	Moderately decayed snags, d.b.h. >50 cm, ht 1.5-15 m
LMSNAGC	Well-decayed snags, d.b.h. >50 cm, ht 1.5-15 m
LTSNAGA	Intact to slightly decayed snags, d.b.h. >50 cm, ht >15 m
LTSNAGB	Moderately decayed snags, d.b.h. >50 cm, ht >15 m
LTSNAGC	Well-decayed snags, d.b.h. >50 cm, ht >15 m
. LSNAGS	All snags, d.b.h. >50 cm, ht >1.5 m
SNAGSA	All intact to slightly decayed snags
SNAGSB	All moderately decayed snags
• SNAGSC	All well-decayed snags
Other:	
SCAN	Presence of super-canopy trees
• @*~*~*~*~*	Depth of litter layer
TREPIT	Density of tree pits

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Location of study sites within the three physiographic provinces.

Regional Patterns of Terrestrial Amphibian Communities in Oregon and Washington

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Abstract

We examined the occurrence and abundance patterns of terrestrial amphibians in the Pacific Northwest, mostly based on captures in pitfall traps at 130 study sites. Seven of eight widespread species showed a marked variation in abundance between the Oregon Coast Range and the Cascade Range in Oregon and Washington. Only two species were associated with an age gradient (young, mature, and old-growth forests): the northwestern salamander was usually most abundant in old growth, whereas the western redback salamander occurred in highest numbers in young stands. *Ensatina* was most abundant in dry old growth in the Cascade Range and was the only species with a marked response across a moisture gradient (wet, moderate, and dry forests). Abundance of species was more often associated with physiographic variables than with vegetation features. On the basis of multidimensional

scaling of species richness, the amphibian community in the Coast Range appears distinct from that in the Cascade Range. The highest species richness was in the Oregon Coast Range, whereas the lowest species richness was in the Cascade Range in Washington. The same analysis was unable to discriminate differences in the species richness of amphibians among young, mature, and old-growth stands. Special habitat features influenced the abundance of amphibians. Ponds and streams are required for several aquatic-breeding amphibians, but these waters were unevenly distributed in the stands we studied. Large, well-decayed down wood was essential for several terrestrial salamanders, and these species may eventually be reduced in numbers or extirpated in managed forests where down wood is scarce. Rocky substrate also appeared to influence the occurrence and abundance of several salamanders. The Pacific Northwest has several endemic species with restricted distributions and specialized habitat requirements. Unless management strategies are tailored to these unique species, they may decline locally or be extirpated.

Introduction

The value of old-growth forests for wildlife habitat and the effect of timber harvest on this resource is the subject of current debate (see Fosburg 1986, Harris 1984, Kerrick and others 1984, Meslow and others 1981, Norse 1990, Salwasser 1987, Wilcove 1987). Old-growth forests dominated by

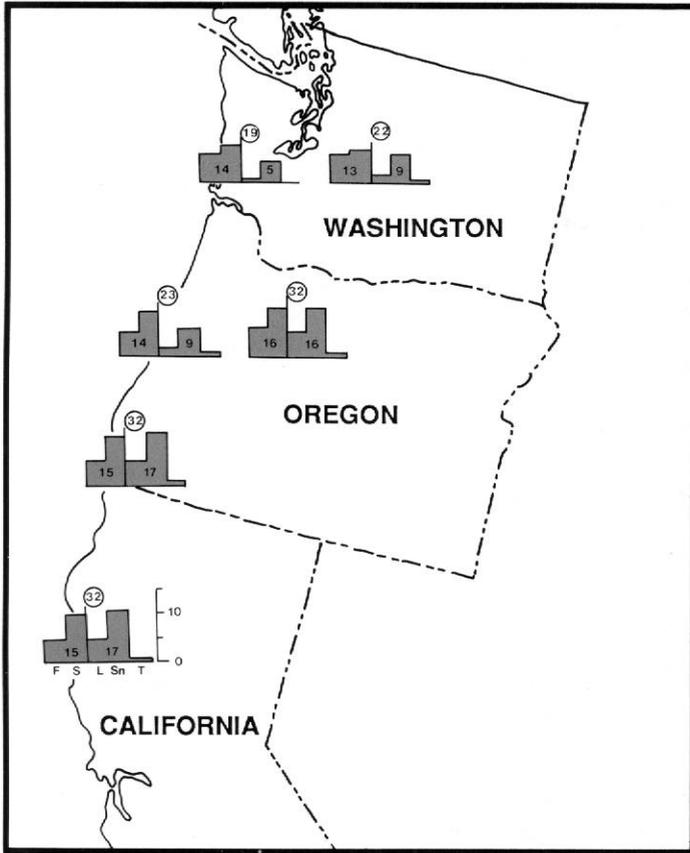


Figure 1—Numbers of species of amphibians and reptiles occurring in the Pacific Northwest (F = frogs, S = salamanders, L = lizards, Sn = snakes, T = turtles). Note the marked decrease in reptile species from south to north.

Douglas-fir have a wide range of tree sizes and ages, a deep multilayered canopy, large individual trees, and accumulations of large pieces of coarse woody debris (Franklin and Spies 1984). These distinctive attributes of old-growth forests may be important habitat elements for several species of the Pacific Northwest herpetofauna.

Most areas in the Pacific Northwest support as many as 19 to 23 species of amphibians and reptiles, based on published distribution maps (Nussbaum and others 1983, Stebbins 1985) and our field studies (fig. 1). Further, these herpetological communities may be ecologically important because of the high numbers and biomass of resident amphibians and reptiles (see Bury 1988).

Recently, the Old-Growth Forest Wildlife Habitat Program (see Ruggiero and Carey 1984) conducted several studies on amphibians and reptiles in forested habitats. Few reptiles were captured, and they are not discussed in this paper.

Reptiles are prevalent in open habitats such as oak woodland or grassland (Raphael 1987, Welsh 1987), where different techniques are needed to sample them adequately.

Results of sampling terrestrial amphibians have been reported for four provinces: Southern Washington Cascade Range, from Mount Rainier National Park south to the Columbia River (Aubry and others 1988; Aubry and Hall, this volume), Oregon Cascade Range (Bury and Corn 1988a; Gilbert and Allwine, this volume c), Oregon Coast Range (Corn and Bury, this volume b), and the Klamath Mountains province in southern Oregon and northern California (Raphael 1987b; Raphael 1988c; Welsh and Lind 1988, this volume). Aquatic amphibians were analyzed separately (Bury and others, this volume b; Bury and Corn 1988b; Corn and Bury 1989).

Here, we attempt to identify which species of the herpetofauna are associated with gradients of forest age and moisture condition in naturally regenerated forests for the three provinces north of the Klamath Mountains. Our specific objectives are:

- To compare the species richness and relative abundance of terrestrial amphibians among different forest stands;
- To elucidate regional differences in the structure and composition of terrestrial amphibian communities relative to their biogeographical patterns; and
- To provide guidelines for managing and protecting these species.

Methods

Methods of sampling amphibians included time-constrained collecting, which is useful for capturing certain terrestrial species, and pitfall trapping, which is effective for sampling most terrestrial species, especially migratory forms. These techniques are based on general herpetological sampling (see Bury and Raphael 1983, Campbell and Christman 1982, Jones 1986, Raphael and Barrett 1981), and specific methods developed for Pacific Northwest forests (Bury and Corn 1987; Corn and Bury 1990; Raphael 1988c).

We compared patterns of abundance among the three provinces by using several statistical approaches. We used two-way analysis of variance (ANOVA) to test for significant differences among provinces in the abundance of species that occur in all three provinces. Study sites were not selected at random because of logistical problems (for example, inaccessible wilderness) and land-use patterns (for example, private ownership or active logging nearby). Thus, we used statistical tests to identify major patterns in the data rather than to test specific hypotheses (see Carey and Spies, this volume).

Species included in the ANOVA analyses were the northwestern salamander, Pacific giant salamander, Olympic salamander, ensatina, western redback salamander, roughskin newt, tailed frog, and red-legged frog. Only data derived from pitfall captures were used in these tests because abundance data from time-constrained collecting may be biased (Corn and Bury 1990, this volume b). Abundance was expressed as number captured per 100 trap-nights. We excluded juveniles of the northwestern salamander (<70 mm snout-vent length [SVL]), roughskin newt (<40 mm SVL), tailed frog (<35 mm SVL), and red-legged frog (<35 mm SVL) from the analyses so as to minimize the effects that seasonal pulses of aquatic breeders moving through the study sites would have on estimates of abundance (see Bury and Corn 1987, 1988a).

Separate two-way ANOVAs were performed for amphibians across gradients of age and moisture. Most stands were naturally regenerated after catastrophic fire, and three age-classes were represented: young (35-79 years old), mature (80-195 years), and old-growth (200-730 years). A moisture gradient (wet, moderate, and dry) was established for the old-growth stands (see Spies and Franklin, this volume).

Pitfall trapping was conducted in 147 stands. We compared pitfall data among 130 stands across the chronosequence and 83 old-growth stands on the moisture gradient. We used a 6 by 6 grid of traps (15 m apart) in each stand, which is described in detail elsewhere (Corn and Bury 1990).

Some differences in techniques were used for each province. In the Oregon Cascade Range, trapping was conducted in 56 stands; all stands were sampled in 1984, and the same grids in the central stands (on or near the H.J. Andrews Experimental Forest) in 1985 (Gilbert and Allwine, this volume c). Stands in the southern Washington Cascade Range ($n = 45$) and the Oregon Coast Range ($n = 46$) were trapped in both 1984 and 1985, and trap grids were moved between years in Washington (Aubry and Hall, this volume) but not in the Coast Range (Corn and Bury, this volume b). Values are expressed as mean captures to facilitate comparisons between provinces that have different numbers of stands. We used 1985 data from the Oregon Coast Range and the Cascade Range in Washington because the analyses of these data within each province combined the captures from both years (Aubry and Hall, this volume; Corn and Bury, this volume b).

We used gradient analyses to investigate relations between the abundance of species and habitat variables (physiographic and vegetative). Physiographic variables were measured on each pitfall grid (see Corn and Bury, this volume b) and included stand age, elevation, aspect (cosine-transformed), percentage slope (arcsine-transformed), and the presence or absence of surface water or exposed talus. Individual vegetative variables were combined into broad stand-scale gradients using canonical discriminant analysis. Separate analyses

resulted in four variables (Spies and Franklin, this volume): DF1A and DF2A from an analysis of stands in the chronosequence, and DF1M and DF2M from an analysis of stands in the moisture gradient. DF1A is positively correlated with stand development (for example, number of large trees, stand age, and variation in tree diameter), and DF2A is positively correlated with coarse woody debris (primarily volume of snags and down wood). DF1M was negatively correlated with the basal area of shade-tolerant trees and apparently represents a temperature gradient (stands from the Coast Range have high scores, Washington stands have low scores). DF2M was negatively correlated with the density of sub-canopy trees and cover of evergreen shrubs, and it represents a moisture gradient (wet stands have high scores).

Because the abundances of most amphibian species varied among provinces, we tested for associations between abundance and continuously distributed habitat variables. We compared abundance among provinces by using the habitat variables as covariates. The presence or absence of variables (water and talus) were tested in a two-way ANOVA with province.

We compared the structure and composition of amphibian communities among provinces by determining the presence or absence of 12 species. Eight species occurred in all provinces, and four others were present in one or two provinces (the clouded salamander, Oregon slender salamander, Dunn's salamander, and the Cascades frog). We combined the results of time-constrained collecting and pitfall trapping to generate lists of species in each stand. Such an approach precludes the use of abundance data, but it provides a more complete list of species than pitfall data alone (Corn and Bury 1990).

Species richness was based on one time-constrained collection (or survey of down wood) and 2 years of pitfall trapping in each of 55 stands. Surveys of down wood (equivalent to time-constrained collection) were done in only 15 of the study sites in the Oregon Coast Range (Corn and Bury, this volume b), so we selected subsamples (the central stands) from both provinces in the Cascade Range. In Oregon, we used data from 19 stands in or near the H.J. Andrews Experimental Forest (Gilbert and Allwine, this volume c), and in Washington, we used data from 21 stands in the Packwood-Randle area (Aubry and Hall, this volume).

We used multidimensional scaling (MDS) to represent the pattern of presence or absence of the 12 species; MDS computes two-dimensional coordinates for a set of stands so that the distances between pairs of stands fit as closely as possible to their measured similarities (Wilkinson 1988). Similarity between pairs of stands was computed with Jaccard's index (Pielou 1984), which is the number of species present in one stand in proportion to the total number of species present in the pair of stands.

Table 1—Mean captures (number per 100 trap-nights) of amphibians across the chronosequence of forest stands (standard deviations are in parentheses)

Species	Oregon Coast Range			Oregon Cascade Range			Southern Washington Cascade Range		
	Old growth n = 25	Mature n = 10	Young n = 8	Old growth n = 22	Mature n = 19	Young n = 9	Old Growth n = 19	Mature n = 9	Young n = 9
Northwestern salamander	0.015 (0.032)	0.014 (0.029)	0.013 (0.026)	0.022 (0.073)	0.010 (0.042)	0.013 (0.026)	0.227 (0.379)	0.041 (0.062)	0.036 (0.060)
Pacific giant salamander	.050 (.053)	.042 (.043)	.043 (.058)	.030 (.071)	.041 (.078)	.045 (.136)	.002 (.010)	0 (.052)	.021 (.062)
Olympic salamander ^a	.029 (.048)	.003 (.011)	.013 (.026)	.011 (.039)	0	0	.007 (.017)	.020 (.052)	.052 (.147)
Ensatina	.454 (.227)	.542 (.525)	.569 (.242)	.453 (.296)	.491 (.360)	.439 (.327)	.825 (.954)	.686 (.612)	1.443 (1.036)
Western redback salamander	.532 (.359)	.490 (.739)	.812 (1.126)	.025 (.061)	.006 (.018)	.006 (.019)	.075 (.183)	.025 (.060)	.628 (.954)
Roughskin newt	.111 (.168)	.076 (.102)	.026 (.025)	.107 (.173)	.065 (.096)	.550 (.777)	.164 (.269)	.041 (.075)	.031 (.061)
Tailed frog	.033 (.061)	.101 (.122)	.035 (.098)	.144 (.591)	.016 (.032)	.172 (.274)	.127 (.101)	.455 (.573)	.067 (.152)
Red-legged frog	.003 (.010)	0	.026 (.031)	.026 (.084)	.025 (.054)	0	.063 (.093)	.116 (.140)	.041 (.054)

^a Olympic salamanders do not occur at the north end of the Cascade Range in Washington or the south end of the Cascade Range in Oregon. Correct sample sizes are: Oregon old growth (12), mature (12), young (6); Washington old growth (13), mature (7), young (8).

Table 2—Separate two-way analysis of variance of abundance versus province and age-class, and abundance versus province and moisture-class

Species	Factor				
	Province ^a	Age ^b	Moisture ^c	Interactions	
				PxA ^d	PxM ^e
Northwestern salamander	XXXX ^f	XXXX		XXXX	
Pacific giant salamander	XXXX				
Olympic salamander					
Ensatina	XXXX		XXXX		
Western redback salamander	XXXX	XXXX			
Roughskin newt	XXXX			XXXX	
Tailed frog	XXXX				
Red-legged frog	XXXX				

^a Southern Washington Cascade Range, Oregon Cascade Range, Oregon Coast Range.

^b Old-growth, mature, young.

^c Old-growth stands only: dry, moderate, wet.

^d Province x age.

^e Moisture x age.

^f $P < 0.05$.

Using the same set of data on species richness, we performed a nonhierarchical clustering of stands using the K-means procedure of SYSTAT (Wilkinson 1988). The K-means procedure produces a specified number of nonoverlapping pools (clusters) of stands. We chose three pools because three provinces and three forest age-classes were analyzed.

Results

Variation Within the Chronosequence

Marked variation was found in the abundance of amphibians across the chronosequence of selected stands (table 1). Ensatina was usually the most common species captured in all stand ages for each province, followed by roughskin newts. Western redback salamanders were an exception, being more abundant in young and old-growth stands in the Oregon Coast Range than either of the other two species.

We found that seven of eight species showed marked variation in abundance among provinces (table 2). Only the northwestern salamander and the western redback salamander were significantly associated with the age gradient when variation among provinces was taken into account. The northwestern salamander was more abundant in old growth (this pattern was not apparent in the Coast Range) than in mature or young stands. They were most abundant in Washington. The western redback salamander was most abundant in young stands and in samples from the Coast Range; the species was rare in the Cascade Range in Oregon. A strong interaction was found between province and stand age for roughskin newts. This species was most abundant in old-growth forests in Washington and in the Coast Range, and in young stands in the Oregon Cascade Range.

Variation Within the Moisture Gradient

Ensatina was the only species with a significant response to the moisture gradient (tables 2 and 3). In both Cascade Range provinces, ensatina was most abundant in dry old-growth stands.