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Ecogeography of the herpetofauna of a northern California watershed: linking species patterns to landscape processes

Hartwell H. Welsh Jr, Garth R. Hodgson and Amy J. Lind

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Ecosystems are rapidly being altered and destabilized on a global scale, threatening native biota and compromising vital services provided to human society. We need to better understand the processes that can undermine ecosystem integrity (resistance-resilience) in order to devise strategies to ameliorate this trend. We used a herpetofaunal assemblage to first assess spatial patterns of biodiversity and then to discover the underlying landscape processes likely responsible for these patterns. Reptiles and amphibians are a phylogenetically diverse set of species with documented sensitivity to environmental perturbations. We examined ecogeographic patterns of these taxa in aquatic and riparian environments across the landscape mosaic of the Mattole River watershed of northern California, USA. We analyzed species distributions relative to three primary vegetation types (grassland, second-growth forest, late-seral forest) and two hydrologic regimes (perennial vs intermittent). We sought evidence for the processes behind these patterns by modeling animal distributions relative to multi-scale compositional, structural, and physical attributes of the vegetation or hydrologic type. Total herpetofaunal diversity was higher along perennial streams, with reptile diversity higher in mixed grassland. Amphibian and reptile richness, and reptile evenness, varied significantly among the three vegetations. Evidence indicated that distinct assemblages were associated with each end of a seral continuum. Four amphibians were more abundant in late-seral forest, while two amphibians and two reptiles were more abundant in second-growth forest, or mixed grassland, or both. Two amphibians were more abundant along intermittent streams. Models for predicting reptile richness, or abundances of the two amphibian assemblages, indicated water temperature was the best predictor variable. Based on these results and the physiological limits of several sensitive species, we determined the primary processes influencing faunal assemblage patterns on this landscape have been vegetation changes resulting from the harvesting of late-seral forests and the clearing of forest for pasture. Comparing past with present landscape mosaics indicated that these changes have transformed the dominant amphibian and reptile species assemblage from a mostly cold-water and cool forest-associated assemblage to one now dominated by warm-water and mixed grassland/woodland species.

H. H. Welsh Jr (hwelsh@fs.fed.us), G. R. Hodgson and A. J. Lind, U.S. Forest Service, Pacific Southwest Research Station, Redwood Sciences Lab., 1700 Bayview Dr., Arcata, CA 95521 USA (present address of A. J. L.: U.S. Forest Service Pacific Southwest Research Station, Sierra-Nevada Research Center, 2121 2nd St., Davis, CA 95616 USA).

A major challenge facing ecosystem science and natural resource management is the early detection of changes that threaten the natural resistance/resilience (Waide 1995) of ecosystems: changes that can threaten an ecosystem's ability to support healthy populations of its native assemblage of organisms (Naeem et al. 1994, Tilman et al. 1994). Although the analysis of ecological pattern and process across large landscapes is fraught

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with challenges (Ricklefs 1987, Cale et al. 1989, Conroy and Noon 1996), an increased focus on larger spatial scales has spawned a more integrative paradigm in ecology (Turner 1989, Levin 1992, Hansson et al. 1995). This integrative approach is generating new methods for solving problems that transcend multiple spatial and temporal scales (Edwards et al. 1993, Kareiva and Wennergren 1995, Roth et al. 1996). In this paper we present a synthetic approach for understanding ecosystem status and trends across broad spatial scales by integrating knowledge of the environmental relationships of multiple species and diverse higher taxa with information on landscape processes. The herpetofauna (reptiles and amphibians) are a phylogenetically remote group of vertebrate organisms that share a high degree of sensitivity to environmental perturbations (DaSilva and Sites 1995, Raxworthy 1996, Welsh and Ollivier 1998). Through a multi-scale analysis of their geographic relationships, it is possible to uncover shared, landscape-level patterns across large, diverse landscapes. By then modeling the environmental relationships that best describe the shared faunal patterns, and testing these candidate predictive models against independent environmental data describing the elements of the landscape mosaic at multiple spatial scales, it is possible to derive new qualitative insights into the processes behind the patterns (see Hilborn and Mangel 1997). Furthermore, by considering the resulting models in the context of the natural history of the individual species, one can further refine these insights and potentially identify the underlying causal mechanisms. Identifying these causal mechanisms is critical to formulating solutions for ameliorating negative effects.

Amphibian and reptile species are excellent indicators of environmental change and stress (Welsh and Ollivier 1998). Here we employed the entire herpetofaunal assemblage, and subsets of the more common species, to examine ecogeographic patterns and evaluate the nature and trends of ecosystem-level processes influencing the landscape mosaic. We reasoned that if a single species of amphibian or reptile can serve as a good metric of environmental change, investigating the entire assemblage would provide a complimentary and more comprehensive analysis of the ecological and anthropogenic processes interacting and influencing a landscape. Also, given that much of the herpetofauna have life histories requiring both terrestrial and aquatic environments, analyzing their multi-scale spatial patterns (micro-, meso-, and macro-geographic) can provide unique insights into the nature of the landscape processes that shape these patterns. Here we focus primarily on the results of our analysis of the macro-geographic relationships of the herpetofauna; relationships with landscape mosaic components or vegetation types. Together, these components comprise the landscape-level ecogeographic patterns of interest within the watershed. We used results from the analysis of finer scale environmental relationships (micro- and meso-geographic) of individual species to understand and interpret the most successful predictive models for the three species assemblages we discovered.

We first sought to examine how the species composition and relative abundances of the herpetofauna differed by vegetation type. Also, because many reptiles and most amphibians have a requirement for permanent water, we asked how species composition and abundance differed between intermittent and perennial streams. We then developed and tested predictive models to link animal patterns and environmental attributes. By establishing such linkages and evaluating them against available ecological and physiological data for individual species, we sought to develop hypotheses to explain landscape-level cause and effect relationships for the patterns uncovered. Studying the ecogeography of such a diverse set of vertebrate species also allows us to predict relative habitat value on this landscape mosaic for other, less tractable species whose natural histories and habitat requirements are similar.

To apply this approach we selected a representative watershed with a diverse reptile and amphibian fauna, a history of variable land uses including farming, ranching, and timber harvesting, but that still contained pristine natural areas. Our specific objectives were to: 1) quantify relationships between animal distributions and the patterns of plant assemblages and hydrology types (perennial versus intermittent streams); 2) to construct and evaluate sets of competing models, using independent data on the composition, structure, and physical attributes of the vegetation types to predict animal abundances; and 3) based on established animal-environment linkages, and knowledge of species' natural histories, hypothesize on the processes responsible for the observed patterns.

Study area

This work occurred within a 6th-order watershed, the Mattole River watershed (hereafter the Mattole), which has the climate and vegetation typical of interior watersheds of comparable size in northern California. The Mattole is a 789 km^2 watershed situated between 40°00′ and 40°30′ north latitude, and is the western-most major river valley in northern California and the continental U.S. (Welsh et al. 2005). It contains one of the few remaining free-flowing rivers in California. The Mattole is in a highly active fault zone, with a triple junction of major continental and oceanic tectonic plates under the Pacific Ocean just off the mouth of the river (McLaughlin et al. 1994). The steep terrain and close proximity to the Pacific Ocean, has resulted in portions of this river valley having the highest rainfall in the state (with

508 cm yr^{-1} at Honeydew, CA). However, the high, steep topography to the west largely insulates this valley from the marine influences of the Pacific Ocean, making the climate typical of other interior watersheds of the northern California Coast Range Mountains. Due to the complex terrain, and high floristic diversity, the Mattole supports a relatively diverse herpetofauna, with 27 species, including eight salamanders, three frogs, one toad, one turtle, five lizards, and nine snakes (Welsh and Hodgson 1997). Two major tributaries of the Mattole which drain primarily U.S. federal lands, Bear and Honeydew Creeks, have been designated for special management considerations (Anon. 1993), because they retain their native biota and, thus, have the potential to be refugia for species, especially salmonid fishes, that are in decline or have been extirpated in other parts of the Pacific Northwest.

Methods

Our study was focused on the riparian and aquatic environments of the Mattole because herpetofaunal diversity is usually greatest in these areas (Brode and Bury 1984). Our sample units were located in a set of tributary streams distributed among the three primary vegetation assemblages that dominate this landscape (Welsh et al. 2005). Using tributary streams for sampling had two primary advantages beyond the high potential diversity of herpetofauna: 1) the Mattole has ca 81 third- to fifth-order (Strahler 1964) tributaries, providing both a logical means to systematically distribute our sampling and large potential sample size; and 2) many tributaries contained both intermittent and perennial reaches, facilitating the study of the influence of stream permanence on the distribution of the herpetofauna.

Study design and reach placement

We initially used aerial photographs and ground reconnaissance to examine the vegetation of the Mattole. This approach revealed that three distinct, relatively homogeneous, vegetative assemblages dominated the landscape (later confirmed by analysis of plot data, Welsh et al. 2005): 1) grassland with interspersed second-growth forest (hereafter mixed grassland), 2) second-growth forest, and 3) late-seral forest. These three vegetation types were not equally distributed in the Mattole, with the first and second types being far more common than the third. Vegetation types varied in plant species composition, particularly in the relative amounts of conifers versus hardwood tree species. However, they were readily identifiable as distinct physiognomic types, and thus provided a suitable coarse-grained environmental matrix for systematically placing our sample units. We used this three-part vegetation mosaic to distribute our animal sampling units (hereafter "stream reaches" or "reaches") relatively equally across the Mattole. While the distribution of reaches was somewhat limited by access to private land, there were sufficient federal lands and enough cooperative landowners, that we were able to disperse our sample throughout the watershed.

During spring and summer of 1994–1996 we sampled 49 stream reaches in 31 Mattole tributaries, with both an intermittent and a perennial reach sampled in those tributaries where available (18 of 31). Each reach consisted of a randomly selected 300 m length of perennial or intermittent stream within each tributary. We defined an intermittent reach as containing flowing or standing water interspersed between segments of dry channel. However, for comparison of animal abundances among reach types, we established intermittent reaches so that they contained the same amount of wetted channel as the perennial reaches (300 m). This was accomplished by measuring the wetted portions of the channel and sampling in the same day. Reach starting points were determined by pacing a random distance between 1 and 100 m starting 50 m upstream from any road or trail access. Reaches were selected in sub-basins dominated (>80% cover) by one of the three primary vegetation types.

Sampling approach

Environmental variables

In each reach we measured or estimated environmental variables that characterized the surrounding sub-basin vegetation structure and composition (e.g. tree counts by size class, ground cover, etc.), in adjacent upslope and immediate streamside riparian areas, by sampling at mid-reach within both 1/10th (12.5 m radius) and 1/5th ha (25 m radius) circles centered on the reach (Welsh et al. 2005). These data were used to test the accuracy of our initial vegetation coverage classifications and to correct questionable reach assignments prior to the analysis of animal-habitat relationships. Once the accuracy of our reach classifications was confirmed, these data were used to ascertain important distinguishing features of the macro- and meso-environments within the three primary vegetation types. These distinguishing features among vegetation types then provided us with sets of potential variables for building predictive models of animal presence/abundance. Additionally, we measured variables that characterized microclimate in the riparian zone (soil and water temperatures, % canopy closure) because microclimates are critical determinants of habitat suitability for ectotherms (Magnuson et al. 1979, Huey 1991). The sampling of microclimates consisted of permanent stations with automated dataloggers (seven stations per reach, one water, six air and relative humidity) to continuously monitor water temperature (placed at tributary mouths at the bottom of deep pools with mixing water) and riparian air temperatures and relative humidities at a set of four reaches within each of the three vegetation types (Welsh et al. 2005).

Animal variables

Using a three-part sampling method, we recorded reptile and amphibian presence and abundance by species and developmental stage, along the 49 stream reaches. The three-part sampling approach consisted of: 1) timed searches (also known as visual encounter surveys; see Crump and Scott [1994]) of each 300-m reach, moving slowly upstream and recording all animals observed in the water, on shore, or in the adjacent riparian area, but without moving potential cover objects (number of observations/time), 2) an area-constrained search of streambed cover objects in three randomly chosen fast- and three slow-water habitats; each one meter long and stretching from bank to bank (number of observations/m^2), and 3) a one-half hour timed search of available seep and/or stream margin habitat, searching all cover (number of observations/time). This three-tiered approach was designed specifically to detect all of the potential species that can occur in the aquatic/riparian environments of the Mattole (Welsh and Hodgson 1997 for details). Forty-seven of these reaches were sampled in a single year (1995). A subset of 18 reaches was sampled in each of three years to examine annual variation. Using a one-factor ANOVA to analyze data from these reaches, we tested the null hypothesis that we would detect no differences among years in total captures by order or class (salamanders, frogs, amphibians, and reptiles) or in the total captures of the eight species we captured in sufficient numbers to test (captured at $\geq 25\%$ of reaches) (Appendix 1). In all cases we failed to reject the null hypothesis and thus included data from single reaches sampled in 1994 and 1996.

For intermittent reaches we counted animals only along the 300 m of wetted channel in order to compare captures for the same amount of aquatic habitat for each reach type. Animals observed along dry portions of intermittent reaches were recorded as incidentals only. Incidental records of animals seen during the collection of environmental data at each reach were also recorded. The incidental records were used only in analyses of species richness (Appendix 1).

Statistical analyses

Environmental variables

Thirty-five macro-environmental variables were examined in a series of discriminant analyses (DA). These variables were sorted into seven ecologically meaningful sets based on their characterization of structural, compositional, or climatic conditions at various levels of the forest environment. A separate DA was conducted on each set to test and correct reach assignments within the three primary vegetation categories. An identical process was used to examine thirty-three meso-environmental variables to determine which variables best distinguished riparian and channel conditions along reaches within the three vegetation types. Both of these analyses are described in detail in Welsh et al. (2005). Results of these analyses provided subsets of independent variables used to build models for predicting the occurrence of the different herpetofaunal assemblages found in the Mattole (see below).

Microclimate data were averaged for the same time periods at each datalogger station in each of four representative sites within each of the three vegetation types. We used data from the hottest period of the summer of 1997, to compare microclimatic regimes among the three vegetation types (details in Welsh et al. 2005). Our intent was to compare available microclimatic regimes within the riparian zones of each vegetation type with known physiological tolerances and behavioral patterns of particular species (cf. Huey 1991, Welsh et al. 2001) in order to help understand and explain the distribution patterns of the various herpetofaunal assemblages.

Animal variables

We examined the associations of vegetation type and hydrologic type with diversity of the total herpetofauna and class-level species richness (total number of species of reptiles or amphibians) and evenness (relative numbers of individuals of amphibians or reptiles) (Magurran 1988). We also examined these associations with individual species that were detected in at least 25% of our reaches (the minimum detection rate we considered sufficient for robust analysis). The 300 m reach was the unit of analysis. In the analyses of vegetation types and hydrologic regimes we used a single year's data per reach. Our research hypothesis was that we would find marked differences, in both the species compositions and relative abundances within species, depending upon both vegetation type and hydrologic regime. We used a two-factor analysis of variance (ANOVA; type III sums of squares) (Anon. 1990) to test the null hypotheses that there were no differences in diversity, class-level richness or evenness, or relative abundance for individual species, among vegetation cover types and hydrologic types. In the case of several species where captures were too low for ANOVA (detected at $<25\%$ of reaches or absent altogether from a vegetation type), we used proportions tests (Zar 1999). Here the proportion of sites in each vegetation type with detections for a given species was the response metric. In 18 of 31 tributaries we sampled multiple reaches. To avoid pseudo-replication (Hurlbert 1984) in our tests for differences in both vegetation type and hydrology, we used a single reach (either perennial or intermittent) from each tributary, drawn at random such that no two reaches were from the same tributary. In our analysis of species richness we included 119 incidental records (Appendix 1). We omitted one extreme outlier (Cowpie Creek), a reach sampled shortly after foothill yellow-legged frog egg masses had hatched, which resulted in an extremely high concentration of larvae. The α level for all tests was $p < 0.10$, which is considered appropriate for detecting ecological trends (Shrader-Frechette and McCoy 1993).

Predicting herpetofaunal assemblages

Those subsets of environmental variables that best discriminated between the three vegetation types at the macro- and meso-environmental scales (8 and 5 variables, respectively) (see Fig. 3 and 4 in Welsh et al. 2005) were used in an all-possible-subsets regression analysis (APS) to build sets of models for predicting richness or abundance of three different herpetofaunal assemblages. Two assemblages of amphibians, and one of reptiles, were apparent from the data (Appendix 1). Reptiles were primarily associated with second-growth forest and mixed grassland, and essentially absent from late-seral forest. Because reptile captures were low overall (Appendix 1), we used reptile species richness as the response variable in this analysis. Two amphibian assemblages were clearly distinguishable between the late-seral and the mixed grassland (Appendix 1). Data from the second-growth forest suggested that this vegetation type is a successional stage between the other two types, as it does not support a unique assemblage (except perhaps for the red-bellied newt; Appendix 1). For purposes of this analysis we used >15 captures overall, and/or significant differences in abundance to assign a given amphibian species to either of these two assemblages. The two assemblages were defined as: 1) mixed grassland-associated amphibians – rough-skinned newt, foothill yellow-legged frog, and the Pacific treefrog, and 2) late-seral forest-associated amphibians – coastal giant salamander, black salamander, southern torrent salamander, and the tailed frog (Appendix 1). The total number of amphibians of these species in each vegetation type became the response variable.

Predictive models, selected by APS, were ranked using the bias-corrected Akaike's Information Criteria (AIC_C), and Akaike weights (Burnham and Anderson 1998). Akaike weights estimate the relative competitiveness of the candidate models for fitting the dataset, given the models under consideration. Akaike weights were also used to estimate the relative importance of each environmental variable in the selected models by summing the weights of those models in which that variable occurred. We assessed goodness-of-fit using a cross-validation procedure (Fielding 2002).

Results

The macro-environment: primary vegetation assemblages of the Mattole

At the macro-environmental scale, the discriminant analysis (DA) of 35 environmental variables indicated pronounced differences among the three vegetation assemblages that dominate the Mattole (Fig. 1) (details in Welsh et al. 2005). The mixed grassland sites were distinguishable from the second-growth sites by the presence of more large hardwood logs in the former, and a more closed canopy in the latter (Fig. 1). The late-seral sites were distinguishable from the other two types by higher numbers of both small hardwoods and large conifers, higher elevations, fewer stumps, a lower percentage of conifer seedlings, and fewer small conifers (Fig. 1). While this analysis appears to support our initial aerial photo analysis of three distinct vegetation assemblages in the Mattole, it also indicates considerable overlap among them (Fig. 1). We believe this is evidence

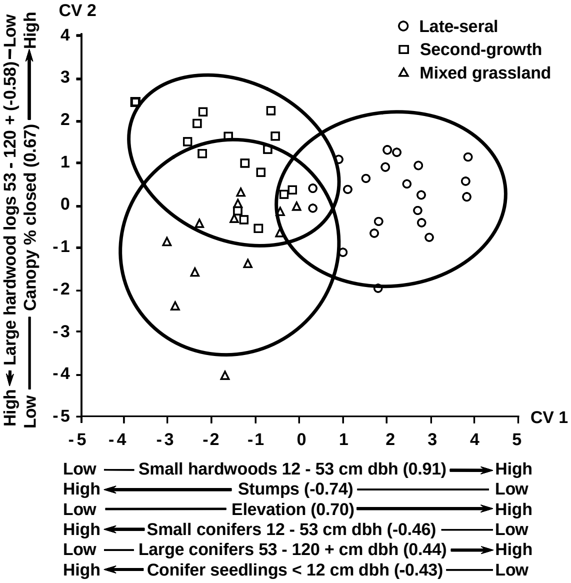

Fig. 1. Ninety-five percent confidence ellipses for 49 sites sampled within the three primary vegetation types of the Mattole. Canonical variable scores are based on a composite discriminant model derived from analysis of 35 macro-environmental variables measured adjacent to (upslope of) the 49 stream reaches sampled for herpetofauna from 1994 to 1996 (details in Welsh et al. 2005). The eight variables on the two canonical axes were those that best differentiated the structure and composition among the three vegetation types at the macro-environmental scale. Numbers in () are standardized coefficients which rank the variables relative to their influence on the discriminant function.

for a successional sequence from mixed grassland to more homogeneous second-growth, grading into late-seral forest. We suspect that the mixed grassland type, while possibly able to persist on unstable and south-facing slopes, is largely sustained on this landscape by frequent fires and livestock grazing.

The meso-environment: the riparian/aquatic environment

The DA of 33 variables measured in the riparian meso-environment of the three vegetation types indicated that the late-seral riparian is distinguishable from the other two types by less exposed soil, lower water temperatures, lower herb cover, and more boulders (Fig. 2). The riparian in the mixed grassland is distinguishable by having more exposed soil, higher water temperatures, more herb and grass ground cover, and fewer boulders in the stream channel (Fig. 2). The reaches within the second-growth shows a range of values along the first canonical variable (CV) axis midway between those of the other two vegetation types (Fig. 2); possibly further evidence of a seral continuum across these vegetation types in the Mattole.

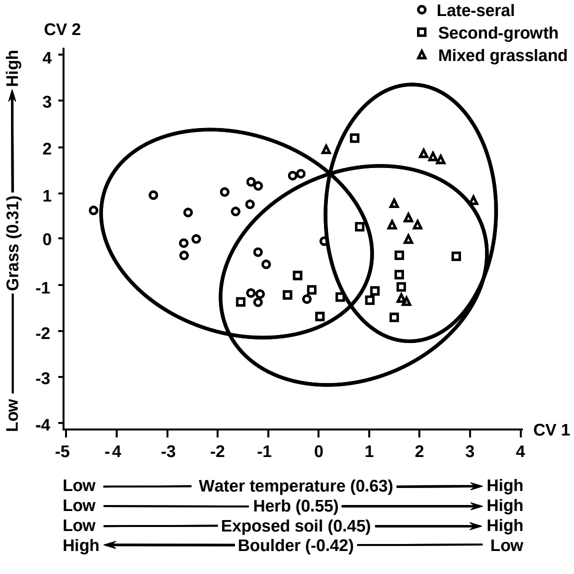

Fig. 2. Ninety-five percent confidence ellipses for 49 sites sampled in three primary vegetation types of the Mattole. Canonical variable scores are based on a composite discriminant model derived from analysis of 33 meso-environmental variables measured within the riparian zones of the 49 stream reaches sampled for herpetofauna from 1994 to 1996 (details in Welsh et al. 2005). The five variables on the two canonical axes were those that best differentiated riparian and stream channel conditions among the three vegetation types at the meso-environmental scale. Numbers in () are standardized coefficients which rank the variables relative to their influence on the discriminant function.

The micro-environment: microclimates within primary vegetation types

Analysis of microclimatic scale water temperature data revealed pronounced differences among vegetation types, with late-seral stream reaches colder, and with lower daily amplitudes, than either second-growth or mixed reaches (see Fig. 3). Air temperature and relative humidity regimes within vegetation types were also dramatically different among vegetation types (see Fig. 5a and b, respectively, in Welsh et al. 2005).

Composition of the herpetofauna

We sampled 22 species of reptiles and amphibians including six species that were recorded as incidentals (used only in the analysis of richness) (Appendix 1). Four snake species and one turtle not detected during this project are also found in the Mattole (see Welsh and Hodgson 1997).

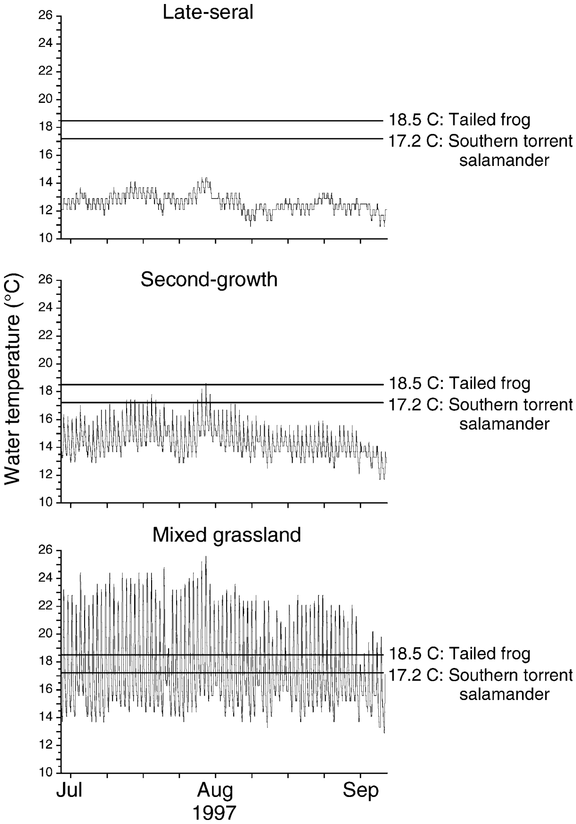

Fig. 3. Water temperature (°C) profiles from the summer of 1997 from three streams, each chosen as representative of streams transecting the following: late-seral, second-growth, and mixed grassland. The solid horizontal lines represent initiation of thermal stress for tailed frog eggs (i.e. cessation of development [Brown 1975]), and adult southern torrent salamanders (i.e. compromised mobility [Welsh and Lind 1996]).

Differences among vegetation types and hydrologic regimes

We found higher diversity (Shannon Index) of herpetofauna along perennial compared to intermittent stream reaches (Table 1). Reptile richness (Fig. 4a), and evenness were significantly greater in the mixed grassland (Table 1). In contrast, amphibian species richness was higher in the late-seral versus the second-growth forest type, but evenness did not differ among vegetation types (Table 1, Fig. 4b). We found no evidence of an interaction effect between forest type and hydrologic regime for any of the herpetofaunal assemblages or the individual species tested (Table 1).

With ANOVA of individual species, we found two of the three most frequently detected amphibians, the coastal giant salamander *Dicamptodon tenebrosus* and the black salamander *Aneides flavipunctatus*, were significantly more abundant in the late-seral versus the mixed grassland (Table 1). These two salamanders were also significantly more abundant along intermittent stream reaches (Fig. 5a and b). The other commonly detected amphibian, the foothill yellow-legged frog *Rana boylii*, was more abundant along the open, sunny reaches of mixed grassland streams compared with second-growth and late-seral types (Table 1).

We also identified differences in occurrence by vegetation type for the five species detected infrequently in our study area (Table 2). The torrent salamander *Rhyacotriton variegatus* was more often found in the late-seral forest than in the mixed grassland (Fig. 6a), while the rough-skinned newt *Taricha granulosa* was more often found in the second-growth and mixed grassland than in late-seral forest (Table 2). The tailed frog *Ascaphus truei* was found only in late-seral forest (Fig. 6b). The two most common reptiles, and the only two with sufficient detections to test for differences, the western fence lizard *Sceloporus occidentalis* and the Pacific Coast aquatic garter snake *Thamnophis atratus*, were both found more often in mixed grassland compared to late-seral forest, with the garter snake also found more often in second-growth compared to late-seral forest (Table 2).

Predicting herpetofaunal assemblages

For each of three herpetofaunal assemblages, we initially evaluated the five best (based on R^2_{adj}) APS models. Each group of models was comprised of sets of environmental variables from the vegetation analysis (Welsh et al. 2005) that best predicted the richness (reptiles) or abundance (amphibians) of that assemblage. We present the best model for each of the three assemblages, and those models that ranked within two AIC_C units of the best model (Table 3). We found five competing models (i.e. within two AIC_c units) for predicting reptile species richness, with Akaike weights ranging from a high of

Table 1. Two-factor analysis of variance (ANOVA) of herpetofaunal assemblage, or individual species, by vegetation cover (L = late-seral, S = second-growth, M = mixed grassland) and intermittent vs perennial stream (P = perennial, I = intermittent) with Tukey multiple comparisons (alpha <0.1). * 0.1–0.01, ** <0.01–0.001. For factors V = vegetation type and IP = intermittent vs perennial stream reach[1]. See Appendix 1 for effect sizes.

Dependent variable	Factor	DF	MSE	F	p	Multiple comparisons
Shannon index						
Total herpetofauna	vegetation type	2	0.027	0.19	0.82	
	intermittent/perennial	1	0.594	4.27	0.049*	P > I
	V × IP	2	0.012	0.09	0.91	
Richness	vegetation type	2	7.031	3.77	0.03*	L > S
Amphibians	intermittent/perennial	1	0.145	0.08	0.78	
	V × IP	2	0.048	0.03	0.97	
Reptiles	vegetation type	2	7.900	4.95	0.02*	M > L
	intermittent/perennial	1	0.037	0.02	0.88	
	V × IP	2	0.128	0.08	0.92	
Evenness						
Amphibians	vegetation type	2	0.008	0.10	0.90	
	intermittent/perennial	1	0.205	2.38	0.14	
	V × IP	2	0.041	0.48	0.62	
Reptiles	vegetation type	2	0.650	4.85	0.02*	M > S
	intermittent/perennial	1	0.000	0.00	0.97	
	V × IP	2	0.000	0.00	0.97	
Species abundances						
Coastal giant salamander	vegetation type	2	640.446	4.50	0.02*	L > M
	intermittent/perennial	1	746.740	5.25	0.03*	I > P
	V × IP	2	195.143	1.37	0.27	
Black salamander	vegetation type	1	1.244	4.48	0.02*	L > M
	intermittent/perennial	2	0.912	3.29	0.08*	I > P
	V × IP		0.133	0.48	0.62	
Foothill yellow-legged frog	vegetation type	2	8.021	8.47	0.002**	M > S, M > L
	intermittent/perennial	1	1.902	2.01	0.17	
	V × IP	2	0.273	0.29	0.75	

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[1] Cell sizes were as follows: perennial late-seral = 8; perennial second-growth = 4; perennial mixed grassland = 4; intermittent late-seral = 6; intermittent second-growth = 4; intermittent mixed grassland = 5.

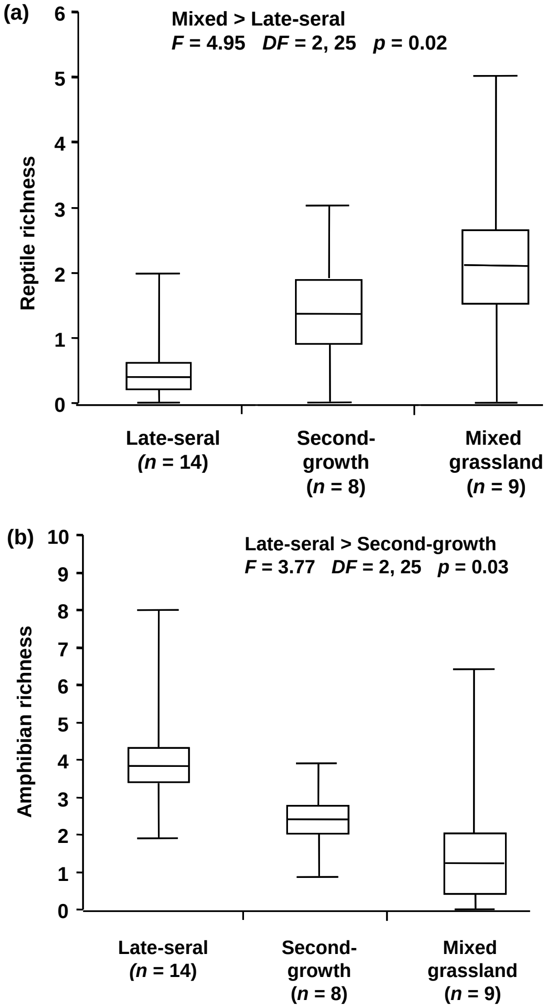

Fig. 4. Comparison of (a) reptile and (b) amphibian richness (number of species) relative to the three primary vegetation types in the Mattole watershed. Box and whisker plots depict the mean, plus or minus one standard error, and the range of each response variable.

0.36 down to 0.14, with model accuracy range from 0.87 to 0.91 (Table 3). These models explained 33–38% of the variation in reptile richness (Table 3). The importance of the covariates in the best models, estimated by calculating the sum of Akaike weights of models in which each occurred, were as follows: water temperature 0.99, grass 0.99, stumps 0.84, herbs 0.30, small hardwoods 0.19, and large hardwoods 0.14. Only one model was competitive for predicting the abundance of mixed grassland-associated amphibians. This model explained 43% of the variation in the abundance of this assemblage, with an accuracy of 0.79 (Table 3). Three models were competitive for predicting the abundance of late-seral-associated amphibians, with Akaike weights ranging from 0.22 to 0.51, and model accuracy ranging from 0.83 to 0.91 (Table 3). The relative importance of covariates were as follows: water temperature 0.98, elevation 0.98, grass 0.73, small conifers 0.25, stumps 0.25, and conifer seedlings 0.22.

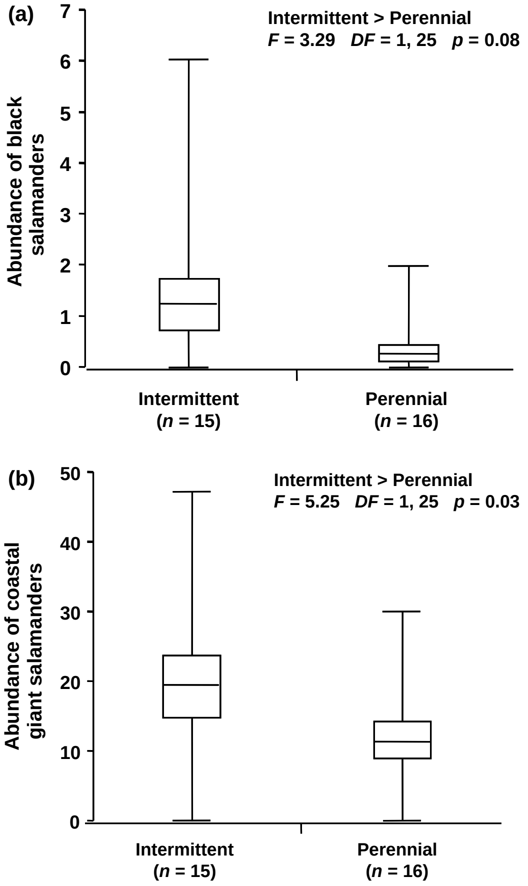

Fig. 5. Abundances of (a) black salamanders *Aneides flavipunctatus* and (b) larval coastal giant salamanders *Dicamptodon tenebrosus* relative to hydrologic regime (perennial or intermittent) in the Mattole watershed.

In two of the preceding analyses, several models were estimated to be highly competitive as best-fits to the sample data. Based on the prediction interval criterion with cross-validation, all models provided a reasonable fit. Therefore, a weighted average of predicted values,

Table 2. Significant ($p < 0.05$) proportion tests of reptiles and amphibians relative to vegetation cover type (L = late-seral, S = second-growth, M = mixed grassland). See Appendix 1 for effect sizes.

Species	Q	Result
Southern torrent salamander	4.23	L > M
Rough-skinned newt	−3.55	S > L
"	−4.10	M > L
Tailed frog	5.38	L > S
"	5.63	L > M
Western fence lizard	−4.09	M > L
Pacific Coast aquatic garter snake	−3.55	S > L
"	−4.10	M > L

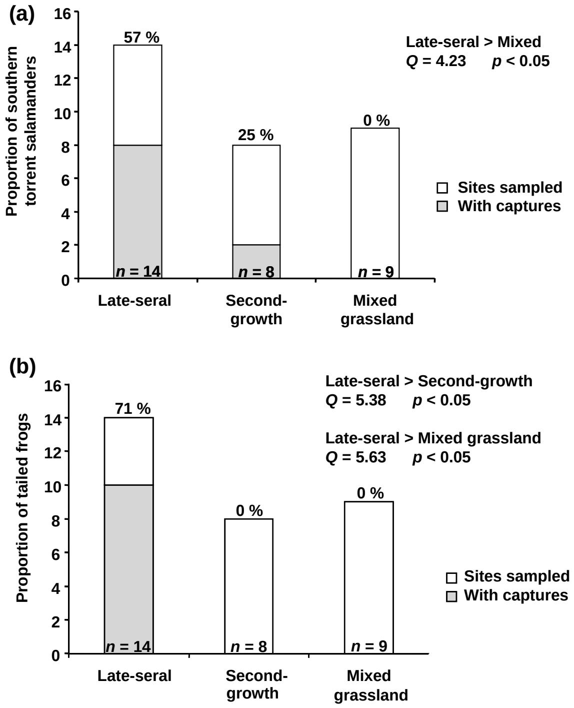

Fig. 6. Proportion of stream reaches with (a) southern torrent salamanders *Rhyacotriton variegatus* and (b) tailed frogs *Ascaphus truei* within each of the three primary vegetation types in the Mattole watershed. Only significant test results are presented.

based upon all of the competing models and their Akaike weights, could be used to provide predictive values for assemblage response. In two of the assemblages (the reptile richness and mixed grassland amphibians) water temperature (here positive with reptile richness and amphibian abundance) was the best single variable, entering all models (Table 3). In both cases, other variables represented more open, warmer environments (e.g. more grass, more herbs, more stumps, fewer hardwoods, less upland canopy) (Table 3). In the late-seral-associated amphibians, water temperature (here a negative relationship), and elevation were equivalent predictors of higher abundances (Table 3). The models for late-seral-associated amphibians contained additional variables indicative of more closed habitats (e.g. a negative relationship with grass, stumps, and conifer seedlings, and a positive relationships with small conifers trees [Table 3]).

Discussion

Linking ecogeographic patterns and landscape processes

First considerations

Because of low mobility and physiological constraints common to most amphibians and reptiles, understanding how distributions are linked with landscape-scale patterns requires examining differences among coarse-scale vegetation mosaic patches that can influence conditions at finer scales of resolution (Pope et al. 2000). Herpetofauna are mostly small, relatively sedentary vertebrates with localized territories or home ranges (Swingland 1983, Sinsch 1990). Consequently individuals are most immediately influenced by conditions at the meso- and micro-environmental scales (Dunham et al. 1989, Huey 1991). Their size and mobility limit

Table 3. The best-approximating models for the herpetofaunal assemblages associated with each end of the seral continuum in the Mattole; late-seral forest and mixed grassland (Appendix 1). Thirteen environmental attributes that best discriminated among the three vegetation types that comprise the continuum (Tables 3 and 5; Welsh et al. 2005) were used in an all-possible-subsets regression analysis (best five models selected based on R^2 [adj.]) to determine those sets of features that best predicted: I) reptile species richness[1], II) numbers of mixed grassland associated-amphibians[2], III) numbers of late-seral forest associated-amphibians[2]. Listed are the best-fitting models for each assemblage, as measured by AIC_C, and all models within 2 AIC_C units of the best model. The Δ AIC_C indicates the difference in the AIC value of a given model and the AIC_C of the best-fitting model. The symbols "+" and "−" indicate the direction of influence of the variables on richness or abundance. The coefficient of determination (R^2) for each model is provided for comparison.

Model covariates	Δ AIC_C	Akaike weight	R^2 (adj.)	Cross-validation
I) Reptile species richness				
Water temperature (+) grass (+) stumps (+)	0.00	0.36	0.38	0.91
Water temperature (+) grass (+) stumps (+) small hardwoods (−)	1.27	0.19	0.38	0.87
Water temperature (+) grass (+) herb (+)	1.71	0.15	0.35	0.90
Water temperature (+) grass (+) stumps (+) herb (+)	1.79	0.15	0.37	0.87
Water temperature (+) grass (+) stumps (+) large hardwoods (−)	1.82	0.14	0.33	0.90
II) Mixed grassland associated-amphibians				
Water temperature (+) grass (+) upland canopy (−)	0.00	1.0	0.43	0.79
III) Late-seral associated-amphibians				
Water temperature (−) elevation (+) grass (−)	0.00	0.51	0.43	0.91
Water temperature (−) elevation (+) stumps (−) small conifers (+)	1.39	0.25	0.44	0.83
Water temperature (−) elevation (+) grass (−) conifer seedlings (−)	1.50	0.22	0.43	0.89

[1] Presence/absence of reptile species includes incidentals (see Appendix 1).

[2] Counts of each species with >15 captures in either the late-seral (coastal giant salamander, southern torrent salamander, black salamander, and tailed frog), or mixed grassland (roughskin newt, Pacific treefrog, foothill yellow-legged frog).

their options for coping with adversity because, unlike larger, more mobile species, they cannot readily escape adverse conditions that persist at coarser scales. Also, because many of the species we studied have aquatic larvae, they are unable to move below ground or into large decomposing logs to avoid climatic extremes.

Furthermore, the physiological constraints of reptiles and amphibians imposed by their ectothermy strongly influence their ability to forage, reproduce, and survive. The essence of these constraints is that herpetofauna require micro-environmental conditions that allow them to regulate both body temperature and body moisture through behavioral responses to the external environment because they lack internal controls for these biophysical parameters (Dunham et al. 1989, Hutchison and Dupre 1992, Rome et al. 1992). These physiological constraints have profound implications because they limit when and where these animals can exist and thrive on the landscape (Brattstrom 1979, Magnuson et al. 1979, Huey 1991). Determining where and how these constraints manifest along environmental gradients can provide critical information on habitat relationships and lead to useful new hypotheses on how such mechanisms may determine incidence and abundance (Morrison 2001). Consequently, in order to understand and explain the differences we detected in the distributions of herpetofaunal assemblages in the Mattole, we focused our attention on finer-scale variation we detected within primary vegetation types, particularly differences in microclimatic regimes. We found confirmation for the validity of this approach in the emergence of water temperature as an important predictor variable (either positive or negative) in all of our assemblage models (Table 3).

Reptiles

The greater richness and evenness of reptiles in the mixed grassland versus late-seral vegetation (Table 1, Fig. 4a) is best explained by the propensity of reptiles to bask, a means of thermoregulation (Huey 1982), and the presence of more open, exposed habitats in the mixed grassland (Fig. 1 and 2). Both the western fence lizard and the Pacific Coast aquatic garter snake are heliotherms that bask to raise body temperatures before they can forage.

Amphibians

In contrast, amphibians had higher species richness in late-seral compared with second-growth forests (Table 1, Fig. 4b). However, several species were not more abundant in the late-seral forests. The foothill yellow-legged frog was more abundant along streams in the mixed grassland compared with the other vegetations (Table 1). This frog is a basking species more common along open, riffle-dominated streams (Hayes and Jennings 1988, Lind and Welsh unpubl.), where it readily moves among micro-environments to thermoregulate. The rough-skinned newt was more abundant in second-growth and mixed grassland compared with late-seral (Table 2). This salamander migrates to ponds and streams in the spring to breed. We believe that this pattern may reflect the selection of more open, warmer streams that enhance egg and larval development (Feder and Burggren 1992).

The remaining amphibian species occurred in a pattern consistent with the selection of cooler, moister environments like those found along late-seral streams (Tables 2 and 3, Fig. 4a and b). The black salamander is a member of the family Plethodontidae, a mostly terrestrial family that requires cool, moist environments (Spotila 1972, Feder 1983). While this is the first report of the black salamander being more abundant in late-seral forest compared with other vegetation types, many other plethodontid species have been reported to decline when forest structure is altered or canopy removed (Welsh and Droege 2001).

Our finding of higher abundances of coastal giant salamanders in streams in late-seral forest compared with those in the mixed grassland (Table 1) is consistent with some earlier findings (Corn and Bury 1989), but not others (Murphy and Hall 1981, Murphy et al. 1981, Welsh and Lind 2002). Corn and Bury (1989) speculated that the differences they found were due to the loss of streambed substrate interstices caused by siltation from logging. Welsh and Ollivier (1998) also found a negative impact of fine sediments on giant salamander abundances in the relatively low gradient streams they sampled. High gradient streams have a greater propensity to flush, rather than store, fine sediments compared with low gradient streams (Murphy and Hall 1981, Hawkins et al. 1983). The differences in giant salamander abundances we found may be related to a difference in stream gradient (and the related ability to flush fine sediments) among the reach sets (see Table 2, fine sediments; in Welsh et al. 2005). The late-seral streams had significantly higher gradients (mean percent slope = 18.57 [SD = 11.88]) than the mixed grassland streams (mean percent slope = 7.83 [SD = 9.92]) (Kruskal-Wallis ANOVA; $\chi^2 = 9.00$, $p = 0.011$). While this explanation is one possibility, it also may be that the differences in giant salamander abundances are a response to higher stream temperatures, with many of the grassland streams exhibiting significantly higher temperatures (mean °C = 15.98 [SD = 2.56]) compared with both the second growth (mean °C = 13.55 [SD = 2.16]), and the late-seral streams (mean °C = 12.75 [SD = 1.68]) (Kruskal-Wallis ANOVA; $\chi^2 = 14.25$, $p = 0.0008$), with the warmest streams being absent of giant salamanders altogether.

The occurrence of the tailed frog and southern torrent salamander, both species of special concern in California (Jennings and Hayes 1994), in a significantly higher proportion of reaches within late-seral versus mixed grassland, and the occurrence of tailed frogs in a higher proportion of late-seral versus second-growth reaches (Table 2), is also likely a result of physiological constraints. Welsh and Lind (1996) reported on a laboratory experiment investigating thermal tolerances of adult southern torrent salamanders which indicated that the first signs of thermal stress (compromised mobility) occurred at 17.2°C. When this threshold is examined graphically against our stream temperature data from the three vegetation types, it is clear that only late-seral streams provide a thermally stress-free summer aquatic environment for this salamander (Fig. 3). Some second-growth streams may provide a thermally suitable environment in the summer, but our representative stream exceeded the critical threshold during both July and August of 1997 (Fig. 3), a typical summer for the Mattole. We believe these data provide the most parsimonious explanation for the lack of torrent salamanders in mixed grassland, and their rare occurrence in second-growth streams of the Mattole (Table 2, Fig. 6a).

While tailed frogs are well distributed in some second-growth forests in cool coastal areas (Diller and Wallace 1999), this is not the case in the Mattole. Tailed frog eggs cease to develop at 18.5°C (Brown 1975). These frogs typically lay their eggs under streambed boulders and cobbles in the spring and they develop over the summer, hatching from late summer into fall (Karraker and Beyersdorf 1997). Based on our representative stream temperature data, only under conditions found in late-seral forest streams in the Mattole is it possible for tailed frogs to reproduce (Fig. 3). Consequently, we believe that differences in water temperature regimes among vegetation types best explains the absence of tailed frogs in mixed grassland and second-growth streams (Table 2, Fig. 6b).

Herpetofauna and ecosystem processes

Forest succession

The patterns of distribution of reptiles and amphibians in the Mattole reflect a watershed in transition, where the once dominant late-seral Douglas-fir/mixed hardwood forests have been nearly eliminated on a landscape altered by intensive forestry practices, conversions of forest lands to agricultural uses, and the proliferation of small homesteads. Such changes are now typical of most watersheds in northwestern California. This process of habitat alteration can have profound effects on native species, with some species likely to increase (e.g. those predisposed to more open habitats and early succession forests), while others are likely to decline (Andren 1994, Wiens 1996). The remaining late-seral forests of the Mattole now cover 4965 ha, or ca 7% of the landscape they covered in 1943 (Mattole Restoration Council 1988; see Fig. 7 in Welsh et al. 2005). Late-seral associated amphibians are presently restricted to the few remaining late-seral stands that still exist in the higher more remote areas of the watershed (note that elevation is as good a predictor of this amphibian assemblage as water temperature [Table 3]).

The overlap in composition between the second-growth forest assemblage and both the reptiles and the late-seral amphibian assemblages (Appendix 1), is consistent with our interpretation of a successional continuum existing across the primary vegetation types (Fig. 1 and 2). The probable continuation of the anthropogenic process of conversion of this landscape to earlier successional stages suggests that the relative abundances of the second-growth and mixed grassland assemblages will shift back and forth through time as the second-growth forest is harvested and re-grows, and as the creation and abandonment of agricultural lands continues. This scenario has historical precedence as both indigenous people and early European settlers used fire to promote grasslands in the Mattole (Roscoe 1985, Blackburn and Anderson 1993).

Perennial versus intermittent hydrology

Many biotic and abiotic attributes of a stream ecosystem change in a predictable manner along the stream continuum from headwaters down through higher order channels (Vannote et al. 1980, Ward 1998). We believe our finding of a greater diversity of herpetofauna along perennial versus intermittent reaches (Table 1) is a reflection of the fact that perennial reaches occur more often in the downstream portions of drainages. As a result, perennial reaches, in addition to the enhancing effects of reliable flowing surface water on biodiversity, also tended to contain greater riparian and aquatic habitat heterogeneity that manifests from the effects of the relatively more complex downstream geomorphological and hydrologic processes (Montgomery 1999). Both factors then, while not unrelated, would contribute to supporting a greater diversity of amphibians and reptiles downstream. Intermittent channels, on the other hand, are more often encountered toward the upper end of the stream continuum, and are typically less complex as a result of fewer and simpler structuring processes at work (Montgomery 1999).

Relative to perennial versus intermittent hydrology, we report differences in abundance of two species, the black salamander and the coastal giant salamander (Table 1, Fig. 5a and b). Our results are, in fact, the first reports of significant differences in abundance for these two species, relative to both hydrologic regime and forest type and suggest that intermittent reaches may play an important role in some key aspects of their natural history. While this question is in need of further study, there are several considerations that may be informative here. Our sample of black salamanders consisted almost entirely of juveniles that occurred in association with the stream bank and seep searches. While this species is terrestrial, and usually not associated with flowing water, it may be that either the young migrate to the cool, damp, shaded areas of these intermittent reaches subsequent to hatching from the eggs, or the adult females lay their eggs adjacent to intermittent streams. In either case, juvenile black salamanders, which are small and thus highly susceptible to desiccation (Feder 1983), would have a higher probability of survival in these damp areas. Female coastal giant salamanders appear to seek headwater areas for egg deposition (Nussbaum 1969), even in those areas not impacted by a history of timber harvest (Welsh unpubl.). Headwaters may be sought by females because of reduced predation from other species and from larger conspecifics of this highly cannibalistic species (Petranka 1998). Because headwater areas are also often associated with intermittent reaches, giant salamanders may be benefiting from the channel disjunctions. The dry channel segments would discourage movement of aquatic predators such as fishes and larger aquatic salamanders, thus enhancing the survival of eggs and larvae. There also may be more dependable cold ground water present in headwater areas to assure that eggs remain viable. In either case, headwater areas may be critical to maintaining viable populations of these salamanders so that basin-level processes and anthropogenic activities that alter stream hydrology (Keppler and Brown 1998) should be carefully evaluated in watersheds where these species occur.

Succession versus hydrology

With the exception of the black and coastal giant salamanders, the other headwater specialists we detected (i.e. tailed frog, torrent salamander) occurred equally along both intermittent and perennial reaches. However, because all of these species occurred in higher abundances in our late-seral reaches, it is important to examine the relative importance of intermittent hydrology and late-seral forest, both conditions which exist almost exclusively higher in the stream continua in the Mattole as a result of past land use practices. From the perspective of the natural histories and physiologies of the native headwater amphibian species, it is clear that cold water is a vital requisite (Welsh and Lind 1996, 2002), as was also born out by our modeling exercise (Table 3). This appears to be the case regardless of hydrologic regime because these species were detected almost exclusively in late-seral environments (Appendix 1), yet only two of the four showed any relationship with hydrology (Table 1). Consequently, we believe the unique microclimatic environments of late-seral forests outweigh the importance of an intermittent hydrology. In the Mattole, the equable microclimates required by cold-water adapted amphibians (Brown 1975, Welsh and Lind 1996, 2002) are currently found almost exclusively in the late-seral vegetation (Fig. 3 herein and Fig. 5a and b in Welsh et al. 2005). This link between late-seral stage forest and cool and stable forest and stream microclimates is well established (Brosofske et al. 1997, Chen et al. 1999).

Of particular concern is our finding that the tailed frog and the southern torrent salamander are both found almost exclusively in late-seral headwater reaches of the Mattole, rarely occurring further down the stream continuum. Earlier research established a close link between the presence of these two species and late-seral forests in northern California (Welsh 1990, Welsh and Lind 1996, 2002), and their distributions in the Mattole indicates that here they are indeed closely linked to these environments (Fig. 6a and b). However, late-seral habitats were more common in the past, and not until very recently have they been restricted, as appears to be the case in the Mattole, in such a manner as to possibly preclude gene flow for headwater species. Aquatic predators, such as fish, and changing aquatic and riparian microclimates may be playing a role in shaping these distribution patterns (Lowe 2002). Late-seral forests with microclimates that can support these species have retreated up the drainages as the lower elevation forest has been harvested, making late-seral vegetation types among the rarest environments in the Mattole (see Fig. 7 in Welsh et al. 2005). Fish and other aquatic predators occupy downstream reaches which further limit the potential for migration and gene flow among headwater sub-populations of these amphibians. Current conditions may already preclude gene flow and long-term viability for these headwater amphibians in the Mattole, and we may be witnessing a watershed level extinction event in progress (Tilman et al. 1994).

Conclusions

Little data are available on how various reptiles and amphibians respond to major land-use practices across broad landscapes (Semlitsch and Bodie 2003). To derive a clear understanding of how landscape dynamics from natural or anthropogenic processes influence the distributions of these small vertebrates is challenging because one must consider and integrate a range of potential spatial and temporal scales (Levin 1992). Yet conservation or management strategies for promoting the viability of these species should consider both local and landscape dynamics (Semlitsch 2000). Furthermore, the establishment of these linkages renders these highly sensitive species particularly useful management tools as indicators of ecosystem perturbations and stress.

Suitable thermal environments are an essential element determining fitness in populations of ectotherms (Huey and Kingsolver 1989). In the Mattole we found that the composition of the riparian and aquatic herpetofauna varied greatly across the seral continuum.

Four amphibians were significantly associated with the remaining late-seral environments and three were associated with more open forests/grasslands. While these faunal differences may appear on the surface to be directly related to differences in vegetation structure, the actual underlying process is somewhat more complex, having to do with the modification of climate by forest structure differentially during succession, as temperatures (air and water) and moisture (relative humidity) vary greatly depending upon seral stage (Fig. 3, Chen et al. 1999). In our companion study (Welsh et al. 2005) we also found that at a larger spatial scale, both the stage and the extent of vegetation greatly influenced the aquatic and riparian microclimates within entire sub-basins, particularly water and air temperature.

We see parallels between our work and that of Lomolino and Perault (2000), who investigated mammal communities in a fragmented temperate rainforest on the Olympic peninsula of Washington. They found the mammal community dramatically altered in both second-growth forests and clear cut areas when compared with late-seral. Similarly, we found that the herpetofaunal assemblages of second-growth forests and mixed grasslands constituted nonrandom subsets of the regional species pool which differed significantly from the assemblage of the old-growth forest. In our case, the apparent decline of the late-seral assemblage in the Mattole is followed by the occurrence of species either more tolerant of, or adapted to, more open, warmer habitats. As with the mammals of the Olympic peninsula (Lomolino and Perault 2000), the herpetofaunal assemblages of the second-growth and grassland areas of the Mattole showed little evidence of converging on the environmental characteristics and assemblage structure of the old-growth forest. This may be because these late-seral forest communities have low resilience and take centuries to develop or recover (Peterson et al. 1997). Consequently, it appears that the late-seral-associated amphibian assemblage of the Mattole is unlikely to persevere unless the remaining remnant late-seral stands are protected, and efforts are made to recover habitat connectivity sufficient for these amphibians to allow migration between isolated stands (but see Harrison and Bruna 1999). The late-seral forests that remain in the Mattole are $<7\%$ of what was historically present (Fig. 7 in Welsh et al. 2005).

The requirement of many amphibians for more than one habitat during their life cycle makes them particularly vulnerable to the impacts of habitat alterations (Pope et al. 2000). For example, Findlay and Houlahan (1997) demonstrated strong effects of landscape composition on wetland species richness out to ≥ 2 km in the landscape surrounding wetlands. The changes that are altering the landscape of the Mattole are consistent with the larger pattern of habitat modification considered one of the major causes of amphibian declines worldwide (Collins and Storfer 2003, Stuart et al. 2004). The decline or loss of highly sensitive species is one of the first signs of an ecosystem in stress (Rapport and Regier 1995). The scattered remnant populations of several species (i.e. tailed frog, southern torrent salamander) in the Mattole are evidence of their being more widely distributed in the past. The few small populations of these species now appear to be sufficiently isolated from one another by distance that they are likely nearing extinction in this watershed (Johnson 1998). These fragmented distributions are the legacy of the large-scale anthropogenic alteration of much of the watershed (Tilman et al. 1994, Harding et al. 1998). The negative impacts of anthropogenic landscape modifications on a wide range of native fauna is now well understood (Saunders et al. 1991, Andren 1994, Fahrig and Merriam 1994, Wiens 1996), and evidence such as reported here indicates that entire amphibian (Tocher et al. 1997, Semlitsch 2000) and reptile (Driscoll 2004 and cites therein) assemblages are clearly effected.

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Appendix 1. Total detections and detections per reach (), reported by primary vegetation type, for species sampled along 49 stream reaches in the Mattole watershed. Forty-seven reaches were sampled in 1995, and one each in 1994 and 1996. * Species encountered incidentally and used only in the analysis of species richness (see text). ** Species encountered in numbers too low for statistical analyses (<25% of reaches) and used only in the analysis of species richness (see text). Bolded count values indicate the species is most associated with that vegetation type.

Taxa	Late-seral (n =21)	Second-growth (n =16)	Mixed grassland (n =12)
Amphibians			
Coastal giant salamander *Dicamptodon tenebrosus*	**456 (21.71)**	232 (14.50)	78 (6.50)
Black salamander *Aneides flavipunctatus*	**21 (1.00)**	5 (0.31)	1 (0.08)
Southern torrent salamander *Rhyacotriton variegatus*	**19 (0.90)**	3 (0.19)	0 (0.00)
Ensatina *Ensatina eschscholtzii**	3	0	0
Wandering salamander *Aneides vagrans**	10	0	0
Calif. slender salamander *Batrachoseps attenuatus***	3	0	0
Rough-skinned newt *Taricha granulosa*	0 (0.00)	27 (1.69)	**148 (12.33)**
Red-bellied newt *Taricha rivularis***	0	14	3
Tailed frog *Ascaphus truei*	**41 (2.00)**	2 (0.13)	0 (0.00)
Pacific treefrog *Hyla regilla***	0	1	**27**
Foothill yellow-legged frog *Rana boylii*	18 (0.86)	43 (2.69)	**555 (46.25)**
Western toad *Bufo boreas***	0	0	1
Reptiles	0	3	3
Western skink *Eumeces skiltonianus***			
Western fence lizard *Sceloporus occidentalis*	0 (0.00)	3 (0.18)	**26 (2.17)**
Northern alligator lizard *Elgaria coerulea**	0	4	0
Southern alligator lizard *Elgaria multicarinata**	1	0	0
Pacific Coast aquatic garter snake *Thamnophis atratus*	0 (0.00)	6 (0.38)	**11 (0.92)**
Common garter snake *T. sirtalis***	1	2	5
Western terrestrial garter snake *T. elegans***	2	1	0
Ring-necked snake *Diadophis punctatus***	0	1	0
Rubber boa *Charina bottae**	0	1	0
Gopher snake *Pituophis catenifer**	0	0	1