Spatial relationships in a dendritic network: the herpetofaunal metacommunity of the Mattole River catchment of northwest California

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We investigated the aquatic and riparian herpetofauna in a 789 km^2 river catchment in northwest California to examine competing theories of biotic community structuring in catchment stream networks. Research in fluvial geomorphology has resulted in multi-scale models of dynamic processes that cyclically create, maintain, and destroy environments in stream networks of mountain catchments. These models have been applied to understanding distributions of invertebrates, algae, fishes and their habitats across entire basin networks, but similar approaches with herpetofauna are rare. We examined multi-scale spatial patterns of multiple species as they related to variation in channel types, channel settings, and within-channel attributes that result from these processes. From 83 reaches distributed randomly throughout the watershed, we distinguished four channel types: 1) high gradient with cascade structure; 2) 2–4% gradient with step-pool structure controlled by moderately steep valleys; 3) slightly entrenched, lower gradient, plane-bed structure; and 4) low gradient, shallow, unconfined, multiple or migrating pool/riffle channels in broad alluvial valleys. The composition of herpetofauna differed in five of six pair-wise comparisons among these channel types, indicating a minimum of three distinct mesoscale assemblages. We used non-parametric multiple regression (NPMR) to examine relationships at multiple spatial scales. NPMR revealed species-specific associations with channel settings and within-channel environments among species sharing the same sets of channel types. Morphological adaptations, biophysical limits and natural histories of each species best explained their associations with distinct sets of attributes surrounding and within channel types. While each set of species has similarly adapted to fluvial and geomorphic disturbance processes structuring channels at the mesoscale, species within each set have adapted to a unique set of attributes that are best discerned when their spatial relationships are examined across multiple spatial scales. We evaluated the various spatial patterns against hypotheses of stream community organization and metacommunity perspectives.

Metacommunites are sets of local biotic communities that exchange individuals of multiple species. Metacommunity theory seeks to explain patterns of species richness and the processes that structure ecological communities across multiple spatial and temporal scales (Leibold et al. 2004). This approach, a logical extension of metapopulation (Levins 1969) and island biogeography (MacArthur and Wilson 1967) theories, includes considerations beyond the numbers of individuals or species. It seeks to explain how the fact that local communities are embedded in larger regional biota affects local phenomena and patterns of variation across communities (Leibold et al. 2004). The metacommunity perspective includes species identities, trophic structure, competition, dispersal modalities, niche differentiation, etc. when attempting to understand distributions within ecological communities (Holyoak et al. 2005a). Metacommunity theory is comprised of four perspectives with which to view spatial and temporal dynamics: 1) patch dynamics in which the species composition of multiple patches represents varying abilities of colonization-competition (metacommunity theory considers all patches identical [Leibold et al. 2004]); 2) species-sorting, resulting from localized spatial heterogeneities favoring some species over others (analogous to niche theory); 3) mass effects, a perspective that focuses on the effects of immigration and emigration on local population dynamics, thereby altering species densities or masses within assemblages; and 4) a neutral perspective in which species are essentially equivalent (e.g. tradeoffs between dispersal and competitive abilities are minimal) (Holyoak et al. 2005b).

In our review of empirical studies used to illustrate these metacommunity perspectives we found that most systems were spatially discrete (e.g. small islands, rock pools, pitcher plants; Holyoak et al. 2005a). Stream ecosystems, to the contrary, are interconnected networks that lack permanently discrete components (Freeman et al. 2007, Grant et al. 2007). We found no indication that advocates of metacommunity theory (Leibold et al. 2004, Holyoak et al. 2005a)

had evaluated the metacommunity framework with regard to structuring of biotic communities in stream networks (Lepori and Hjerdt 2006 for a recent review). In this paper we assess the abilities of metacommunity theory and stream community theory to explain the distributions of the aquatic and riparian herpetofauna in an entire free-flowing river catchment.

The two dominant schools of thought pertaining to the organization of ecological communities in streams differ primarily in how they view the effects of disturbance on stream biodiversity: 1) models that assume communities are shaped by biotic interactions emphasize positive effects (e.g. colonization by species that would be out-competed in stable environments); whereas, 2) models that consider that communities are shaped by physical habitat factors emphasize negative effects (e.g. the exclusion of species lacking adaptations to stress) (Lepori and Hjerdt 2006). The patch dynamics of stream theory differs from that of metacommunity theory as it represents different parts of a heterogeneous lotic environment (i.e. the patch mosaic; Pringle et al. 1988). The species-sorting and mass effects perspectives of metacommunity theory both assume heterogeneity among the attributes of local sites so that different species may be favored depending on local abiotic features.

We used the riparian and aquatic herpetofauna (amphibians, reptiles and turtles) of a large, entire and free-flowing river catchment which allowed us to study community and metacommunity dynamics across spatial scales within a complete and naturally bounded network (Reeves et al. 1995). This approach differs markedly from earlier studies of herpetofaunal assemblages (mostly amphibians) used to evaluate metacommunity theory, which have analyzed spatially discrete systems such as ponds in terrestrial matrices (Urban 2004, Resetarits 2005, Van Buskirk 2005, Richter-Boix et al. 2007, Werner et al. 2007a). Stream networks by contrast are interconnected and influenced periodically by physical disturbances that alter attributes within, around and among system components (e.g. channels), and vary in frequency, intensity, and duration (Resh et al. 1988).

The river continuum concept (Vannote et al. 1980) offered a model of how biotic processes and component aquatic and riparian organisms are spatially organized relative to the physical properties manifesting from the interactions of hydrology and watershed geomorphology. Similarly, a patch dynamics model has been proposed as the principle organizing mechanism of biotic communities in fluvial systems (Pringle et al. 1988, Townsend 1989). These concepts have been variously modified and revised to include the influences of upslope and channel geomorphologic processes (Montgomery 1999), a temporal dimension (Ward 1989), a catchment network perspective (Gomi et al. 2002), and the influences of spatial hierarchy and tributary confluences on network structure and habitat patch dynamics (Benda et al. 2004). Many workers now view the formative influences on stream aquatic and riparian environments and their communities as consisting of a combination of processes with both continuum-like and patchy characteristics (Townsend 1996), processes that are effectively united in the process domains concept (Montgomery 1999). Consistent with this concept is the view of these systems as inter-connected and inter-active dendritic networks (Grant et al. 2007).

It is clear that geomorphic context and disturbance history can profoundly influence lotic ecological systems, yet the ecological effects of fluvial/geomorphic processes are poorly understood and spatial perspectives have been lacking from conceptual models (Montgomery 1999). Consequently, efforts to accurately map and understand the spatial aspects of entire catchments and determine the importance of physical attributes to various biota and ecological processes are few (Minshall et al. 1983, Huryn and Wallace 1987, Naiman et al. 1987). Studies relating herpetofaunal distributions to aspects of catchment networks are also few (Lowe and Bolger 2002, Sheridan and Olson 2003, Peterman et al. 2008, Sepulveda and Lowe 2009).

Herpetofauna consist of three phylogenetically remote groups of higher vertebrates (CNAH 2008), offering a set of markedly different yet ecologically interacting species with which to examine spatial dynamics across broad ecological and taxonomic space. This allows for a relatively robust evaluation of community organizing hypotheses. Furthermore, using the herpetofauna combines aquatic and terrestrial (i.e. riparian) domains, thus encompassing two distinct but intimately linked (Nakano and Murakami 2001) components of the network environment. This provides a more complex and realistic landscape and a more spatially inclusive investigation of potential community organizing modalities.

By focusing on an entire free-flowing river catchment, the riverine landscape (Ward et al. 2002, Wiens 2002), we were able to study how the spatial patterns of the aquatic and riparian herpetofauna relate to the natural processes that shape and define a complete, naturally defined dendritic network. By comparing revealed distribution patterns with life histories (Stearns 1992), niche traits (Chase and Leibold 2003) and other distinguishing attributes of member species, we could evaluate the ability of various community organizing hypotheses to account for spatial patterns at multiple spatial scales within and up to the catchment level as revealed by different animal assemblages. We posited that a high consistency between the distributions of groups of species and particular channel types would constitute evidence of local community structure. We sought to determine the existence of such communities by 1) establishing the existence of distinct channel types (Montgomery and Buffington 1997) as evidence of different geomorphologic and hydrologic disturbance regimes (i.e. process domains; Montgomery 1999). We then 2) evaluated herpetofaunal distributions relative to different channel types to uncover shared patterns. This was followed by 3) a multi-scale spatial analysis of species with shared patterns among channel types to examine relationships with other attributes both surrounding and within channels. We used this information to 4) compared species' characteristics (e.g. natural histories, physical niche components, biophysical limits, etc.) to seek commonalities within patterns between species-specific characteristics and the use of channel environments. Finally we examined consistencies and differences in spatial patterns and species' attributes, seeking evidence for hypotheses of metacommunity theory (Holyoak et al. 2005a) and/or stream community theory (Lepori and Hjerdt 2006). We did not hypothesis test per se, (i.e. we did not falsify hypotheses) but rather reviewed evidence for consistency with predictions of these various community organizing

perspectives, an important step in generating testable hypotheses.

Study area

The Mattole River catchment (hereafter the Mattole) is a 789 km², 6th-order watershed in northwestern California (Fig. 1). It is the western-most river valley in the continental U.S. and contains one of the last free-flowing rivers. 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 river mouth (McLaughlin et al. 1994). The resulting steep terrain (up to 1219 m), and close proximity to the Pacific Ocean, have resulted in this valley having the highest rainfall in the state (average of 508 cm yr^{-1} at Honeydew, CA). However, the extreme topography to the west insulates most of this valley from the marine influences of the Pacific Ocean, making the climate typical of other interior catchments of the Coast Range Mountains of California. Due in part to the complex terrain and high floristic diversity (details in Welsh et al. 2005b), the Mattole supports a diverse temperate herpetofauna comprised of 28 species: eight salamanders, four frogs, one toad, one turtle, five lizards, and nine snakes (Welsh and Hodgson 1997).

Methods

We measured both coarse- and fine-scale attributes of a well distributed set of channel reaches and their surrounding environments (see below), focusing on attributes that based
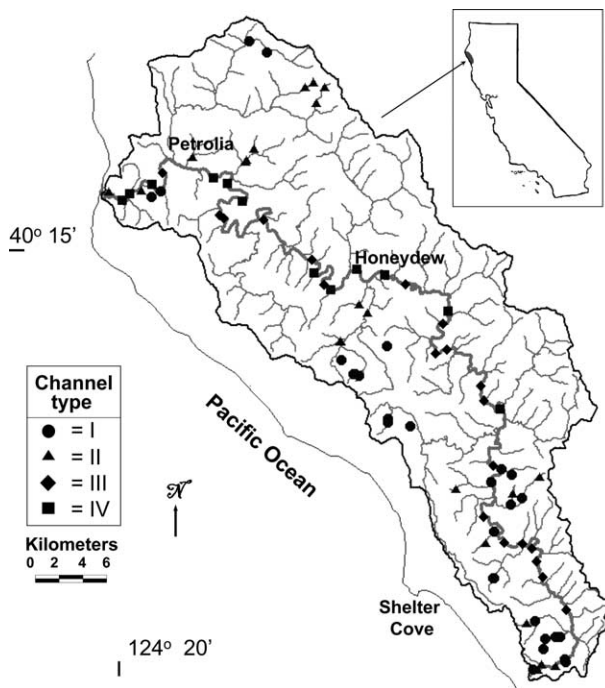

Figure 1. The 789-km² Mattole watershed, northwestern California, USA. Symbols indicate 300-m sample reaches on the main stem river (n = 34) and tributaries (n = 49).

on the literature and our previous research (Welsh et al. 2005a, b), are both affected by geomorphic and hydro-dynamic processes, and that may influence the presence and/or abundance of the herpetofauna. Initially we used channel attributes (slope, drainage area, relative roughness, and bed-surface grain size) to identify unique channel types (described by Montgomery and Buffington 1997) as indicative of geomorphologic process domains in watersheds of the Pacific Northwest. Using these pre-defined channel types provided an independently-derived framework of the dendritic network against which to examine herpetofaunal spatial patterns.

To study herpetofaunal distributions relative to these geomorphic zones, we collected data on aquatic and riparian species and channel attributes with two sampling efforts, both consisting of randomly placed 300-m reaches: 1) from 31 named tributary streams distributed systematically, on U.S. government land and accessible private land throughout the catchment (first reported in Welsh et al. 2005a) (n = 49) and 2) along the main stem river (n = 34) (Fig. 1). The two datasets overlapped spatially where the tributary dataset included reaches in the headwaters of the main stem; together they comprise a dataset representing the entire dendritic network (n = 83 reaches). Sampling occurred in daylight and clear weather during late spring and summer low flows when animals were highly visible and all life stages of pulse-breeding species were present in channel environments.

Main stem reaches

We divided the 112 km main stem of the Mattole River into four sections (each ~37 km) to distribute our sampling systematically along the length. We randomly located eight or nine 1 km sections in each river portion and randomly selected starting points for one reach in each 1 km section for a total of 34 reaches (Fig. 1). We measured four cross-channel transects per reach, distributed systematically within, to estimate depths for wetted and bank-full widths. Canopy closure was measured with a spherical densiometer on each side of the wetted channel and at the mid-point. We sampled substrate particle sizes at 10 equally spaced locations per transect to estimate roughness and bed-surface grain sizes. Water temperature (°C) was recorded at mid-channel. We could not measure valley widths directly due to obstructing topography and vegetation, so we used digital 7.5 minute quadrangle maps (DRGs) in a GIS environment (ArcView 2002) to derive these estimates as well as drainage areas and river channel slopes.

Animal data for the main stem reaches were collected in 1998 using visual encounter surveys (VES; Crump and Scott 1994) with three persons, one per bank and a third in the mid-channel, working in an upstream direction. Data collected with each individual included species, age (size) class, and mesohabitat (riffle, run, pool, etc.; Hawkins et al. 1993). This sampling occurred in the summer when river depths are relatively low and animal counts at their highest.

Tributary reaches

Tributary data were collected in spring and early summer from 1994 to 1996 in 49 reaches using a three-tiered approach comprised of VES, area-constrained cross-stream belts (three each in fast and slow water), and ½-h searches of seep habitat (details in Welsh and Hodgson 1997). Forty-nine reaches with random starts were situated in 31 named tributaries, and then measured to characterize physical attributes comparable to those of the main stem reaches. Data were taken at six cross-stream belts or the bottom of each reach where we measured substrates, canopy closure and water temperatures. GIS was used to determine values for the landscape level variables around the reaches.

Detection

In order to visit and sample a large number of sites across an extensive and complex landscape (i.e. the snapshot approach; Salvia et al. 1999), logistic constraints prevented us from taking the time required to conduct the repeated sampling required of the mathematical models used to estimate species-specific detection probabilities (MacKenzie et al. 2005). Given our objectives, proven methodologies, expertise with the herpetofauna and approach of collecting abundance (rather than simple occupancy) data across a large number of sites (Supplementary material), we determined that the extra efforts required to correct abundance estimates for potential false negative detections was not essential to obtaining valid answers to the questions posed (Johnson 2008). Furthermore, we could not meet model assumptions that the reaches were closed between sampling occasions or that our ability to detect animals in subsequent surveys was not influenced by the first survey. Our sampling effort was extensive and equal among reaches so that estimates (i.e. the ratios) of animals detected across channel types for each species would be consistent, even had we failed to detect some individuals due to sampling biases that might downwardly influence the true accuracy of our findings (MacKenzie 2006). Consequently we believe any minor variations in the detectability of individuals or species did not adversely influence our results.

However, in order to test this assumption, we evaluated our sampling protocols by analyzing data from two earlier studies where the same methods were used to detect species that present the greatest detection challenge, those that live in streambed interstices (i.e. the southern torrent salamander *Rhyacotriton variegatus*, larval and neotenic coastal giant salamanders *Dicamptodon tenebrosus*, and larval Pacific tailed frogs *Ascaphus truei*). This analysis yielded detection probabilities of 1.00 for the giant salamander (in both studies), 0.80 and 0.79 for the tailed frog, and 0.77 for the torrent salamander (detected in only one study), indicating that our protocols were sufficient to avoid any meaningful influences from false negatives.

Analyses

Determining geomorphologic channel types

To differentiate the 83 reaches based on channel characteristics we used non-metric multidimensional scaling (NMDS) with Sorensen's distance in PCOrd (McCune and Grace 2002). Sorensen's distance measures Euclidean distance in multi-dimensional space based on a linear model (McCune and Grace 2002). NMDS is well suited for ordinations in high-dimensional space with non-normal data (McCune and Grace 2002). We analyzed physical attributes including slope, roughness, basin area, and grain size of channel substrates. Our approach differed slightly from Montgomery and Buffington's (1997) in that we used percent of substrate particles in seven size classes rather than the single variable "mean grain size". Several variables were log transformed prior to analysis (see footnotes on tables).

Defining herpetofaunal assemblages relative to channel types (the mesoscale)

To assess herpetofaunal differences across channel types, we used the raw counts of the 16 common species from both tributary and main stem datasets (Supplementary material) in a multi-response permutation procedure (MRPP) using Sorensen's distance (McCune and Grace 2002). Prior to calculating Sorensen's distances, data were naturally weighted based on relative sample size (McCune and Grace 2002). Given that the MRPP analysis was significant (i.e. five of seven comparisons of species composition between channel types differed from what was expected under the null hypothesis), we followed with univariate analyses of variance (ANOVA) and proportion tests. Differences in herpetofaunal richness (number of species) among channel types were examined by ANOVA using all species observed per reach from all sampling methods. Incidental observations (animals seen outside of formal sampling sessions; Supplementary material) were included only in the analysis of richness to improve the accuracy of this metric. Due to minor differences in sampling between main stem and tributary reaches, we were conservative, and only used counts per species from each 300-m reach VES (13 amphibians [larvae omitted] and 12 reptiles; Supplementary material) in an ANOVA of evenness (relative numbers of individuals/species on a scale of zero to 1.0). This analysis was performed in SAS (SAS 2003).

Occurrence of the 16 most common species was examined by channel type by reducing the relative abundances to present/not detected data and using proportion tests followed by Tukey-Kramer multiple comparisons (SAS 2003). For the two pulse-breeding amphibians with complex life cycles (foothill yellow-legged frog *Rana boylii* and western toad *Anaxyrus boreas*), larval (including metamorphs) and post-metamorphic (includes adult, sub-adult and juvenile) life stages were analyzed separately in recognition of their different uses of the environment.

Abiotic conditions, distribution patterns and spatial scales

Given possible influences both within and among spatial scales, we deemed it important to examine the influences of broader environmental conditions in which channel types are embedded (the macroscale; e.g. basin area) as well as conditions along and within each reach (the microscale). While many of the latter attributes influence and determine micro-environmental conditions (see below), we viewed the former as likely having influences that cross spatial scales,

and when both are considered together it can provide a clearer resolution of animal spatial patterns than is provided by the channel types alone (i.e. the mesoscale; Holt 1993). In this regard, the variable "basin area" requires some explanation. The concept of hydrological connectivity (Bracken and Croke 2007) integrates factors that comprise the fluvial linkages inherent in riverine landscapes (Jencso et al. 2009). This fluvial interconnectedness has profound implications for the establishment and maintenance of these ecological networks (Pringle 2003, Freeman et al. 2007, Wipfli et al. 2007). Consequently, annual discharge (water volume yr^{-1}) is a variable that can summarize the frequency and volume (= magnitude) of this linkage, characterizing the relative hydrologic disturbance among sites in the catchment network. Basin area (the amount of a catchment above a reach) then can serve as a surrogate for the relative amount of annual discharge because it quantifies the relationship between runoff source and distance to a given reach (Bracken and Croke 2007), establishing a gradient of relative disturbance for all channel sites. This allowed us to examine animal patterns in a complex riverine network on a continuous axis representing the primary disturbance factor in the system.

We also included water temperature and canopy closure in our analysis based on the previously demonstrated influences on the spatial patterns of many of these species (Welsh et al. 2005a, b). We sought to examine if and how these two variables might act across spatial scales of organization, or combine with other attributes, to influence spatial patterns.

In our analyses, we considered species with similar distributions among channel types as members of unique local assemblages within the metacommunity at an intermediate scale (mesoscale), however, we also recognizing the possibility that processes at different levels of resolution (i.e. both coarse, fine and multi-scale perspectives; Peters et al. 2007) are likely to influence spatial patterns. At mid-resolution this could include different mesohabitats within reaches such as pools and riffles (Hawkins et al. 1993) as well as at a fine-resolution such as different micro-environments within these mesohabitats (Frissell et al. 1986). We sought to examine those environmental gradients within channel types as expressed by the same abiotic variables we used to distinguish these types, plus water temperature and canopy closure, to determine if and how these combined factors may be influencing spatial patterns and community structure. In this analysis, we used only the range of values for these variables found within the channel types where each species occurred.

Microscale (e.g. substrates) and macroscale (e.g. basin area) relationships between channel attributes and each set of species or life stages (as defined by their mesoscale associations with the same channel types) were assessed with non-parametric multiplicative regression analysis (NPMR; McCune 2006) using the software HyperNiche ver. 1.0 (McCune and Mefford 2004). NPMR, designed for multivariate niche modeling, seeks to optimize a fit of species detection data along multiple environmental gradients (i.e. in multi-dimensional attribute space) rather than adhering to a specific model form like linear or Poisson regression. NPMR considers interactions among all predictor variables in a given model (McCune 2006). NPMR estimates a response for each variable at a given point in predictor space by weighting heavily points that are near a target point and giving less weight to distant points along a gradient (using a minimum of three points). In model generation we set the minimum neighborhood size to five percent of each sample. In NPMR, a Gaussian weighting function is used to describe how broadly information is employed from nearby areas of the predictor space around a target point (referred to as the "tolerance" of a species along a particular gradient) (McCune 2006); as such, it models the niche breadth for that particular attribute. Tolerance is then the bandwidth used in the multiplicative kernel smoother, given in the units of the environmental attribute (McCune 2006). A species that is broadly tolerant relative to a particular environmental factor uses information from a large neighborhood of data points (McCune 2006). Data points describing the tolerance for all of the variables (= the ecological neighborhood) are then employed to model the niche of each species or life stage along multiple axes. We used a local mean estimator and Gaussian weighting function in an all-possible-subsets regression to determine sets of possible models. Models were assessed using a leave-one-out cross-validated R^2 (xR^2), which is equal to one minus the ratio of the residual sum of squares over the total sum of squares; this procedure provides a built-in check on over-fitting (Antoine and McCune 2004). We used the HyperNiche exhaustive search mode to determine the best single variable and best multi-variable model (up to eight predictor variables) for each species or life stage based on highest xR^2 (Giordani 2007). HyperNiche provides a sensitivity analysis that allowed us to evaluate the relative importance of the variables in each multivariate NPMR model. Sensitivity is expressed as a ratio independent of the units of the variable. The greater the sensitivity, the more influence that variable has in a model; one means that on average changing the value of a predictor results in a response of equal magnitude and zero means no detectable effect on the response. We report only those variables with sensitivity ≥ 0.5. Species relationships with independent variables are reported as positive (+), negative (−), or hyperbolic (^= either a humped or U-shaped distribution). We set p ≤ 0.10 as appropriate for detecting ecological trends (Schrader-Frechette and McCoy 1993) in all tests.

Results

Distinguishing channel types

The NMDS ordination with ten abiotic variables (Table 1) distinguished four channel types among the 83 reaches (Fig. 2). Channel type I matched closely Montgomery and Buffington's (1997) category "cascades", channel type II matched that of "step pools", channel type III with "plane-bed", and channel type IV with "pool riffle". Moving downstream from the headwaters these channel types are described as follows: type I are cascade reaches with relatively high-gradients and narrow, gorge-defined channels with cascade structures; type II are step-pool reaches with moderately entrenched channels with 2–4% gradients, structurally controlled by moderately steep valleys; type III

Table 1. Means (standard deviations) of geomorphologic variables used to distinguish four channel types in the Mattole using non-metric multidimentional scaling (NMMS). Channel type I = cascades, channel type II = step pools, channel type III = plane-beds, and channel type IV = pool riffles. *Relative roughness is the ratio of the ninetieth percentile grain size to the bankfull flow depth (Montgomery and Buffington 1997).

Variable	Channel type			
	I (n = 27) Mean (SD)	II (n = 23) Mean (SD)	III (n = 21) Mean (SD)	IV (n = 12) Mean (SD)
Slope (%)	5.86 (5.58)	5.17 (4.30)	0.44 (0.28)	0.28 (0.20)
Roughness*	1.52 (0.74)	1.34 (0.81)	0.05 (0.05)	0.04 (0.02)
Area (ha)	216.37 (286.97)	188.96 (266.80)	27296.38 (21513.41)	52585.33 (18370.19)
Substrates (%)				
Fines	7.08 (6.29)	13.92 (12.49)	5.92 (6.44)	3.50 (3.75)
Sand	8.49 (4.94)	8.91 (6.73)	13.31 (8.10)	18.81 (6.17)
Gravel	16.90 (4.99)	17.73 (10.10)	30.19 (12.03)	28.72 (8.15)
Pebble	21.60 (6.42)	18.37 (6.42)	30.45 (10.79)	32.08 (5.91)
Cobble	23.56 (6.94)	22.80 (12.69)	13.62 (9.98)	15.24 (3.79)
Boulder	22.37 (15.59)	18.26 (14.26)	6.51 (8.52)	2.65 (4.33)
Bedrock	10.41 (13.55)	0.00 (0.00)	1.45 (1.40)	0.00 (0.00)

are plane-bed reaches, slightly entrenched, lower-gradient, meandering channels with a well developed flood plain; and type IV are pool/riffle reaches with exposed bars, turbulent riffles, and slow pools.
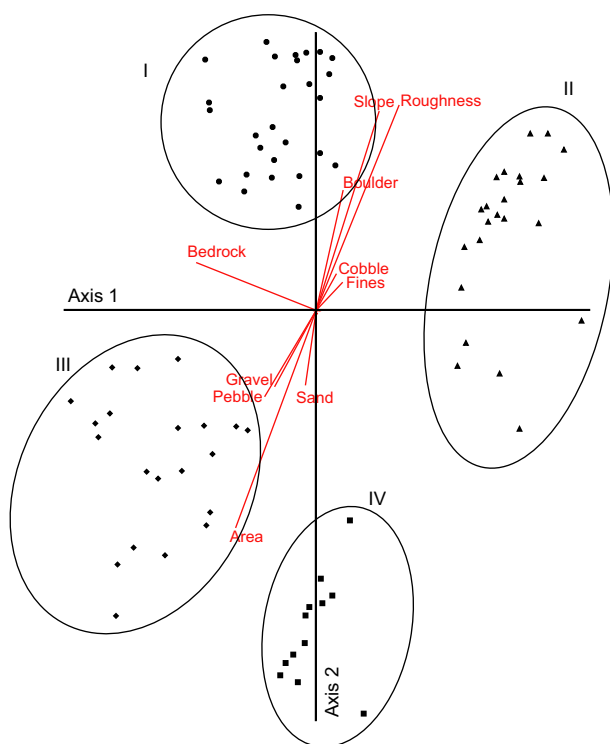

Figure 2. Non-metric multidimensional scaling (NMDS) of 83 sample reaches in the Mattole (see Fig. 1) based on slope, roughness, basin area, and substrate composition (variables log transformed prior to analysis; see methods for details). Type I = high-gradient, narrow, gorge-defined channels with cascade structures; type II = moderately entrenched channels with step-pool structure controlled by moderately steep valleys; type III = slightly entrenched, lower-gradient, plane-bed channels with well developed flood plains; type IV = low gradient, shallow, unconfined, multiple or migrating riffle/pool channels typical of broad alluvial valleys.

Distinguishing spatial patterns among the herpetofauna

Herpetofaunal biodiversity across the catchment

With four techniques combined we detected 34 942 individuals of 22 species, 11 amphibians and 11 reptiles (Supplementary material). An additional 370 detections were made outside of protocol, and used only in the analysis of richness (Supplementary material). Not including larvae, the highest count for a single reach was 367 individuals, 134 of which were post-metamorphic foothill yellow-legged frogs. Reptile and amphibian richness for single reaches both peaked at eight species (not at the same locality). Reptile richness increased along the axis of basin area, increasing from tributary headwaters to the river mouth, with four of six pair wise comparisons differing (Table 2). Amphibian richness was relatively stable, with different species replacing each other along this same axis. Reptile evenness along the basin area axis reached the maximum of 1.0 at sites near the river mouth, declining steeply upstream, approaching zero in headwaters. Reptile evenness differed between combined types I and II and combined types III and IV, but not between the members of either pair (Table 2). Amphibian evenness was relatively stable, and did not vary along the basin area axis (i.e. by channel type) (Table 2).

The MRPP of 16 common species (no larvae or metamorphs) (Supplementary material) indicated pronounced differences in the composition of species assemblages among the four channel types. Five of the six pair-wise comparisons had significant differences, with only channel types I and II not supporting distinct assemblages (Table 3).

Herpetofaunal assemblages and channel types (the mesoscale)

Sixteen species, nine amphibians (including both larval and adult life stages of the foothill yellow-legged frog and the western toad) and seven reptiles, were detected in numbers sufficient to analyze relationships with the channel types (Supplementary material). This analysis indicated nine species were distributed un-equally among the four types (Table 4). The southern torrent salamander was found more

Table 2. ANOVA results of assemblage metrics comparing herpetofaunal composition by channel type. All data (including incidentals) were used for richness; 300-m VES data only were used for evenness (see methods). *Natural log transformed, †Tukey-Kramer multiple comparisons.

Dependent variable	DF	MSE	F	p	Multiple comparisons†
Richness					
Amphibians*	3	0.183	1.63	0.1887	
Reptiles (+turtles)	3	2.615	12.19	<0.0001	III >I, III >II, IV >II, IV >II
Evenness					
Amphibians	3	0.139	0.25	0.8606	
Reptiles (+turtles)	3	0.127	13.95	<0.0001	III >I,III >II, IV >I, IV >II

in type I compared with II, III, and IV. The coastal giant salamander was found more in types I and II than in III and IV, and more in type III than IV. The black salamander *Aneides flavipunctatus* was detected more in types I and II than in III and IV. The Pacific tailed frog was found more in type I compared to III and IV. The remaining amphibians all expressed different spatial patterns. The rough-skinned newt *Taricha granulosa*, larval western toads *Anaxyrus boreas*, the red-bellied newt *T. rivularis*, and both life stages of the foothill yellow-legged frog *Rana boylii* were detected more often in type III compared with I and II. The rough-skinned newt, larval western toad and both life stages of yellow-legged frog were detected more in type IV than I and II (Table 4).

Reptiles displayed a general pattern of greater detections in channel types III and IV compared with I and II (Table 4). The western pond turtle *Actinemys marmorata*, western fence lizard *Sceloporus occidentalis*, northern alligator lizard *Elgaria coerulea*, common garter snake *Thamnophis sirtalis*, and the Pacific aquatic garter snake *T. atratus* were all detected more in types III and IV compared with I. All of these reptiles, except the common garter snake, were also detected more in type III compared with II. The pond turtle, fence lizard and Pacific aquatic garter snake were detected more in type IV compared with II. The fence lizard was the only reptile found more in type IV than III. Only one reptile, the common garter snake, differed between types I and II (Table 4).

We detected several upland species with differences in their distributions relative to channel types: the terrestrial garter snake *T. elegans*, western skink *Plestiodon skiltonianus*, Pacific chorus frog *Pseudacris regilla* and western toad (post-metamorphic) (Table 4). Given their extensive use of upland environments in the Mattole (Welsh unpubl.), the chorus frog, western toad, and the two reptiles, are not specifically adapted to aquatic and riparian areas, and we did not consider them to be members of the assemblages we found in these environments. While we do not further analyze their spatial relationships here, they do use these areas to reproduce (i.e. the anurans), forage and possibly for other life history requisites.

The distributions of seven amphibians and four reptiles are shown relative to the four channel types in Fig. 3. The greatest difference among those species whose distributions matched closely with channel types occurred between the two low order, higher gradient types (I and II) and those with lower gradients and larger drainage areas (III and IV) (Fig. 3). Differences between types I and II were not significant, and those between III and IV were relatively weak (Table 3). We also found that the pairs of channel types showing the greatest faunal differences were also readily distinguishable based on microclimate. We found canopy closure and water temperature similar between types I and II, and between III and IV, but differing greatly between the pairs (Fig. 4); these two attributes were highly negatively correlated (r = −0.937). Based on differences in roughness, substrate composition etc. (Table 1), these channel type pairs can be described as steeper, mostly bedrock or colluvial, headwater channels (types I and II) and lower gradient, primarily alluvial channels (types III and IV) (for additional characteristics see Montgomery and Buffington 1997).

Abiotic factors and channel type assemblages: headwater channel species

Twenty of 22 detections of southern torrent salamanders occurred in channel type I, with two in type II (Supplementary material). The NPMR analysis revealed that water temperature (−) was the best single variable but a poor predictor of increased numbers ($xR^2 = 0.079$). The best multivariate model, comprised of roughness (+), fines

Table 3. Multi-response permutation procedure (MRPP) with multiple comparisons of 16 species (Supplementary material) among four channel types. Variables were weighted prior to calculating Sorensen (proportional city-block) distances (see Methods). δ =within group Sorensen distance, A =chance corrected within-group agreement.

	Observed δ	δ under null hypothesis			T	p	A
		Expected	Variance	Skewness			
All groups	0.630	0.763	<0.0001	−1.17	−18.51	<0.0001	0.175
I vs II	0.637	0.639	<0.0001	−1.82	−0.37	0.2624	0.003
I vs III	0.654	0.778	<0.0001	−2.08	−17.34	<0.0001	0.159
I vs IV	0.578	0.736	<0.0001	−2.24	−16.08	<0.0001	0.215
II vs III	0.676	0.782	<0.0001	−1.74	−14.64	<0.0001	0.136
II vs IV	0.596	0.740	0.0001	−2.01	−13.85	<0.0001	0.195
III vs IV	0.619	0.633	<0.0001	−1.33	−2.29	0.0321	0.023

Table 4. Proportion tests (Pearson's Chi-Square) with Tukey-Kramer multiple comparisons of amphibians (9 species) and reptiles (7 species) among four stream channel types using present/not detected data. [1]Combined adults, juveniles and sub-adults, [2]combined larvae and metamorphs.

Dependent variable	DF	χ^2	p	Multiple comparisons
Amphibians				
S. torrent salamander	3	19.91	0.0002	I >II, I >III, I >IV
Coastal giant salamander	3	45.61	<0.0001	I >III, I >IV, II >III, II >IV, III >IV
Rough-skinned newt	3	26.19	<0.0001	III >I, III >II, IV >I, IV >II
Red-bellied newt	3	15.84	0.0012	III >I, III >II
Black salamander	3	10.17	0.0171	I >III, I >IV, II >III, II >IV
Western toad (post-metamorph)[1]	3	5.54	0.1362	
Western toad (larvae)[2]	3	28.48	<0.0001	III >I, III >II, IV >I, IV >II
Pacific chorus frog	3	2.22	0.5286	
Pacific tailed frog	3	16.66	0.0008	I >III, I >IV
F. H. yellow-legged frog (adults)[1]	3	23.91	<0.0001	III >I, III >II, IV >I, IV >II
F. H. yellow-legged frog (larvae)[2]	3	52.42	<0.0001	III >I, III >II, IV >I, IV >II
Reptiles and turtles				
Western pond turtle	3	39.47	<0.0001	III >I, III >II, IV >I, IV >II
Western fence lizard	3	36.07	<0.0001	III >I, III >II, IV >I, IV >II, IV >III
Western skink	3	3.42	0.3318	
Northern alligator lizard	3	15.40	0.0015	III >I, III >II, IV >I
Common garter snake	3	13.35	0.0039	II >I, III >I, IV >I
W. terrestrial garter snake	3	3.42	0.3318	
Aquatic garter snake	3	41.72	<0.0001	III >I, III >II, IV >I, IV >II

($-$), boulder ($+$), bedrock ($\wedge$), water temperature and canopy ($+$) was better, but still a weak predictor ($xR^2 = 0.365$) (Table 5). No torrent salamanders were detected in water $>13.5°C$ or with canopy closure $<91\%$, bedrock was the most sensitive (0.582) with detections up to 19% bedrock but none beyond that amount.

We found 35 tailed frogs in channel type I (12 adults, 23 larvae) and eight in type II (six adults, two larvae) (Supplementary material). The NPMR analysis indicated that canopy closure ($+$) was the single best predictor of increased tailed frogs (life stages combined), but it was relatively poor ($xR^2 = 0.055$). The best model, comprised
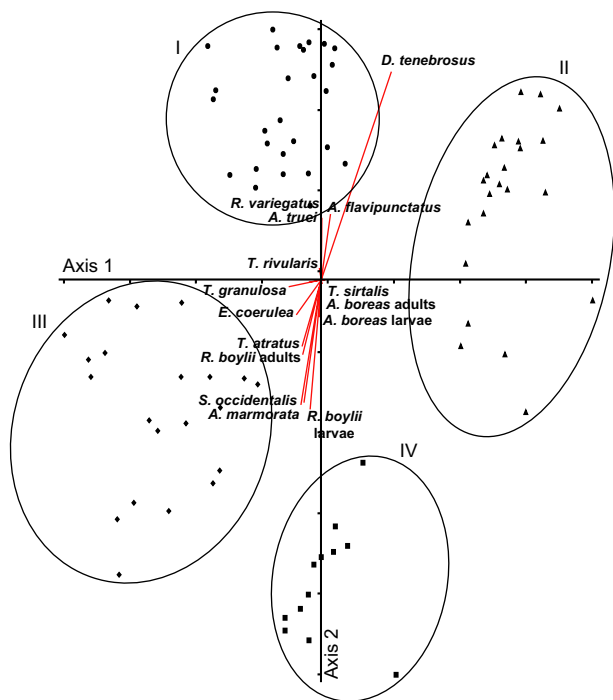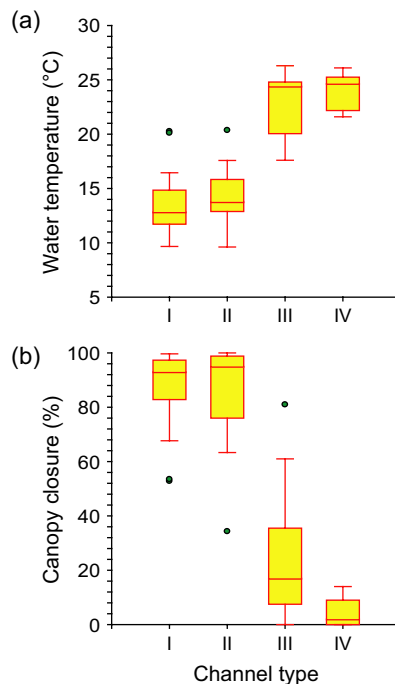

Figure 3. NMDS of 83 reaches from the Mattole watershed with the distributions of eleven amphibian and reptile species relative to the four channel types (see descriptions in Fig. 2). Species depicted are those distributed primarily in headwater (I and II), alluvial (III and IV), or all four channel types; in several of these cases types III and IV supported greater abundances (for details see Table 4, Supplementary material).

Figure 4. Water temperature (°C) and canopy closure (percent) by channel type for the four channel types in the Mattole watershed (see descriptions in Fig. 2). The top and bottom of the box represents the 25th and 75th percentiles (IQR), and the middle line represents the median value. The lines extend to 1.5 times the IQR.

Table 5. Non-parametric multiplicative regression (NPMR) models (best single variable and best multivariate model) for twelve species with distributions that fell into four distinct assemblage patterns based on channel types. The data for the abiotic variables used in this analysis were those only from the channel types where each species occurred. Tolerance () is in the units of the response variable and refers to the niche width along that variable. xR^2 is a leave-one-out cross-validated R^2. See methods for more details. *natural log transformed, †Arcsine square root transformed.

Models	xR^2
Channel types I and II	
Black salamander*	
Area* (0.6 ha)	0.259
Slope† (0.3%), Area* (0.6 ha), Cobble (8.5%), Boulder (38.0%)	0.500
Pacific tailed frog*	
Canopy (6.6%)	0.055
Roughness (0.6), Sand (3.7%), Boulder (11.7%), Bedrock (7.0%), Canopy (9.8%)	0.168
Southern torrent salamander*	
Water temperature (1.6°C)	0.079
Roughness (1.0), Fines (8.3%), Boulder (11.7%), Bedrock (7.0%), Water temperature (2.7°C), Canopy (26.3%)	0.365
Coastal giant salamander	
Area* (0.6 ha)	0.574
Roughness (0.3), Area* (1.4 ha), Bedrock (28.0%), Canopy (10.0%)	0.719
Channel types III and IV	
Western toad (larvae)	
Area* (0.2 ha)	0.145
Area* (0.6 ha), Sand (15.1%), Gravel (24.5%), Water temperature (0.9°C)	0.435
Western pond turtle	
Bedrock (6.7%)	0.159
Slope (28.0%), Roughness (0.1), Fines (2.3%), Bedrock (11.2%)	0.347
Northern alligator lizard	
Slope (22.4%)	0.084
Slope (11.2%), Pebble (33.9%), Cobble (6.9%), Boulder (14.3%)	0.332
Channel types I, II, III and IV	
Rough-skinned newt*	
Canopy (10.0%)	0.291
Slope (3.8%), Area* (1.4 ha), Gravel (30.0%), Water temperature (1.7°C), Canopy (10.0%)	0.484
Foothill yellow-legged frog (adults)*	
Canopy (10.0%)	0.594
Slope (7.6%), Area (0.6 ha), Gravel (27.7%), Cobble (19.7%), Canopy (10.0%)	0.653
Foothill yellow-legged frog (larvae)*	
Water temperature (1.7°C)	0.875
Area* (5.0 ha), Pebble (11.3%), Cobble (11.2%), Water temperature (0.8°C)	0.934
Western fence lizard*	
Water temperature (0.8°C)	0.595
Pebble (6.8%), Boulder (10.7%), Water temperature (0.8°C)	0.726
Aquatic garter snake*	
Area* (0.6 ha)	0.608
Slope (13.3%), Sand (15.8%), Gravel (9.2%), Pebble (15.8%), Boulder (32.2%), Water temperature (4.2°C)	0.728
Idiosyncratic distributions	
Red-bellied newt (larvae)*	
Water temperature (1.7°C)	0.237
Sand (7.7%), Gravel (13.1%), Pebble (22.6%), Cobble (9.6%), Water temperature (1.7°C), Canopy (54.8%)	0.593
Common garter snake	
Cobble (2.8%)	0.198
Slope (9.6%), Roughness (1.4), Gravel (11.5%), Cobble (2.8%), Boulder (29.8%)	0.298

of roughness ($^$), sand ($^$), boulder (+) and canopy closure was only a slight improvement ($xR^2 = 0.168$) (Table 5). No tailed frogs were detected where canopy closure <82.8%; sand was the most sensitive variable (0.768) with tailed frogs detected up to 12% sand but none were found over that amount.

We found 405 coastal giant salamanders (larvae and paedomorphs) in channel type I, 367 in type II and 12 in channel type III (Supplementary material). The best single predictor of increased giant salamanders was basin area (−) ($xR^2 = 0.574$). The best multivariate model consisted of roughness (+), basin area, bedrock ($^$) and canopy closure (+) ($xR^2 = 0.719$) (Table 5). No giant salamanders were detected in areas with canopy closure <53.5%.

Twenty-three of 27 black salamanders detected were juveniles found in wetted substrates under cobbles at streamside, 18 by type I and nine by type II channels (Supplementary material). Basin area (−) was the best single predictor of increasing detections ($xR^2 = 0.259$). The best multivariate model, slope (+), basin area, cobble ($^$) and boulder (+), was greatly improved ($xR^2 = 0.500$) (Table 5). Basin area was the most sensitive variable (0.654) with no detections above 119 ha.

Alluvial channel species

Larval and metamorphic western toads were found in channel types III (627 individuals) and IV (6537 individuals) (Supplementary material). The best single predictor was basin area ($^$) ($xR^2 = 0.145$), showing a threshold effect with no toads found in channel draining <21 045 ha. The best multivariate model, basin area, sand ($^$), gravel (+) and water temperature ($^$), was greatly improved ($xR^2 = 0.435$) (Table 5). Water temperature was the most sensitive variable (0.605) with larval toads detected in a narrow range from 21.6–25.7°C.

Eighteen western pond turtles were detected in channel type III and 21 in type IV (Supplementary material). The best single predictor of increased turtles was bedrock (−) ($xR^2 = 0.090$). The best multivariate model, slope (−), roughness (+), fines ($^$) and bedrock, was better, but still weak ($xR^2 = 0.347$) (Table 5). "Fines" was the most sensitive variable (0.560) with turtle detections up to 5% but none beyond. Bedrock also showed a threshold effect with no turtles >17.5%.

Sixteen northern alligator lizards were detected along type III and seven along type IV channels (Supplementary material). The best single predictor, slope (+), was weak ($xR^2 = 0.084$). The best multivariate model, slope, pebble (−), cobble ($^$) and boulder ($^$), was better, but unremarkable ($xR^2 = 0.332$) (Table 5).

Species present in all channel types

The most abundant species found was the foothill yellow-legged frog, occurring in all four channel types, but with much higher abundances in types III and IV (Supplementary material). The NPMR analysis indicated the best single predictor variable for adults was canopy closure (−) ($xR^2 = 0.594$). The best multivariate model consisted of slope (−), basin area (+), gravel ($^$), cobble ($^$) and canopy closure ($xR^2 = 0.654$) (Table 5). Basin area had high sensitivity (0.952) indicating a dramatic increase

in the number of frogs detected in channels draining basin areas >10 000 ha. For larval yellow-legged frogs the best single predictor variable was water temperature (+) ($xR^2 = 0.875$), with no tadpoles detected <13°C. The best multivariate model, basin area (+), pebble (+), cobble (^) and water temperature, was the best model overall ($xR^2 = 0.934$) (Table 5).

The rough-skinned newt (488 adults, 19 larvae) occurred in all channel types (Supplementary material). The best single variable was canopy closure (^) ($xR^2 = 0.291$). The best multivariate model was slope (−), basin area (^), gravel (+), water temperature (+) and canopy closure ($xR^2 = 0.484$) (Table 5).

The western fence lizard occurred in all channel types but was much more abundant along types III and IV (Supplementary material). The best single predictor was water temperature (+) ($xR^2 = 0.596$), which was highly sensitive (0.867) with no detections <12.5°C. The best multivariate model was pebble (+), boulder (−) and water temperature ($xR^2 = 0.726$) (Table 5).

The Pacific aquatic garter snake, while present in all channel types, was much more abundant in alluvial versus colluvial channels (219 vs 21, respectively) (Supplementary material). The best single predictor variable was basin area (^) ($xR^2 = 0.608$). The best multivariate model, slope (−), sand (^), gravel (+), pebble (+), boulder (−), water temperature (+) and canopy closure (−), was an excellent predictor ($xR^2 = 0.728$) (Table 5). Canopy closure was highly sensitive (1.05), with a peak in detections at ~7% and declining gradually to zero as it approached 100%.

Idiosyncratic distributions

The red-bellied newt (123 larvae, five adults) occurred in channel types I, III, and IV (Supplementary material). The best single variable, water temperature (^), was a fair predictor ($xR^2 = 0.237$), with a distinct range from 15 to 26°C. The best multivariate model, sand (^), gravel (−), pebble (−), cobble (+), water temperature and canopy closure (^) was far better ($xR^2 = 0.593$) (Table 5).

The common garter snake (37 individuals) was absent in channel type I, and most abundant along alluvial channels (Supplementary material). The best single variable, cobble (^), was highly sensitive (2.67) but a weak predictor ($xR^2 = 0.198$), showing a peak in detections at ~12%. The best multivariate model, slope (−), roughness (−), gravel (^), cobble and boulder (^), was a slight improvement ($xR^2 = 0.298$) (Table 5).

Discussion

Montgomery (1999, Fig. 7, 8) described the disturbance processes associated with colluvial, confined, and floodplain (alluvial) channels in mountain catchments. Fire and wind can affect changes throughout mountain drainage networks, avalanches influence mostly low order channels, debris flows primarily influence the mid-channel network, and fluvial processes such as floods and channel migration primarily influence high order, low gradient channels. Stream networks are re-shaped periodically (often annually) by disturbances such as streambed mobilization and the

movement of large woody debris at high flows (Lowe et al. 2006), processes that alternately create and destroy habitats within channel networks. All of these disturbances, their timing, magnitude, and duration, interact with local geomorphologic conditions to determine where particular channel types manifest and are maintained. The abiotic variables used to define the channel types, and then employed in the NPMR analysis along with water temperature and canopy closure, provided excellent physical niche models for six species or life stages, fair models for three others, and weak to poor models in the remaining five cases (Table 5). However, even the weak models, some suggesting the lack of a strong relationship with the physical environment, provided useful information about the possible structuring modalities among the sub-sets of assemblages within the Mattole metacommunity. Below we examine previous research on physiological limits, natural histories and habitat requirements, in conjunction with our analysis of abiotic associations, for members of each of the assemblages associated with a specific set of channel types (Table 5). Here we seek evidence of similarities among species in each assemblage that could explain both their shared mesoscale distributions, and the means by which they co-exist in the same channels.

Headwater channel species

Headwater channels are usually steep, often with emergent cold ground water and few fine sediments; they lack major scouring events, and thus contain a stable mix of variable sizes of substrate particles and the concomitant complex substrate interstices (i.e. high roughness) that typify areas subject to low levels of fluvial disturbance. Furthermore, headwater channels in mature forests contain cool, moist microclimates that remain so even in summer as a result of buffering by complex, multi-story canopy (Welsh 1990, Chen et al. 1999).

The southern torrent salamander occurred primarily in undisturbed channel type I environments. It is one of the few North American amphibians with morphological adaptations specifically for headwater conditions (Valentine and Dennis 1964). Our niche model for torrent salamanders described a headwater environment with low fines, complex coarse substrates, cold water (<13.5°C) and high canopy (>91%). The torrent salamander is the most sensitive of all North American salamanders to desiccation (Ray 1958) and is adapted specifically for life in cold water (Brattstrom 1963, Bury 2008). Welsh and Lind (1996) described the niche as cold, clear, slow-flowing, shallow water under high canopy closure typical of late-seral forest, concluding that their unwavering restriction to these conditions indicated an ecological dependence (Ruggiero et al. 1988).

Pacific tailed frogs were restricted to headwater channels, with a four fold increase in their numbers in type I channels. We did not detect these frogs where canopy closure was <82%, with this variable the best single predictor. The current distribution of this ancient frog in the Mattole has been greatly limited by contemporary timber harvesting (Tang et al. 1997), with remaining populations fragmented and isolated to a few remaining

stands of old-growth forest (Welsh et al. 2005a). This patchy distribution is likely the result of water temperatures that now exceed the upper thermal limits of egg development during the summer when these frogs oviposit under stream substrates (Welsh et al. 2005a). Larval tailed frogs have morphological adaptations (Gradwell 1971) and biophysical constraints (Brattstrom 1963, Bury 2008) for life in cold, clear, running waters. These adaptations and physiological limits constitute an ecological dependence (Ruggiero et al. 1988) on cool stable thermal conditions most reliably found in headwater channels under mature and late-seral forest canopy at altitudes below 1000 m (Welsh and Lind 2002). These conditions are commonly altered by timber harvesting along tributaries above fish-bearing reaches under existing Pacific Northwest harvest regulations (Welsh et al. 2000, Olson et al. 2007). The population level response to this poor forest management is the reduction or elimination of gene flow (Spear and Storfer 2008), and a reduced likelihood that the frogs will re-populate recovered stream channels within their range. While our niche model captured many of the headwater channel attributes associated with tailed frogs (Adams and Bury 2002, Welsh and Lind 2002, Dupuis and Friele 2006), it was a poor predictor overall. We attribute this poor performance to the absence of tailed frogs in recovered and now suitable channel environments resulting from a restricted ability to re-populate an impacted landscape (Spear and Storfer 2008). This same phenomenon may also explain our weak predictive model for the torrent salamander, which has experienced a similar fate in the Mattole (Welsh et al. 2005a). The torrent salamander is known to be a poor disperser with concomitant high genetic differentiation among geographically proximate populations (Wagner et al. 2006).

The majority (>700) of aquatic coastal giant salamanders occurred in channel types I and II. The niche model for this salamander was highly indicative of headwater environments typical of these channels. Despite the importance of canopy closure (no detections <53.5%), this low canopy threshold, and earlier studies (Welsh and Lind 2002), indicate a broader niche than that of the other aquatic headwater channel species. This appears to hold as well for their thermal requirements (Bury 2008, Welsh and Hodgson 2008). None-the-less, they respond negatively to the re-setting of the forest seral continuum (Curtis and Taylor 2003). Their numbers also decline in response to excessive amounts of fine sediments (Welsh and Ollivier 1998), an effect that can last for decades in anthropogenically-disturbed low gradient streams (Ashton et al. 2006). Despite the broader niche compared with the headwater species above, our predictive model indicates that giant salamanders are ecological specialists (Futuyma and Moreno 1988) requiring partially shaded stream environments with heterogeneous coarse substrates found primarily in low order channels in relatively small mountain catchments.

The black salamander is the only terrestrial salamander in this study; most of our detections were juveniles found in wetted substrates under cover along stream banks. Consequently, our niche analysis pertains primarily to juvenile summer use of streamside environments. This analysis indicated higher numbers associated with low order (i.e. small basin area) headwater channel environments typified

by steep slopes, intermediate amounts of cobble and abundant boulders, results indicating that the salamanders select specific micro-environments associated with stream-side cover substrates (i.e. damp, cool, seep habitat) along these channels. Our results suggest that either some females (who deposit eggs in terrestrial environments) may nest near headwaters, or the young migrate to these areas shortly after hatching, possibly seeking microclimates that prevent desiccation in the dry season. Despite the association of juvenile black salamanders with headwater environments, we do not know what proportion of a population seek these conditions, if and how long the conditions may be required, or how the larger population is distributed on the landscape. Data from rainy season sampling indicates that all life stages do occur in upland habitats (S. Reilly pers. comm.).

Alluvial channel species

Alluvial channels are generally lower gradient, less confined channels that undergo frequent substrate sorting from seasonal fluvial disturbances that alternately create and destroy point bars, back water pools, and channel meanders (Montgomery 1999). Aside from winter flows, water velocities in alluvial channels tend to be lower than in headwater channels due to more gradual slopes, resulting in lower substrate roughness, fewer boulders, and more pebble, gravel and cobble. Because of the predictable nature of these disturbances, many species that use alluvial channel environments have evolved cyclical occupancy patterns, associated with reproduction or the availability of food resources, and seasonal upland movements allow them to avoid annual fluvial disturbances (see below).

Larval western toads were the second most abundant species we found in alluvial channels. Western toads breed in still or slow-moving waters (Muths and Nanjappa 2005) like backwater channels or pools. These habitats are common in alluvial channels in the spring and summer where river meanders create warm shallow back waters that provided optimal breeding and rearing habitats. Basin area with a distinct threshold for detections at >21 000 ha was the best single predictor of toad tadpoles. Water temperature was the most sensitive variable in the multivariate model, indicating a narrow range with tadpoles absent <21.6°C and the majority found from 21.6 to 25.7°C. This model indicated toad tadpoles associated with the fine substrate conditions more common along alluvial channels, including up to 27.5% sand (the highest = 32.5%) and 42.5% gravel (the highest we measured). However, adult western toads are mostly nocturnal and, with one exception, were not detected during diurnal sampling. We detected 25 post-metamorphic toads but these data showed a lack of association with the variables we examined, possibly because of the transient nature of post-metamorphic toads along these channels.

The western pond turtle lives in diverse freshwater environments in western North America, where it is often found along slow-flowing channels with sufficient basking sites or warm water (Bury and Germano 2008). Our model was weak but did indicate turtle detections increased along alluvial channels with lower gradients (slope <1.0%), increased roughness, and <17.5% bedrock. Escape cover

in submerged refuges is an essential requirement, second only to the ability to thermoregulate (Reese and Welsh 1998), which may explain the relationship with increased roughness. The association with bedrock is suggestive of river bends where large pools (a favored turtle mesohabitat) form in response to scour associated with this geologic feature. The sensitivity to increased amounts of fine sediments (no detections >5%) may indicate an adverse influence on turtle food resources or foraging ability.

We found northern alligator lizards only along channel types III and IV. However, we are aware that they are abundant in forested upland areas of the Mattole (Welsh et al. unpubl.). We interpret the detections of this typically terrestrial lizard along alluvial channels, and the poor physical niche model (Table 5), as evidence of the likely exploitation of a seasonal food resource, the readily available and numerous anuran tadpoles (Cunningham 1956).

Species occurring in all channel types

The following descriptions of the "all channels types" assemblage could be seen to support the interpretation that the alluvial assemblage members described above are nested within this greater assemblage (Tockner et al. 2006). While this view can be supported at the mesoscale, the concept of nestedness is highly scale-dependent and potentially misleading. Members of the alluvial channel assemblage are restricted to those channel types alone, where as members of the "all channels types" are found more widely, occurring in all channel types. Furthermore, regardless of an overlap in alluvial channels, a more inclusive spatial analysis reveals different and distinct uses of space by each species, both where they co-occur and where they do not. An examination of biophysical requirements, natural history, and behavioral modalities of each assemblage member indicates that these attributes combine to dictate a unique use by each of both coarser and finer scale spatial aspects of the aquatic/riparian network environment.

The foothill yellow-legged frog was the most commonly encountered species, with all life stages present in all channel types. However, all the life stages were much more abundant along alluvial channels. There were no detections of tadpoles <13°C, and numbers increasing substantially as water temperature increased (for this single variable $xR^2 = 0.875$). Reduced canopy cover was the best predictor of increased adult frogs. Increases of both life stages were positively associated with larger basin areas and more fine substrates, conditions much more typical of alluvial channels. This stream-dwelling frog is a heliotherm (basker); adults are often found in open sun during the day on gravel bars and on emergent boulders and cobbles (Fellers 2005). Adults deposit egg masses during the spring in microsites within relatively shallow, slow-flowing water, typically attaching egg masses, often in open sunlight, to the downstream sides of coarse substrates like cobbles and boulders (Lind 2005, Wheeler and Welsh 2008).

The rough-skinned newt was found in all channel types, with more detections in channel types III and I, respectively. Detections occurred where canopy closure was <84%, in channels that drained medium sized basins, with water temperatures >13°C, slopes under 10% and substrates comprised of gravel ranging from 9 to 42.5%. These conditions were more prevalent in alluvial channels, but also occurred in low gradient portions of headwater channels. In the aquatic phase the rough-skinned newt uses slow-moving or standing water for reproduction, with adults migrating seasonally between aquatic and terrestrial habitats, depending on elevation and life stage (Marks and Doyle 2005a). Our niche model probably reflects lotic channel conditions selected by adults for reproduction, but we have observed this species in ponds where they are present throughout the year (Welsh unpubl.) so we can not rule out the possibility that these same lotic aquatic conditions function in other aspects of their natural history.

Despite a presence along all channel types, the western fence lizard was far more abundant along alluvial channels, where numbers increased in areas with warmer water, high pebble substrate, and boulders <25%. This lizard is not a riparian obligate but individuals will utilize dry channel environments, seeking areas where streambeds are exposed as flows retreat in the dry season creating conditions where they can forage from perches on large coarse substrates on invertebrates emerging from the wetted channel (Sabo and Power 2002). The strong relationship with warm water is likely a surrogate for areas of high availability of emergent invertebrate prey.

The Pacific aquatic garter snake was found along all channel types, but was much more abundant along alluvial channels. Greater drainage area was the best predictor of these highly aquatic snakes, with substrate and thermal attributes of alluvial channels also important. The mix of five different substrates in the niche model suggests that these snakes may select areas with heterogeneous mixtures of particle sizes. This could also be an artifact of the relative ease of seeing snakes on areas of fine substrates compared with rougher substrates where the snakes can be more cryptic and difficult to detect. However, given their use of a wide range of channel environments (Welsh et al. 2010), we believe their high numbers along alluvial channels is likely a response to greater prey availability. All age classes of aquatic garter snakes feed on amphibians, with adults shifting to bigger prey such as giant salamanders and salmonids fishes that only the larger snakes can pursue in deeper, swifter waters (Lind and Welsh 1994). Young snakes forage on tadpoles and small fishes in shallow stream margins (Welsh and Lind 2000). Alluvial channels offer both higher numbers and a higher diversity of prey for all age classes in conjunction with abundant open areas for thermoregulation.

Idiosyncratic distributions

The red-bellied newt, like the rough-skinned newt, migrates between terrestrial and aquatic environments (changing physiological phases), where it reproduces in flowing waters such as mountain brooks with clean rocky substrates (Marks and Doyle 2005b). Our model indicated aquatic conditions where they are found in both headwater and alluvial channels, but that appear to be more common in type III channels. Optimum conditions for these newts appear limited by a narrow range of water temperatures

(15–26°C) in areas with coarser substrates. The two newt species showed a high degree of overlap, co-occurring in both headwater and alluvial channels. However, the rough-skinned newt was much more widespread in the watershed. The red-bellied newt is restricted to southern portions of the Mattole, reaching their northern extent ∼5 km north-west of Honeydew (Kuchta 2005). We suggest that suitable aquatic micro-environments with high cobble, low gravel and pebble, and <15% sand, may be conditions that are absent further west and north, which could impose limits on their distribution much beyond Honeydew.

In this study the common garter snake was not detected along headwater channels but present along the other three types. However, this species is not a riparian obligate and occurs commonly in upland habitats (Welsh unpubl.). "Cobble" was the best but weak predictor of their occurrence, with the multivariate niche model only a slight improvement. These snakes were found more often in areas with gentle slopes and low roughness with intermediate amounts of gravel, cobble and boulder. Primarily terrestrial, common garter snakes will forage near and in water. The relationships we found with primarily alluvial channel conditions, and the poor niche model, suggests they are probably responding to high prey availability (e.g. yellow-legged frogs) and cover that facilitates their predation on these amphibians (Pope et al. 2008).

Community structuring

We examined relationships between the spatial patterns of the herpetofauna and catchment level fluvial/geomorphic process domains (Montgomery 1999) by documenting the associations with the products of these domains, the channel settings, their configurations (i.e. channel types), and their internal attributes. Our objective was to gain insight into the relationships between the fluvial network and the biology of members of each channel-associated assemblage within the metacommunity. Abiotic attributes appear to be acting on animal distributions at three spatial scales: the macro-scale (e.g. basin area), the meso-scale (i.e. channel types and their primary components such as pools, riffles, runs) and the micro-scale (e.g. microclimates and substrates at specific sites where animals were found). We found headwater and alluvial channels each supported distinct, uniquely-adapted species assemblages that were subsets of the larger meta-community (Table 5). We also found an assemblage of generalist riparian/aquatic species present in all channel types, each with distinct differences in relative abundance across the types. These species each appeared to respond to a unique set of attributes within or in the surrounding channel environment (Table 5). In addition, four species appeared to be responding more to prey availability than abiotic conditions (Table 5; northern alligator lizard, western fence lizard, aquatic garter snake, common garter snake); these relationships likely reflect seasonal use of these channel environments. Two species showed idiosyncratic distributions relative to the four channel types (Table 5, red-bellied newt and common garter snake). Lastly, we detected four species whose distributions and natural histories indicated little relationship with specific parts of the catchment network (Table 4, western toad, Pacific chorus frog, western

skink, and western terrestrial garter snake); these were not included in our analysis of assemblage structure.

Ectothermy has profound implications for habitat selection (Huey 1991) and other vital life history requisites among these taxa (Huey and Kingsolver 1989). The primary consequence is that available microclimates in the immediate environment are strong determinants of where a species can exist, reproduce, and maintain individual and population fitness (Magnuson et al. 1979). As such, it appears that the unique assemblages of reptiles and amphibians within the catchment metacommunity are the result of multi-scale fluvial and geomorphic processes and the attributes they create, interacting with the physiological limits and natural histories of each species. Species-specific associations with basin area, canopy cover and particular substrates, are expressions of the physiological limits and behavioral repertoires of each, and these facts are consistent with the concept of realized niche. Seen at the mesoscale, members of each channel type assemblage can be viewed as demonstrating niche overlap where they share physical space (e.g. in a pool or riffle), but each utilizes different and unique aspects surrounding and within these channel environments. These findings are reminiscent of the classic differences between individualistic (Gleason 1926) and climax (Clement 1936) schools in plant ecology, where it appears that views from different spatial scales resulted in different conclusions about the structuring of plant assemblages, with each valid depending upon the scale of resolution invoked.

While we make no claim to having falsified any hypotheses, the evidence reviewed here is contrary to the neutral model of interspecific equivalence. It supports instead the view that, regardless of spatial overlap within assemblages, each species expresses a unique spatial pattern based on physiological and behavioral constraints resulting from their respective realized niches (Chase and Leibold 2003). For example, the members of the two most distinct mesoscale patterns appear to be in part respond-ing to thermal amelioration in the mostly closed canopy steep headwater channels, or its absence in the more open low-gradient alluvial channels. The range of available microclimates combined with that of substrates within these channel types provides a mosaic of conditions with each species using distinct but inter-related attributes, thereby forming multi-species assemblages (Morris 2003, Resetarits 2005).

It appears that fluvial and geomorphic disturbance processes are the ultimate determinant of network distribu-tion patterns. These processes dictate both channel sur-roundings and internal conditions, directly influencing vegetation structure (Montgomery 1999), which dictate microclimates (Chen et al. 1999); together with the fluvial processes they determine available within-channel environ-ments and fine-scale distributions of individuals. Each species member of an assemblage is responding to a distinct combination of abiotic attributes, controlled by processes acting at a range of spatial scales and across scales (Peters et al. 2007). These attributes dictate each species' options and ultimately their spatial relationships and interactions. Accordingly, we would describe the processes that struc-ture these assemblages as follows: meteorological events drive periodic fluvial disturbances that act together with

geomorphic and botanic processes to create unique channel environments, each with a set of microclimates and fine-scale physical attributes that determine the spatial arrangement of the member species of each assemblage. Interactions among co-existing species that would occur in the dynamic environments of this disturbance-driven network would be short-lived so any competitive advantage would be temporary and transitional. In effect, perpetual change drives the interplay of life in this network and likely many other ecosystems when the full dimensions of space and time are considered. Such system dynamics make competitive exclusion at larger scales extremely remote (Huston 1979), and favor instead the long-term co-existence of competing species (cf. Chesson and Huntly 1997). These results are most consistent with the species-sorting perspective of metacommunity theory because of the strong abiotic influences on populations and species interactions and the concomitant responses of the predator species.

Although the species-sorting perspective of metacommunity theory best explains the structuring of the different elements of the Mattole metacommunity, combining this with the mass-effects perspective better explains some distributions. Larvae and metamorphs of the foothill yellow-legged frog and western toad reach high numbers for short durations in specific channel environments. Consistent with species-sorting, each is associated with different local abiotic conditions (lotic and lentic sites, respectively) within the same channels. However, these early life stages metamorphose and leave the channel network in large numbers to disperse into upland habitats with the onset of fall rains, more consistent with the mass-effects perspective. Consequently, the spatial dynamics of these two anurans, and also perhaps some of their predators, are better explained by combining these two metacommunity perspectives (Amarasekare 2000). Amphibians with complex life cycles require studying each life stage (Wilbur 1984) and integrating multiple perspectives to address their spatial dynamics (Joly and Morand 1994, Urban 2004, Richter-Boix et al. 2007, Werner et al. 2007b).

Our findings here on the role of network habitat heterogeneity, and our earlier results that also demonstrated the importance of riparian and aquatic microclimates (Welsh et al. 2005a), are remarkably consistent with the findings of Cardinale et al. (2006) who explored multiple hypotheses to explain micro-floral diversity patterns in stream systems. They found patterns of algal and periphyton diversity in tributaries of the mid-Atlantic (USA) varied along two interacting axes, one of time since disturbance and one of productivity. The hydrogeomorphic process domains that shape channel types (Montgomery 1999) are based on disturbances, with their frequencies, magnitudes and durations associated with different portions of the channel network (Montgomery 1999, Fig. 7 and 8). Aquatic plant productivity in a channel network, while certainly influenced by process domains (Montgomery 1999), is primarily a result of the amount of solar energy reaching the streambed allowing plant photosynthesis and influencing water and substrate temperatures. The amount of solar radiation captured along a channel is determined by aspect, topography and the forest canopy. Similar to algae and periphyton, amphibian and reptile reproduction (=productivity) is greatly influenced by solar radiation (i.e. 10 of our 14 models contained water temperature, canopy or both; Table 5) and how it affects microclimates (Wells 2007). While not directly comparable given differences in taxa, approach and methodology, we are struck by the similarities between our study and Cardinale et al. (2006). In both cases disturbance regimes interacting with solar radiation appear to shape patterns of diversity among resident network organisms (see also Huryn and Wallace 1987, Kiffney and Roni 2007, Werner et al. 2007a).

The multi-scale aspects of the use of space by the majority of members of the aquatic/riparian herpetofaunal metacommunity of the Mattole are consistent with the recently developed species-sorting perspective of metacommunity theory (Leibold et al. 2004). However, it is also consistent with the disturbance-based riverine patch dynamics concept (Townsend 1989; see also Pringle et al. 1988, Resh et al. 1988) in conjunction with the niche-based (Chase and Leibold 2003) view of ecological processes. Townsend's (1989) concept describes a system of dynamic variation in stream habitats and associated communities with disturbance as the re-set mechanism. Townsend's (1989) views are closely aligned with the Southwood (1977) concept of species-specific habitats. Townsend's (1989) concept envisions an ever-changing, disturbance-driven, patch mosaic, with constantly renewing diverse habitats that accommodate a range of different species-specific tactics and strategies (Southwood 1988), enabling the co-existence of a full complement of stream organisms (see also Townsend and Hildrew 1994, Townsend 1996). Different species exercise their particular niche-based competitive advantages as time and space permit, with competition, predation, extinction, and re-colonization acting as secondary processes within the dynamic matrix of physical habitats. Townsend (1989) proposed this hypothesis to explain stream community dynamics based on Pickett and White's (1985) view of disturbance dynamics in diverse ecosystems (where it applies as well to strictly terrestrial community dynamics, although here the temporal axis is often more stochastic with longer periods of stability). Hutchinson (1951, 1953) was among the earliest to link disturbance with species co-existence (see also Wilkinson 1999). Regardless, given the complexity of disturbance processes (van der Maarel 1993), debate on their influence on ecological communities will no doubt continue (Roxburgh et al. 2004, Johst and Huth 2005), with evidence from tropical forests with relatively long-term stability indicating that disturbance may have varying influence on maintaining biodiversity along a tropical moisture gradient (Bongers et al. 2009). It may be that higher biodiversity in the tropics is the result of strong environmental gradients in these climatically favorable regions (e.g. Andes, Himalayas), along with their re-setting by diverse disturbance regimes (e.g. from gap dynamics and fluvial processes to plate tectonics), interacting with more unique lineages extant over long periods (Wiens et al. 2009) that combine to create optimal templates for greater speciation.

In a recent review of stream community theories (Lepori and Hjerdt 2006), the authors found that fluvial disturbance, either the positive effects emphasized by those favoring biotic interactions, or the negative effects

emphasized by those favoring physical processes, was a common theme among hypotheses. Interestingly, they found the differing views to be scale dependent at small spatial scales fluvial disturbances had negative effects on biodiversity; at larger spatial scales, and over longer terms, these same disturbances had positive effects. They concluded that understanding the processes creating and maintaining heterogeneity in riverine networks requires a broader perspective, emphasizing the importance of both scale and context in developing sound theory, and indicating a need for multi-dimensional perspectives to unravel these complex processes (Lepori and Hjerdt 2006).

Conclusions

Community ecology has seen the recent emergence of metacommunity perspectives, offering four views to explain spatial relationships among sets of local communities (or assemblages) linked by dispersal and comprised of multiple potentially interacting species (Leibold et al. 2004). These concepts have been proposed as a means of advancing our understanding of multi-species spatial dynamics across multiple scales of spatio-temporal organization. The meta-community perspectives include: mass-effects, patch dynamics (used differently than by Townsend 1989; see below), species-sorting, and a neutral model (Holyoak et al. 2005b). Recent work examining the application of these perspectives in aquatic systems with amphibian assemblages has focused on lentic or pond systems; these studies found that a combination of these concepts best explained observed patterns (Urban 2004, Van Buskirk 2005, Richter-Boix et al. 2007). Of the four perspectives, species-sorting, based on the explanatory power of niche theory, best explained the majority of our data. This hypothesis is consistent with the view that across larger scales (e.g. large catchments) dynamic disturbance-driven heterogeneous environment interacts with unique species attributes to shape the spatial patterns of the herpetofauna. Inter-species interactions like predation and competition (and mass effects) appear to play proximate roles in the temporal cycling of their individual numbers at finer spatial scales.

Townsend's (1989) patch dynamics model should not be confused with the patch dynamics perspective of metacommunity theory that assumes all patches are identical (Leibold et al. 2004), a use contrary to its initial application in plant ecology (Thompson 1978) and subsequently in stream ecology (Pringle et al. 1988, Townsend 1989). The metacommunity usage is contrary to that of Thompson (1978) and Townsend (1989), and appears to derive from the competition-colonization trade-offs of species among identical patches (Levins and Culver 1971). Moreover the Townsend (1989) model of community organization is close to, if not identical with, the species-sorting perspective of metacommunity theory. We could find no differences between these two concepts, and believe that Thompson's (1978) use has precedence for the term ''patch dynamics'' as well as its application to a niche-based community organizing hypothesis (Pickett and White 1985). This situation is unfortunate because both camps are attempting to understand and describe universal community organizing processes. In reviewing the metacommunity literature, we could find no evidence that its proponents (Leibold et al. 2004, Holyoak et al. 2005a) evaluated the literature on stream ecology and its various community structuring hypotheses (Lepori and Hjerdt 2006). We find it of interest that these two schools of community organization appear to have developed independent of one other, and suspect it may be the result of the focus by metacommunity theorists predominately on discrete systems while those who studied stream networks focused on systems that are quite the opposite. Metacommunity perspectives also, perhaps because they implicitly rather than explicitly address space (Leibold et al. 2004), minimize the role of the dynamic restructuring of localities and hence the role of disturbance on community composition (i.e. Pickett and White 1985). A key concept for understanding the role of disturbance in ecosystems is that of ''patch dynamics''; these two concepts in combination identifies the source and means by which heterogeneous local and regional environments are maintained, as well as the nature of the processes that can promote high resilience and high biodiversity in ecosystems (van der Maarel 1993, Wilson 1994). In order to avoid any confusion over the use of this term and its first application (Thompson 1978), we would encourage metacommunity proponents to propose an alternative for their use of ''patch dynamics'' and to address the differences (if any) with Townsend's (1989) use of this term, and the niche-based hypothesis of community organization and their species-sorting perspective.

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