Faunal assemblages and multi–scale habitat patterns in headwater tributaries of the South Fork Trinity River – an unregulated river embedded within a multiple–use landscape

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Abstract

Faunal assemblages and multi–scale habitat patterns in headwater tributaries of the South Fork Trinity River – an unregulated river embedded within a multiple–use landscape.— Headwaters can represent 80% of stream kilometers in a watershed, and they also have unique physical and biological properties that have only recently been recognized for their importance in sustaining healthy functioning stream networks and their ecological services. We sampled 60 headwater tributaries in the South Fork Trinity River, a 2,430 km^2, mostly forested, multiple–use watershed in northwestern California. Our objectives were: (1) to differentiate unique headwater types using 69 abiotic and vegetation variables measured at three spatial scales, and then to reduce these to informative subsets; (2) determine if distinct biota occupied the different tributary types; (3) determine the environmental attributes associated with the presence and abundance of these biotic assemblages; and (4) using niche modeling, determine key attribute thresholds to illustrate how these biota could be employed as metrics of system integrity and ecological services. Several taxa were sufficiently abundant and widespread to use as bio–indicators: the presence and abundance of steelhead trout (*Oncorhynchus mykiss*), herpetofauna (reptile and amphibian) species richness, and signal crayfish (*Pacifastacus leniusculus*) represented different trophic positions, value as commercial resources (steelhead), sensitivity to environmental stress (amphibians), and indicators of biodiversity (herpetofauna species richness). Herpetofauna species richness did not differ, but abundances of steelhead trout, signal crayfish, and amphibian richness all differed significantly among tributary types. Niche models indicated that distribution and abundance patterns in both riparian and aquatic environments were associated with physical and structural attributes at multiple spatial scales, both within and around reaches. The bio–indicators responded to unique sets of attributes, reflecting the high environmental heterogeneity in headwater tributaries across this large watershed. These niche attributes represented a wide range of headwater environments, indicating responses to a number of natural and anthropogenic conditions, and demonstrated the value of using a suite of bio–indicators to elucidate watershed conditions, and to examine numerous disturbances that may influence ecological integrity.

Key words: Headwater tributaries, Bio–indicators, Multi–scale, Ecological integrity.

Resumen

Comunidades faunísticas y patrones de hábitats multiescala en las cabeceras de los afluentes del río South Fork Trinity – un río de caudal no regulado encajado en un paisaje de usos múltiples.— Las cabeceras pueden representar el 80% de los kilómetros de recorrido en una cuenca fluvial y poseen unas propiedades físicas y biológicas únicas, cuya importancia hasta hace poco no se habían reconocido para el sostenimiento de un funcionamiento sano de las redes de cuencas y sus servicios ecológicos. Tomamos muestras de 60 cabeceras de los afluentes del río South Fork Trinity, una cuenca de 2.430 km^2, boscosa en su mayor parte y de múltiples usos, situada en el noroeste de California. Nuestros objetivos eran: (1) diferenciar tipos de cabeceras únicos utilizando 69 variables abióticas y vegetales, medidas a tres escalas espaciales, y luego reducirlos a subconjuntos informativos; (2) determinar si distintos biotas ocupaban los distintos tipos de afluentes; (3) determinar las características medioambientales asociadas con la presencia y abundancia de dichas comunidades bióticas; y (4) utilizando una modelización de nichos, determinar los umbrales de los atributos claves para ilustrar cómo estos biotas podrían emplearse para la medición de la integridad del sistema y los servicios ecológicos. Varios

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taxones fueron suficientemente abundantes y extendidos para utilizarlos como bioindicadores; la presencia y abundancia de la trucha arco iris (*Oncorhynchus mykiss*), la riqueza en especies de la herpetofauna (reptiles y anfibios) y el cangrejo señal (*Pacifastacus leniusculus*) representaban diferentes posiciones tróficas, el valor como recursos comerciales (la trucha arco iris), la sensibilidad al estrés ambiental (anfibios), e indicadores de la biodiversidad (riqueza de especies de la herpetofauna). La riqueza de especies de la herpetofauna no difirió, pero la abundancia de la trucha arco iris, del cangrejo señal, la riqueza de anfibios, difirieron significativamente entre los tipos de afluentes. Los modelos de los nichos indicaron que los patrones de distribución y abundancia, tanto en los ambientes acuáticos como en los ribereños, estaban asociados con atributos físicos y estructurales a multiples escalas espaciales, tanto dentro como alrededor de los tramos acuáticos. Los bioindicadores respondieron a series únicas de atributos, reflejando la elevada heterogeneidad ambiental en las cabeceras de los afluentes en toda esta gran cuenca. Dichos atributos de los nichos representaban una amplia gama de ambientes de cabeceras fluviales, indicando respuestas a una serie de condiciones naturales y antropogénicas. Se demostró el valor de utilizar una serie de bioindicadores para elucidar las condiciones de las cabeceras y para examinar las numerosas perturbaciones que pueden influir sobre la integridad ecológica.

Palabras clave: Cabeceras de afluentes, Bioindicadores, Multiescala, Integridad ecológica.

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Introduction

Understanding ecosystem dynamics and cross–scale interactions (Peters et al., 2007) are challenging in dendritic riverine ecosystems where geomorphology, hydrology, and landscape processes influence biotic communities at multiple spatial and temporal scales (Ward, 1989, 1998; Wiens, 2002; Allan, 2004; Lowe et al., 2006). Whole watersheds are logical units for examining these ecological processes because they are contained within distinct natural boundaries (*i.e.*, Montgomery, 1999; Benda et al., 2004; Lowe et al., 2006). There is also a growing body of knowledge about watershed–scale processes and how they shape and influence ecosystem services (*e.g.,* Naiman & Bilby, 1998; Fagan, 2002; Wiens, 2002; Allan, 2004). This knowledge can guide comparative studies and allows key principles of ecosystem processes to be uncovered (*e.g.,* Grant et al., 2007). It can also promote the development of management strategies designed to enhance and protect the functionality of these systems (Lowe et al., 2006). By learning how far ecosystems can be perturbed without harming their integrity, resource managers can make informed decisions regarding natural resources. Ecological processes like stable food webs that provide abundant fish for harvest, or high and stable biodiversity that can facilitate ecosystem resilience, are essential to maintain sustainable riverine ecosystems. Only ecosystems that are managed sustainably will provide perpetual services without losing process elements and system integrity (Westra et al., 2000; Hooper et al., 2005; Karr, 2006).

First, 2nd and 3rd–order channels (Strahler, 1957) (hereafter headwaters) can comprise over 80% of channel length in a watershed (Dunne & Leopold, 1978). These small tributaries and their integral riparian environments are hotspots for watershed faunal diversity (*e.g.*, Naiman & Decamps, 1997; Ward, 1998; Ward & Tochner, 2001; Fernandes et al., 2004; Sabo et al., 2005). The loss of this diversity can have negative consequences for entire ecosystems and their ability to function and provide sustainable services (*e.g.*, Naeem, 1994; Loreau et al., 2002; Duffy, 2003; Dobson et al., 2006). Here, we focus on the ecological attributes of headwater tributaries and their unique aquatic and riparian animal assemblages (Lowe & Likens, 2005; Richardson et al., 2005). Headwater streams provide key functional links with terrestrial (Nakano & Murakami, 2001) and downstream environments (Wipfli et al., 2007; Freeman et al., 2007); they improve water quality, sort, clean, and deliver coarse organic substrates needed by stream organisms for cover and reproduction, and provide nutrients for fish. Knowledge of how watershed level processes can potentially affect these functions is paramount for managing and maintaining the ecological integrity of riverine ecosystems (Meyer et al., 2007).

Our first objective was to describe unique low–order tributary types within the South Fork Trinity River (SFTR) watershed based on attributes representing a wide range of conditions, ecological processes, and disturbance regimes. To do this we used a combination of upland, riparian, and aquatic attributes associated with 60 randomly selected tributaries from across the entire watershed. We initially considered 69 variables, representing three spatial scales and numerous ecological processes, in a cluster analysis to distinguish unique tributary types. We followed with a series of scale–specific discriminant analyses, which served to reduce the number of independent variables and to detect those most informative attributes within and across scales. Our second objective was to determine if the abundance, evenness and species richness of common species or species groups differed between reach types, seeking potential bio–indicators. Our third objective was to model the distribution patterns of the bio–indicators using refined sub–sets of those independent variables used to differentiate the reach types. Understanding the environmental gradients that influence these bio–indicators can reveal important thresholds and key relationships that enable their uses as indicators of ecosystem integrity.

Material and methods

Study area and sampling

The SFTR is a 2,430 km^2 catchment in the Klamath–Siskiyou bioregion of northwestern California, USA. (fig. 1). This bioregion is a globally significant area of biodiversity due to its age, range of geomorphologies, soil types and moisture gradients, conditions that have created high endemism and many relict species (Whittaker, 1960, 1961; Welsh, 1994; DellaSalla et al., 1999; Sawyer, 2006). The SFTR is dominated on the west side by Douglas–fir (*Pseudotsuga menziesii*) mixed conifer/hardwood forest, with lesser amounts of ponderosa pine (*Pinus ponderosa*), montane hardwood–conifer, montane hardwood, montane riparian, and blue oak (*Quercus douglasii*)–gray pine (*Arceuthobium occidentale*) forests (Mayer & Laudenslayer, 1988); drier forest types are more dominant on the east side. Ownership is a mixture of federal (US Forest Service) and private lands. Periodic fires constitute an important natural disturbance with the SFTR experiencing median fire intervals of 11.5–16.5 years (Taylor & Skinner, 2003). The conservation strategy of the US Northwest Forest Plan (Thomas et al., 2006) lists the SFTR as a key watershed for the preservation of salmonid fishes.

A stratified random approach was used to distribute 60 sample locations across the entire watershed in order to capture the full range of headwater aquatic and riparian conditions (fig. 1). Headwaters were located using a Geographic Information System (GIS; ESRI, Redlands, CA) grid (cell size 1 km^2) overlaid on the watershed. Fifteen equally sized polygons were created from north to south, with four 1 km^2 cells randomly selected in each one. The centers of these grid cells were used to locate the closest headwater tributary. GIS–derived locations were visited and searched for potential sample reaches within 2 km of each starting point.

The search criteria consisted of locating a ≥ 300 m stream reach of accessible perennial surface flow shallow enough to sample without diving. Reaches near abrupt changes in vegetation (*i.e.*, edge) and those surrounded by highly heterogeneous forest types were avoided. Although the SFTR contains many small roads used for timber harvesting and private access, this network was not used to find locations; channel access at or near roads required locating reaches ≥ 50 m upstream.

Data collection

We sampled sub–basins 14 to 1,900 ha in size and measured variables at three nested spatial scales that are not mutually exclusive.

The sub–basin scale

Attributes at the sub–basin scale were coarse in resolution, including topographic features and vegetation mosaic elements representative of the entire sub–basin. Features included relative amounts of the primary forest types, annual minimum and maximum air temperatures and solar illumination, and geographic features including aspect and mean elevation. Values for sub–basin attributes were determined in GIS to characterize the larger spatial context in which reaches were embedded (appendix 1; 22 sub–basin scale variables).

The reach scale

Reach scale variables characterized the proximate tributary environment by measuring the structure and plant species composition immediately surrounding each reach (*e.g.*, tree species composition by size class, ground cover vegetation). Variables were collected in three circular plots centered on the reach and spaced equally at 50, 150, and 250 m. Each reach included 1/10th and 1/5th ha concentric circles, and one soil station per side, 25 m above the channel (appendix 1: 28 reach scale variables).

The habitat unit scale

Habitat unit scale variables characterized conditions within each reach, including canopy cover and stream channel morphology. We deployed water temperature data–loggers from June to October at the bottom of each reach to measure summer water temperatures. These data were used to calculate a mean weekly maximum water temperature (MWMT; Dunham et al., 2005). MWMT is derived by averaging the daily maximum water temperatures for the hottest week of the summer. At this latitude, greater daily extremes occur in summer and are more limiting than winter minimums for cool temperate–adapted fauna such as salmonids and many amphibians (Magnuson et al., 1979; Huey, 1991). We estimated fine sediments by calculating mean sediment depths from 10 pools in each reach (*e.g.*, Welsh & Ollivier, 1998) (appendix 1: 19 variables).

Animal sampling

Two teams collected fish, amphibian and reptile data during daylight hours in June through September from 2000–2003. The herpetofauna team used a four–tiered aquatic/riparian/upland approach consisting of: (1) a channel–focused visual encounter survey (VES; Crump & Scott, 1994) of each 300 m reach, (2) 10 area–constrained (ACS) cross–channel aquatic sampling belts, (3) one ½–hour seep–focused VES search, and (4) one upland (terrestrial) 4–hour VES search conducted on clear days between 10 am and 4 pm (Welsh & Hodgson, 1997). The channel–focused VES consisted of a single observer walking slowly upstream recording all observations. The observer walked three to four paces, stopped and scanned the wetted channel and bank–full width for animals. The 10 ACS consisted of one to two observers systematically searching a defined stream area, using acrylic view boxes to search underwater before, during, and after removing all detachable channel substrates. A small dip net, held immediately downstream of the view box, captured dislodged animals. Locations of the ACS belts were determined by dividing the reach into five 60 m sub–sections and locating each belt using random numbers. Within each sub–section, one "fast water" and one "slow water" habitat unit was selected based upon relative water velocity (*e.g.*, Hawkins et al., 1993). Within each habitat unit, 1 m long cross–stream belts were situated in accessible habitat; areas that prohibited thorough searching (i.e., large downed logs) were avoided. The seep VES consisted of searches in seeps or springs detected during the channel VES. The upland VES occurred at least 10 m above riparian vegetation and was conducted for two–person hours on each side of a reach; data were collected at 40 reaches in 2003. The herpetological richness analysis included incidentals from 20 reaches re–sampled in 2001 and 2002.

Fish data were collected in 2001, but due to reduced late–summer flows and equipment failure only 55 of 60 reaches were sampled. The two–person fish team used a Smith–Root backpack electrofisher to sample fish. While electrofishing, we minimized current and set voltage to reduce animal trauma while facilitating capture (Reynolds, 1996). Each 300 m reach was divided into three sections. Within each 100 m subsection, we used six random numbers to locate sample units (18 units sampled per reach). When arriving at the first random distance from the bottom of each section, we electrofished the closest intact habitat unit (fast or slow) using a multiple–pass method. Block nets were not used because tributaries were small and water velocities low. Stunned animals were captured with nets and held in stream water. Animals seen but not captured were counted and identified to species and size category. To ensure conservative estimates, the number of un–captured animals enumerated during the successive *n* + 1 passes could not exceed the number encountered during pass *n*, unless obvious differences in size were observed. After the first habitat unit, the next random distance upstream was used to find the nearest opposite type (fast or slow water). The fish team sampled ≥ four days before or after the herpetofauna team.

Data analysis

Cluster analysis of environmental variables

Our overall objective was to examine the full range of aquatic and riparian conditions that characterized SFTR headwaters, and relate those conditions to particular faunal distributions. Therefore, we did not constrain our sampling to a specific set of attributes other than stream order. This enabled us to incorporate the considerable heterogeneity along multiple environmental gradients and across multiple spatial scales to characterize both reaches and the surrounding sub–basins in which they were embedded. However, we did assume that sufficient commonalities would exist among the 60 tributaries that would allow us to detect a reasonable number of unique sets based on their shared positions in the dendritic network and along environmental gradients. This would enable us to both compare reach types and to discern possible reasons for differences in animal distributions and abundances. To this end, we used non–hierarchical K–Means cluster analysis (Hintze, 2000), which minimizes the within–cluster sums of squares. We eliminated one variable each from six highly correlated ($r \geq 0.70$) pairs, resulting in 69 variables from three spatial scales (appendix 1), variables were used with a K–Means algorithm (with 100 random starts and 1000 iterations) to determine unique reach types and assign group membership for each of the 60 reaches.

Multi–scale discriminant analysis

The clustering procedure established four unique reach groups, but it provided no information on the relative importance of the 69 variables. We employed discriminant analysis (DA) to determine which variables differed among the four types and to rank their relative importance (Green & Vascotto, 1978; McCune & Grace, 2002). Ecological subsets were arranged by spatial scale and analyzed in a hierarchical series of DAs (SAS Institute Inc., 2003) to identify those variables that best determined group membership in each subset and at each scale. Variables at each scale were divided into subsets representing structural, compositional, or climatic attributes of the landscape, forest stand or stream environment (appendix 1) (*e.g.*, Welsh & Lind, 1995). Four–group DAs were performed on each subset at each scale (appendix 1). The null hypothesis tested was that there were no differences between reach types for the variables within each subset. For model–building, variables were entered if the *P* value for the partial *F* statistic was ≤ 0.10 and removed it if it was > 0.05. A linear or quadratic discriminant function was calculated based on the variables selected. Bartlett's modification of the likelihood ratio analysis was used to test the homogeneity of variance–covariance matrices (SAS Institute Inc., 2003).

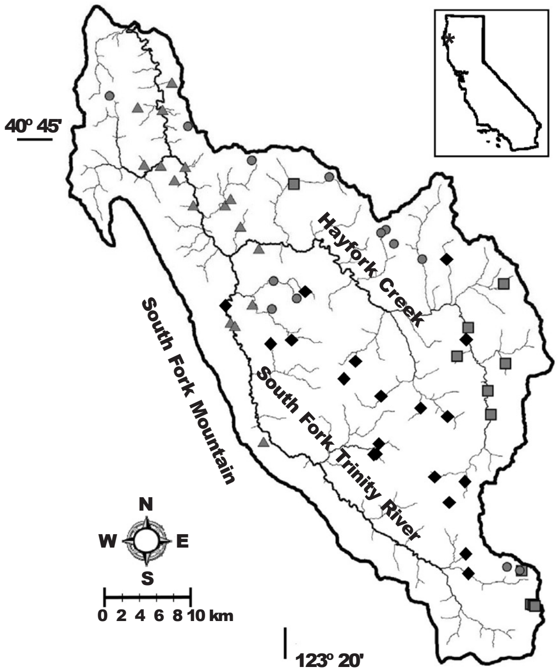

Fig. 1. The South Fork Trinity River Watershed, California, USA, with sampling locations of the 60 headwater reaches. Circles represent reach Group 1 (n = 13), triangles represent reach Group 2 (n = 16), squares represent reach Group 3 (n = 11), and diamonds represent reach Group 4 (n = 20). See methods for details on the determination of group membership.

Fig. 1. La cuenca del río South Fork Trinity, California, USA, con las 60 localizaciones de muestreo cercanas a las cabeceras. Los círculos representan el Grupo 1 de localizaciones (n = 13), los triángulos el Grupo 2 (n = 16), los cuadrados el Grupo 3 (n = 11), y los diamantes el Grupo 4 (n = 20). Para los detalles sobre la pertenencia a un grupo determinado, ver los métodos.

We then combined the significant variables from the DAs of the ecological subsets and performed composite DAs at each spatial scale. Our objective was to derive a reduced set of variables that best distinguished the reach types at each scale. We then ran a final multi–scale DA with the reduced number of variables from each scale–specific DA. With this iterative approach we were able to find those variables that were best able to discriminate between the reach types at each scale, and across scales, and thus reduce the initial number of environmental variables from the cluster analysis to just those that provided both the greatest discriminatory power and the most information on how the tributary types differed. We tested the ability of our DA models to accurately predict whether or not the data from a given reach fit a particular reach type (*i.e.*, classification success) using both a jackknife procedure and a re–substitution test (SAS Institute Inc., 2003). Cohen's Kappa statistic (Titus et al., 1984) was computed for each model to indicate the classification success compared with chance. For this test, we equalized the prior probabilities of group membership because the true proportion of sites in each of the reach groups was unknown prior to the analysis (SAS Institute Inc., 2003).

Analysis of animal distributions

We ran ANOVAs (SAS Institute Inc., 2003) to examine the abundances, richness and evenness of faunal assemblages and individual species among the reach types, testing the null hypothesis of no difference in abundance for each assemblage or species across the four types. Our approach was based on the assumption that differences in animals among the reach types could be directly or indirectly linked to the different ecological attributes of these types. An example of an indirect link is the occurrence of tailed frogs (*Ascaphus truei*), a cold–water–adapted species whose presence can represent the capacity of streams to support similarly adapted fauna such as coho salmon (*Oncorhynchus kisutch*; Welsh & Hodgson, 2008). For parametric ANOVA we used log or square root transformations to reduce skewness. The distribution of crayfish could not be normalized so we used a non–parametric Kruskal–Wallis ANOVA. When ANOVAs were significant, we used the Student–Newman–Keuls (SNK) *a posteriori* multiple comparisons to test group differences. We set $\alpha \leq 0.10$, as this level reduces chances of type II errors and is more appropriate for detecting ecological trends (Shrader–Frechette & McCoy, 1993).

Predictive models

To examine the relationships between the environmental attributes (appendix 1), and amphibian richness, and those individual species that varied by stream group based on ANOVA, we evaluated competing predictive models comprised of subsets of these attributes. Lizard diversity and western fence lizard (*Sceloporus occidentalis*) abundance varied significantly among stream groups based on ANOVA, but they are not riparian or aquatic obligates and their predictive models were weak so they were omitted in this final analysis. Using Spearman correlation analyses, we reduced the environmental attributes to those significantly correlated ($\alpha \leq 0.1$) with each of five bio–indicators. Relationships between these attributes and faunal metrics were assessed with non–parametric multiplicative regression analysis (NPMR) (McCune, 2006) using the software HyperNiche version 1.0 (McCune & Mefford, 2004). NPMR, designed for multivariate niche modeling, seeks to optimize a fit of detection data along multiple environmental gradients (*i.e.*, in multi–dimensional attribute space) rather than adhere 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 at a given point in the predictor space by heavily weighting points that are near a target point, and giving less weight to distant points (using a minimum of three points); data points employed in the model comprise the ecological neighborhood. In model generation, we set the minimum neighborhood size to five percent of each sample. The term "tolerance" is used to describe how broadly information is borrowed from nearby areas in predictor space while attempting to estimate the value of a particular attribute around a target point (McCune, 2006); it is thus akin to the niche breadth for that 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 to a particular attribute uses information from a large neighborhood of data points (McCune, 2006). We used a local mean estimator and Gaussian weighting function in all–possible–subsets regression for each set of 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 (Antoine & McCune, 2004). We used the HyperNiche exhaustive search mode to determine best models, with up to six predictor variables, based on xR^2 (*e.g.*, Giordani, 2007). Relationships between bio–indicators and variables are reported as positive (+), negative (–), or humped/U–shaped (^).

Results

Cluster analysis

The K–Means cluster analysis considered options from two to six groups, with the four group solution the most informative; variation in the data explained dropped from 76.1 to 71.7% beyond four groups, declining more steeply thereafter. The numbers of tributaries in these groups were 11, 13, 16, and 20. We examined the Euclidean distance matrix values for the four group solution, and present scatter plots illustrating group separation (fig. 2).

Discriminant analyses

Distinguishing tributary groups at the sub–basin scale

We performed a DA of 22 sub–basin variables to detect differences in the landscape settings of the four tributary groups (table 1). We found five geographic, three climatic, three disturbance, and one geologic attribute differed among the reach groups at the sub–basin scale (table 1). The best model was that of geographic relationships; the climate model was second, and the disturbance regime model third (table 1). When these 12 variables were combined in a sub–basin scale DA, seven contributed to the composite model; four geographic, two climatic, and one geologic (table 1).

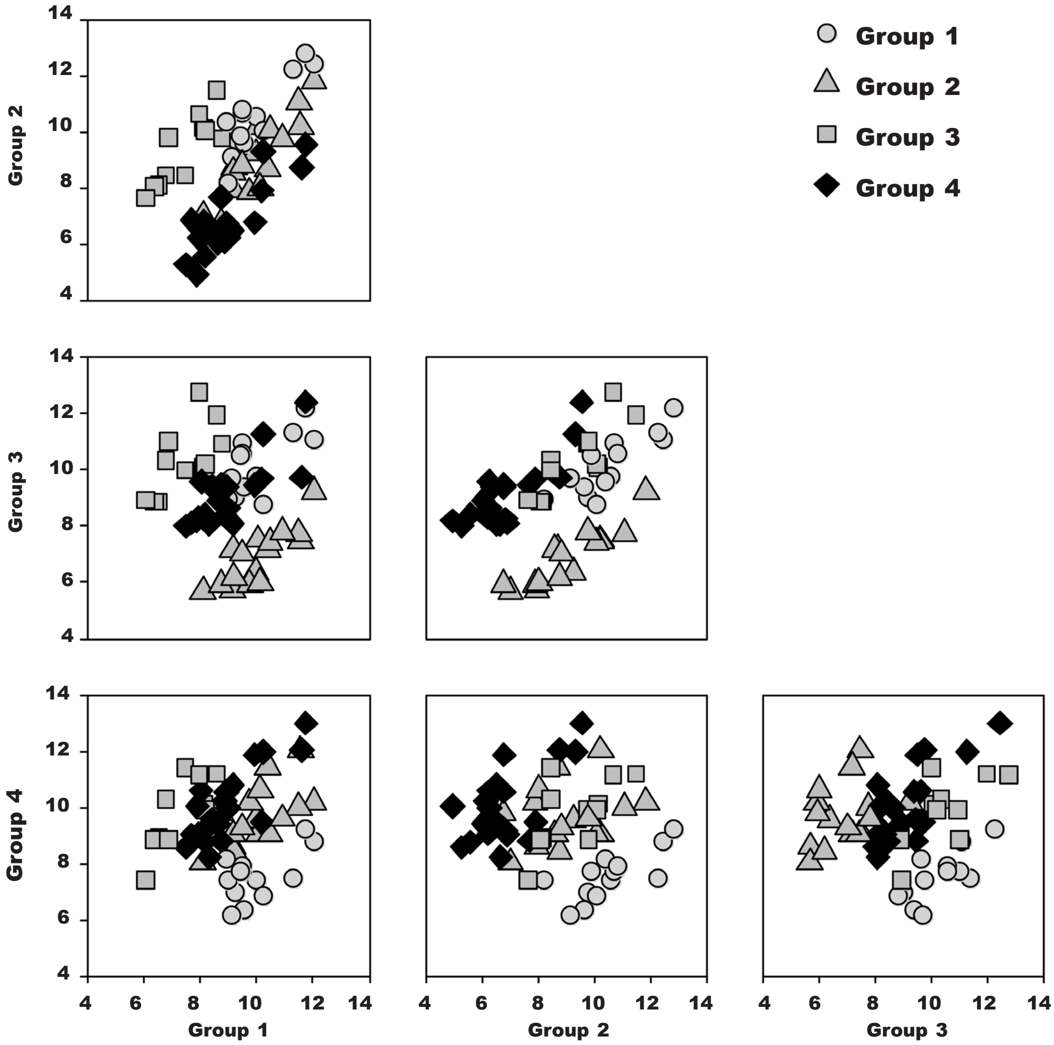

Fig. 2. Scatter plots of Euclidian distances showing six views of the separation of the four group solution from the K–Means cluster analysis (R Development Core Team, 2009).

Fig. 2. Diagrama de dispersión de las distancias euclidianas, que muestra seis visiones de la separación de los cuatro grupos a partir del análisis de conglomerados K–Means (R Development Core Team, 2009).

Distinguishing tributary groups at the reach scale

Twenty–eight variables were used to examine differences in terrestrial environments adjacent to the tributary groups (table 2). The best model consisted of tree and log attributes, with five forest structure and tree composition variables differing (table 2). Other models indicated differences in understory and ground–level vegetation, ground cover, and the amount of upland forest canopy (table 2). The composite model derived from the DA of these 13 variables contained six attributes, three showed differences in numbers of small and large conifers, and medium hardwoods, and three indicated differences in riparian forest width, and amounts of ferns and leaf litter (table 2).

Distinguishing tributary groups at the habitat unit scale

Nineteen channel attributes were measured within the reaches (table 3). The aquatic conditions model was the best, indicating differences among groups in the amount of overhead channel canopy, percent of fine sediments (S–Star), and mean weekly maximum water temperature (MWMT) (table 3). Differences in aquatic substrates were indicated for percent boulders, pebbles, gravels, and visually estimated fine sediments (table 3). The composite model at this scale consisted of overhead canopy, fine sediments (S–Star), MWMT, percent boulders, and visually estimated fines (table 3).

Table 1. Results of discriminant analyses of 22 sub–basin variables. Variables were sub–set into four ecological components and analyzed separately: P. PRISM data; C. Count data; % Percent data; † Variable transformed for statistical analysis. Variables included that did not enter the models are: geographic relationships (basin aspect, † basin area); disturbance regimes († plantation [%], young conifers [%], late–seral trees [%], † grass and shrubs [%], † fire, stumps [C]); parent geology († HF geology); composite (road density, † road crossings, northing, mean temperature [P], hardwood trees [%]). CV. Canonical variable. (Means and standard deviations are for untransformed data.)

Tabla 1. Resultados de los análisis discriminantes de las 22 variables de las subcuencas. Las variables se clasificaron en cuatro componentes ecológicas y se analizaron por separado: P. Datos PRISM; C. Datos de recuento; % Porcentajes; † Variable transformada para el análisis estadístico. Las variables incluidas en los análisis pero que no entraron en los modelos son: relaciones geográficas (aspecto de la cuenca, † área de la cuenca); regímenes de perturbación († plantación [%], coníferas jóvenes [%], árboles seriales tardíos [%], † hierba y arbustos [%], † fuego, tocones [C]); geología original († geología HF, rocas metamórficas precretácicas); composición (densidad carreteras, † cruces carreteras, distancia hacia el norte, temperatura media [P], árboles leñosos [%]). CV. Variable canónica. (Las medias y las desviaciones estándar son de los datos no transformados).

	K–Means cluster groupings								Pooled within–group standardized CV		
	1 (n = 13)		2 (n = 16)		3 (n = 11)		4 (n = 20)				
Variables	Mean	SD	Mean	SD	Mean	SD	Mean	SD	CV1	CV2	CV3
Geographic relationships											
Easting	31.28	15.39	14.44	5.54	50.95	8.91	38.72	9.49	0.85	0.71	–0.93
Northing	46.53	19.10	53.97	12.37	26.29	19.22	28.21	11.26	–0.01	1.11	–0.87
Elevation	1226.00	171.15	647.50	189.76	1190.91	445.72	989.70	273.30	0.24	0.76	0.33
Illumination in December	135.33	26.32	96.05	24.67	86.48	31.86	98.26	23.88	–0.29	0.41	0.83
Slope (%)	0.18	0.07	0.19	0.08	0.12	0.08	0.06	0.04	–0.57	0.52	–0.69
Wilks' lambda = 0.072; *F* (*df* = 15,144) = 15.25; *P* < 0.0001											
Jackknife success (%) = 75.0; Cohen's Kappa = 0.660; *P* < 0.0001											
Climate											
Precipitation (P)	129.63	16.40	131.65	10.52	116.45	15.62	131.36	16.50	0.64	0.11	0.97
Mean temperature (P)	11.08	0.62	11.58	0.68	11.53	1.02	10.18	0.79	1.42	0.68	–0.13
Minimum temperature (P)	3.52	1.45	3.15	0.66	5.56	1.20	2.65	1.42	–1.25	0.44	0.50
Wilks' lambda = 0.261; *F* (*df* = 9,132) = 10.76; *P* < 0.0001											
Jackknife success (%) = 63.3; Cohen's Kappa = 0.507; *P* < 0.0001											
Disturbance regimes											
Road density	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.00	0.62	–0.88	–0.04
† Road crossings	1.08	1.85	3.06	4.48	1.45	2.11	9.00	10.11	0.37	0.74	–0.70
Hardwood trees (%)	0.20	0.20	0.21	0.17	0.24	0.16	0.40	0.20	0.62	0.07	0.85
Wilks' lambda = 0.433; *F* (*df* =12,141) = 4.36; *P* < 0.0001											
Jackknife success (%) = 51.7; Cohen's Kappa = 0.355; *P* < 0.0001											

Table 1. (Cont.)

	K–Means cluster groupings								Pooled within–group standardized CV		
	1 (n = 13)		2 (n = 16)		3 (n = 11)		4 (n = 20)				
Variables	Mean	SD	Mean	SD	Mean	SD	Mean	SD	CV1	CV2	CV3
Parent geology											
† RCM geology (%)	0.33	0.47	0.84	0.34	0.00	0.00	0.78	0.36	1.00		
Wilks' lambda = 0.506; *F* (*df* = 3,56) = 18.20; *P* < 0.0001											
Jackknife success (%) = 45.0; Cohen's Kappa = 0.280; *P* < 0.0001											
Composite model											
Easting	31.28	15.39	14.44	5.54	50.95	8.91	38.72	9.49	0.98	–0.74	–0.02
Minimum temperature (P)	3.52	1.45	3.15	0.66	5.56	1.20	2.65	1.42	–0.37	0.91	–0.69
Illumination December	135.33	26.32	96.05	24.67	86.48	31.86	98.26	23.88	–0.18	–0.22	1.01
Elevation	1226.08	171.15	647.50	189.76	1190.91	445.72	989.70	273.30	0.15	0.75	0.56
† RCM geology (%)	0.33	0.47	0.84	0.34	0.00	0.00	0.78	0.36	–0.38	–0.65	–0.12
Slope (%)	18.08	7.24	18.87	7.96	12.09	8.17	6.50	3.68	–0.77	0.25	0.12
Precipitation (P)	129.63	16.40	131.65	10.52	116.45	15.62	131.36	16.50	0.27	–0.56	–0.25
Wilks' lambda = 0.024; *F* (df = 24,143) = 15.63; *P* < 0.0001											
Jackknife success (%) = 85.0; Cohen's Kappa = 0.797; *P* < 0.0001											

Distinguishing tributary groups across spatial scales

Combining variables from the three scale–specific composite models into a multi–scale model resulted in a final model comprised of 10 variables —five from the sub–basin scale, three from land–surrounding–the–reaches, and two from within the reaches (table 4). This model indicated that tributaries in the SFTR watershed were best distinguished by easting, sub–basin slope, illumination in December, annual minimum air temperature, mafic volcanic rock and chert, numbers of conifers 28–60 cm DBH, numbers of hardwoods 28–60 cm DBH, riparian width, MWMT, and percent of fine sediments (S–Star) (table 4). Using canonical scores from the greatly reduced set of variables in this multi–scale model (10 *vs*. 69 in the cluster analysis) we plotted the relationships of the 60 tributaries in three dimensions (fig. 3). The final multi–scale model improved group separation and provided useful information on the environmental gradients that separated the reach groups compared to the cluster analysis.

Stream groups and animal distributions

We found no differences in reptile or amphibian evenness, or in reptile richness among tributary groups. However, amphibian richness differed, with Group 2 having significantly greater richness than the other three groups (table 5). Several species including the southern torrent salamander (*Rhyacotriton variegatus*), the black salamander (*Aneides flavipunctatus*), the rough–skinned newt, and the Pacific chorus frog (*Pseudacris regilla*), were detected in numbers too low to test individually with ANOVA, but none–the–less contributed to differences in amphibian richness. Two anurans were sufficiently widespread and abundant for ANOVA. The foothill yellow–legged frog (*Rana boylii*) was more abundant in tributaries of Group 2 compared to the other types and the tailed frog was more abundant in tributaries of Group 1 compared with the other groups (table 5). Lizards (all species combined) were more abundant along tributaries of Group 4 compared with those of Group 2, and the western fence lizard was more abundant along tributaries of Group 4 compared

Table 2. Results of discriminant analyses of 28 attributes surrounding the reach. Variables were sub–set into four ecological components and analyzed separately: † Variables transformed for statistical analysis (see table 1 for variable codes). Variables included in the analyses that did not enter the models are: trees and logs († Hardwood 61–120 cm DBH [C], mean stand age, maximum stand age, conifer > 120 cm DBH [C]; † Hardwood 15–27 cm DBH [C], logs [C]); Understory vegetation (shrub, %); Ground level vegetation († herb, %); Ground cover († soil [%], rock [%], organic debris [%], litter depth [%]); Forest climate (upland canopy variation [%], soil temperature, air temperature); Composite (conifer 61–120vcm DBH [C], † conifer seedling [%], † hardwood seedling [%], † grass [%], moss [%], log [%], upland canopy closure [%]); CV. Canonical variable. (Means and standard deviations are for untransformed data.)

Tabla 2. Resultados de los análisis discriminantes de 28 atributos de los cursos. Las variables se subclasificaron en cuatro componentes ecológicas y se analizaron por separado: † Variable transformada para el análisis estadístico (véase la tabla 1 para los códigos de las variables). Las variables incluidas en los análisis pero que no entraron en los modelos son: árboles y troncos († madera dura 61–120 cm DAP [C], edad media de la madera en pie, edad máxima de la madera en pie, coníferas > 120 cm DAP [C]; † Madera dura 15–27 cm DAP [C], troncos [C]); Vegetación del sotobosque (arbustos, %); Vegetación a nivel del suelo († hierba, %); Superficie del suelo († suelo [%], roca [%], desechos orgánicos [%], profundidad del mantillo [%]); Clima forestal (variación del dosel en tierras altas [%], temperatura del suelo, temperatura del aire); Composición (coníferas 61–120 cm DAP [C], † brotes de coníferas [%], † brotes de madera dura [%], † hierba [%], musgo [%], troncos [%], cobertura del dosel en tierras altas [%]); CV. Variable canónica. (Las medias y las desviaciones estándar son de datos no transformados.)

	K–Means cluster groupings								Pooled within–group standardized CV		
	1 (n = 13)		2 (n = 16)		3 (n = 11)		4 (n = 20)				
Variables	Mean	SD	Mean	SD	Mean	SD	Mean	SD	CV1	CV2	CV3
Trees and logs											
† Hardwood 28–60 cm DBH (C)	4.38	3.84	18.12	8.61	1.91	2.47	4.40	3.65	–0.78	–0.09	0.31
† Riparian forest width (m)	3.03	1.70	4.75	1.67	6.48	4.38	5.60	2.54	0.28	0.69	–0.44
Conifer 15–27cm DBH (C)	27.31	12.72	7.25	4.49	18.73	10.48	18.90	7.55	0.16	–0.71	–0.54
Conifer 28–60cm DBH (C)	19.31	8.74	4.94	2.89	23.64	13.97	13.20	7.29	0.58	0.32	0.48
Conifer 61–120cm DBH (C)	18.62	9.23	9.75	8.32	22.73	8.70	13.25	7.85	0.37	0.17	0.60
Wilks' lambda = 0.136; *F* (*df* = 18,145) = 8.25; *P* < 0.0001											
Jackknife success (%) = 70.0; Cohen's Kappa = 0.595; *P* < 0.0001											
Understory vegetation											
† Conifer seedling (%)	0.18	0.15	0.07	0.06	0.09	0.08	0.10	0.05	–0.35	0.95	
† Hardwood seedling (%)	0.09	0.05	0.21	0.14	0.05	0.05	0.13	0.05	0.99	0.20	
Wilks' lambda = 0.550; *F* (*df* = 6,110) = 6.40; *P* < 0.0001											
Jackknife success (%) = 53.3; Cohen's Kappa = 0.377; *P* < 0.0001											
Ground level vegetation											
† Fern (%)	0.07	0.07	0.08	0.07	0.03	0.03	0.03	1.87	0.78	0.63	
† Grass (%)	0.10	0.08	0.04	0.04	0.09	0.06	0.06	0.04	–0.64	0.77	
Wilks' lambda = 0.639; *F* (*df* = 6,110) = 4.60; *P* < 0.0003											
Jackknife success (%) = 40.0; Cohen's Kappa = 0.200; *P* < 0.0083											

Table 2. (Cont.)

	K–Means cluster groupings								Pooled within–group		
	1 (n = 13)		2 (n = 16)		3 (n = 11)		4 (n = 20)		standardized CV		
Variables	Mean	SD	Mean	SD	Mean	SD	Mean	SD	CV1	CV2	CV3
Ground cover											
Leaf (%)	0.85	0.06	0.70	0.19	0.81	0.08	0.61	0.19	0.04	0.98	–0.43
Moss (%)	0.03	0.02	0.18	0.09	0.04	0.05	0.08	0.07	0.99	0.35	0.10
Log (%)	0.10	0.05	0.07	0.04	0.05	0.03	0.07	0.03	–0.36	0.14	0.97
Wilks' lambda = 0.330; *F* (*df* = 9,132) = 8.42; *P* < 0.0001											
Jackknife success (%) = 53.3; Cohen's Kappa = 0.385; *P* < 0.0001											
Forest climate											
Upland canopy closure (%)	0.83	0.11	0.91	0.05	0.83	0.08	0.75	0.14	1.00		
Wilks' lambda = 0.730; F (df = 3,56) = 6.90; *P* = 0.0005											
Jackknife success (%) = 43.3; Cohen's Kappa = 0.236; *P* < 0.0035											
Composite model											
Conifer 15–27cm DBH (C)	27.31	12.72	7.25	4.49	18.73	10.48	18.90	7.55	0.29	0.19	–0.85
Conifer 28–60 cm DBH (C)	19.31	8.74	4.94	2.89	23.64	13.97	13.20	7.29	0.55	–0.02	0.55
† Hardwood 28–60 cm DBH (C)	4.38	3.84	18.12	8.61	1.91	2.47	4.40	3.65	–0.89	0.11	0.01
† Riparian forest width (m)	3.03	1.70	4.75	1.67	6.48	4.38	5.60	2.54	0.14	–0.65	0.20
† Fern (%)	0.07	0.07	0.08	0.07	0.03	0.03	0.03	1.87	–0.68	0.14	–0.03
Leaf (%)	0.85	0.06	0.70	0.19	0.81	0.08	0.61	0.19	0.08	0.64	0.61
Wilks' lambda = 0.086; *F* (*df* = 21,144) = 9.28; *P* < 0.0001											
Jackknife success (%) = 78.3; Cohen's Kappa = 0.709; *P* < 0.0001											

to all other groups (table 5). Steelhead trout were more abundant in tributaries of Group 4 compared to the other three groups (table 5). Crayfish were more abundant in tributaries of Group 4 compared with Group 1 (table 5).

Predictive models of bio–indicators

The NPMR of amphibian richness used 21 environmental variables that were significantly correlated (appendix 1). The best single variable predicting greater amphibian richness was northing (+) (xR^2 = 0.226; table 6). The model improved with the addition of elevation (–), stumps (–), hardwood seedlings (+), and moss (+), respectively (xR^2 = 0.558; table 6).

The NPMR of the foothill yellow–legged frog used 19 variables correlated with this species (appendix 1). The best single variable was soil temperature (+) (xR^2 = 0.243; table 6). This model improved with the addition of sub–basin area (+), % of sub–basin in tree plantations (–), % of sub–basin in hardwoods (–) and elevation (–), respectively (xR^2 = 0.514; table 6).

The NPMR of larval tailed frogs used 25 variables correlated with this species (appendix 1). The best single variable was the number of small conifers (+) (xR^2 = 0.099; table 6). The model improved with the addition of % soil ground cover (–), % leaf litter (+), % debris ground cover (+) and % stream gravel (+), respectively (xR^2 = 0.366; table 6).

The NPMR of steelhead trout used 25 variables correlated with this species (appendix 1). The best single variable was sub–basin area (+) (xR^2 = 0.510; table 6). This model improved with the addition of the number of road crossings (+), % soil ground cover (+), % upland rock (+) and % stream gravel (–), respectively (xR^2 = 0.719; table 6).

Table 3. Results of discriminant analyses of 19 attributes within the reach. These variables were sub–set into four ecological components, each analyzed separately: † Variable transformed for statistical analysis (see table 1 for variable codes). Variables included in the analyses that did not enter the models are: aquatic conditions (reach aspect, † habitat width, S* sediment index, maximum depth, water temperature daily amplitude, flow in fast habitats, embeddedness in slow habitats); Aquatic substrates († bedrock [%], large woody debris [%], cobble [%], detritus [%], † sand [%]); Composite (pebble [%], gravel [%]); CV. Canonical variable. (Percent data is indicated by (%); means and standard deviations are for untransformed data.)

Tabla 3. Resultados de los análisis discriminantes de 19 atributos de los cursos. Dichas variables se subclasificaron en cuatro componentes ecológicas, y cada una de ellas se analizó por separado: † Variable transformada para el análisis estadístico (ver tabla 1 para los códigos de las variables). Las variables incluidas en los análisis pero que no entraron en los modelos son: condiciones acuáticas (aspecto del cauce, † anchura del hábitat, S índice sedimentario, profundidad máxima, oscilación máxima diaria de la temperatura del agua, flujo en los hábitats rápidos, encajamiento en los hábitats lentos); Sustratos acuáticos († lecho rocoso [%], restos de madera grandes [%], guijarros [%], detritus [%], † arena [%]); Composición (cantos rodados [%], grava [%]); CV. Variable canónica. (Los datos porcentuales se indican mediante (%); las medias y las desviaciones estándar son para los datos no transformados.)*

	K–Means cluster grouping								Pooled within–group		
	1 (n = 13)		2 (n = 16)		3 (n = 11)		4 (n = 20)		standardized CV		
Variables	Mean	SD	Mean	SD	Mean	SD	Mean	SD	CV1	CV2	CV3
Aquatic conditions											
Canopy over stream (%)	0.91	0.05	0.96	0.03	0.91	0.07	0.89	0.04	–0.11	1.03	0.08
S* fines (%)	0.70	0.21	0.45	0.18	0.36	0.21	0.31	0.08	0.82	–0.10	0.58
MWMT	13.26	1.20	14.91	1.49	14.55	2.96	16.53	1.81	–0.62	0.14	0.81
Wilks' lambda = 0.322; *F* (*df* = 9,132) = 8.67; *P* < 0.0001											
Jackknife success (%) = 58.3; Cohen's Kappa = 0.436; *P* < 0.0001											
Aquatic substrates											
Boulder (%)	0.03	0.04	0.16	0.13	0.13	0.11	0.21	0.10	–0.40	0.85	–0.41
Pebble (%)	0.16	0.09	0.21	0.07	0.22	0.07	0.19	0.06	–0.77	0.48	0.87
Gravel (%)	0.30	0.12	0.21	0.08	0.20	0.08	0.16	0.05	0.86	–0.03	–0.25
† Fines (%)	0.19	0.19	0.07	0.07	0.02	0.02	0.02	0.02	0.62	0.79	0.10
Wilks' lambda = 0.269; *F* (*df* = 12,140) = 7.54; *P* < 0.0001											
Jackknife success (%) = 53.3; Cohen's Kappa = 0.373; *P* < 0.0001											
Composite model											
Canopy over stream (%)	0.91	0.05	0.96	0.03	0.91	0.07	0.89	0.04	–0.10	0.94	–0.30
S* fines (%)	0.70	0.21	0.45	0.18	0.36	0.21	0.31	0.08	0.50	–0.13	0.48
MWMT	13.26	1.20	14.91	1.49	14.55	2.96	16.53	1.81	–0.55	0.24	0.58
Boulder (%)	0.03	0.04	0.16	0.13	0.13	0.11	0.21	0.10	–0.31	0.49	0.43
† Fines (%)	0.19	0.19	0.07	0.07	0.02	0.02	0.02	0.02	0.47	0.48	0.34
Wilks' lambda = 0.213; *F* (*df* = 15,144) = 7.21; *P* < 0.0001											
Jackknife success (%) = 60.0; Cohen's Kappa = 0.457; *P* < 0.0001											

The NPMR of crayfish used 20 correlated variables (appendix 1). The best single variable was mesohabitat width (^; hump–shaped) (xR^2 = 0.304; table 6). The model improved with % of mafic volcanic rock and chert (+), % of young hardwoods (+), % of fern cover (–) and embeddedness (–), respectively (xR^2 = 0.557; table 6).

Table 4. Results of discriminant analyses of 20 environmental attributes from three spatial scales. *P*–value to enter was set at 0.10 and *P*–value to remove was set at 0.05: † Variable transformed for statistical analysis (see table 1 for variable codes). Variables included in the analyses but that did not enter the models are: elevation, precipitation (P), conifer 15–27 cm DBH (C), † fern (%), leaf (%), canopy over stream (%), boulder (%), † fines (%). CV. Canonical variable. (Means and standard deviations are for untransformed data.)

Tabla 4. Resultados de los análisis discriminantes de 20 atributos ambientales de tres escalas espaciales. El valor de P *para añadir se situó a 0,10, y el valor de P para quitar se situó a 0,05: † Variable transformada para el análisis estadístico (ver tabla 1 para los códigos de las variables). Las variables incluidas en los análisis pero que no entraron en los modelos son: elevación, precipitación (P), coníferas 15–27 cm DAP (C), † helechos (%), hojas (%), dosel sobre la corriente (%), piedras grandes (%), † granos finos (%). CV. Variable canónica. (Las medias y las desviaciones estándar son de datos no transformados.)*

	K–Means cluster groupings								Pooled within–group		
	1 (n = 13)		2 (n = 16)		3 (n = 11)		4 (n = 20)		standardized CV		
Variables	Mean	SD	Mean	SD	Mean	SD	Mean	SD	CV1	CV2	CV3
Composite of composites											
Easting	31.28	15.39	14.44	5.55	50.95	8.91	38.73	9.49	–0.73	0.27	–0.78
Slope (%)	0.18	0.07	0.19	0.08	0.12	0.08	0.06	0.04	0.50	0.05	0.12
Illumination December	135.33	26.32	96.05	24.67	86.48	31.86	98.26	23.88	0.53	0.62	–0.71
Minimum temperature (P)	3.52	1.45	3.15	0.66	5.56	1.20	2.65	1.42	0.18	–0.05	1.26
† RCM geology (%)	0.35	0.47	0.85	0.34	0.00	0.00	0.81	0.36	0.22	–0.17	–0.45
Conifer 28–60cm DBH (C)	19.31	8.74	4.94	2.89	23.64	13.97	13.20	7.29	–0.05	0.51	0.24
† Hardwood 28–60cm DBH (C)	4.38	3.84	18.13	8.61	1.91	2.47	4.40	3.65	0.65	–0.29	–0.01
† Riparian width	3.03	1.70	4.75	1.67	6.48	4.38	5.60	2.54	–0.37	–0.50	0.23
MWMT	13.26	1.20	14.91	1.49	14.55	2.96	16.53	1.81	–0.49	–0.31	–0.25
S* fines (%)	0.70	0.21	0.45	0.18	0.36	0.21	0.31	0.08	0.29	0.55	–0.34

Wilks' lambda = 0.008; *F* (*df* = 33,136) = 16.78; *P* < 0.0001

Jackknife success (%) = 86.7; Cohen's Kappa = 0.819; *P* < 0.0001

Discussion

Our objectives were to detect unique sets of headwater tributaries, determine the riverscape patterns, disturbance processes, and environmental gradients associated with each set, and to link the distributions and abundances of riparian and aquatic biota with informative subsets of these attributes (*e.g.*, Dale et al., 1994; Roth et al., 1996; Whittier et al., 2006). The intent here was that by establishing these linkages we would provide the basis for employing key elements of this fauna as bio–indicators of ecological services and network integrity. Any study that purports to relate environmental conditions across multiple spatial scales and faunal elements must by necessity incorporate a large number of independent variables. Consequently, we needed to reduce a large set of variables from multiple scales into informative subsets for both the tributary groups and the fauna. We sought to relate these reduced sets of variables to the presence and abundance of readily sampled fauna with sensitivity to system degradation (*e.g.*, Welsh & Ollivier, 1998; Lowe & Bolger, 2002; Wilson & Dorcas, 2003), structuring of benthic communities (Parkyn et al., 1997), or commercial value (*i.e.*, steelhead trout).

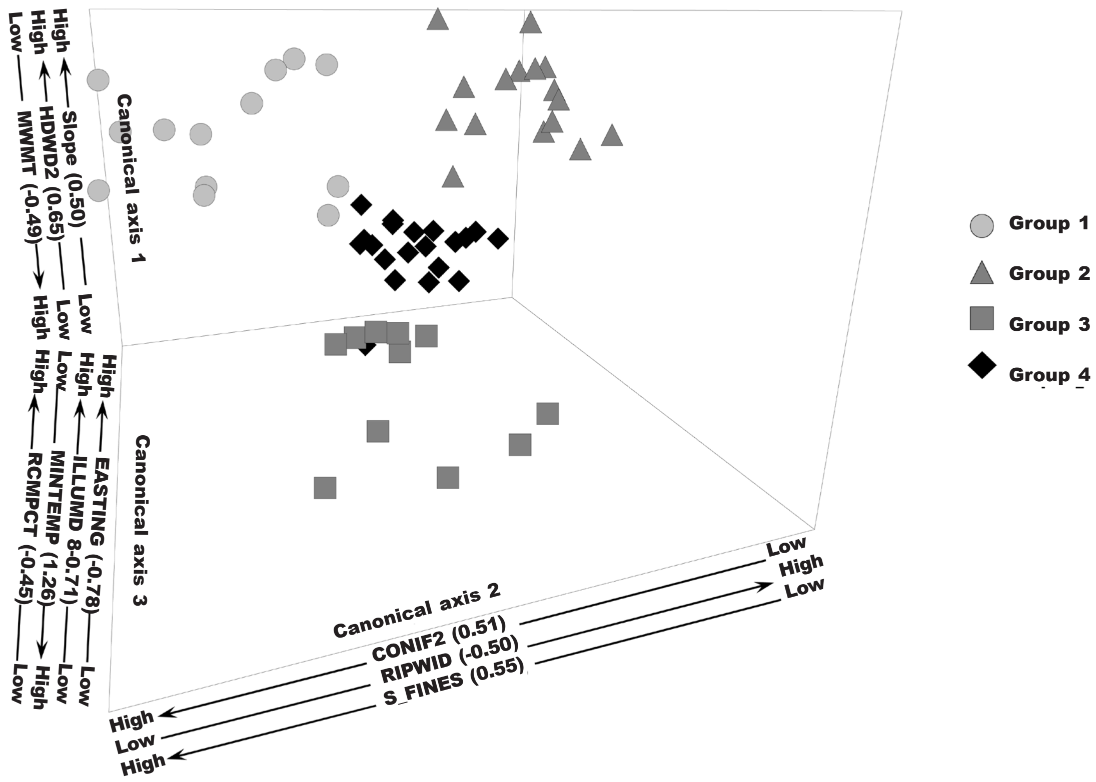

Fig. 3. Three–dimensional scatter plot of canonical scores from the multi–scale discriminant model (table 4). See appendix 1 for definitions. For illustration we used the highest absolute canonical score to assign each variable to a particular canonical axis, however, each variable loads on each of the axes.

Fig. 3. Diagrama de dispersión tridimensional de los datos canónicos del modelo discriminante multiescala (tabla 4). Para las definiciones, ver el apéndice 1. Para realizar la ilustración utilizamos el dato canónico absoluto más alto para asignar cada variable a un eje canónico en particular, a pesar de que cada variable carga valores en cada uno de los ejes.

Our study differs from previous studies that examined multi–scale environmental relationships of stream–dwelling animals (*e.g.*, Lowe & Bolger, 2002; Roni, 2002; Welsh & Lind, 2002; Stoddard & Hayes, 2005) because many of these studies selected study sites based on categorical distinctions or disjunct distributions. Most studies that claim to examine drivers of environmental suitability for particular taxa at multiple spatial scales, *a priori* select sites along existing ecological gradients. These studies, therefore, often implicitly substitute anthropogenically forced spatial differences for naturally occurring spatial or temporal differences (Landres et al., 1999). By randomly selecting sites throughout the SFTR watershed and determining groups *a posteriori*, our study is unbiased in this respect and thus reveals environmental gradients that occur throughout the SFTR. Our assessment of faunal assemblage responses to this environmental structure was determined at a metacommunity scale (Leibold et al., 2004).

The classification success for ecological components within spatial scales ranged from 51–75% (sub–basin scale), 40–70% (land–surrounding–the–reach scale), and 53–58% (within–reach scale). Within scales, classification success of the composite models improved markedly over the ecological sub–sets, with 85% success at the sub–basin, 78% at land–surrounding–the–reach, and 60% at the within–reach scale. The classification success improved even more with the final across–scales watershed level model, achieving 87% correct. As sets of variables were refined at each step, the improved success indicated an enhanced ability to discern a much reduced, yet more informative, set of attributes able to distinguish tributary types. Similar approaches using multivariate analyses have proven useful in other studies seeking to reduce the dimensionality of large data sets by finding the fewest meaningful variables to differentiate sets of sites (*e.g.*, Radwell & Kwak, 2005; Shrestha & Kazama, 2007 and references therein).

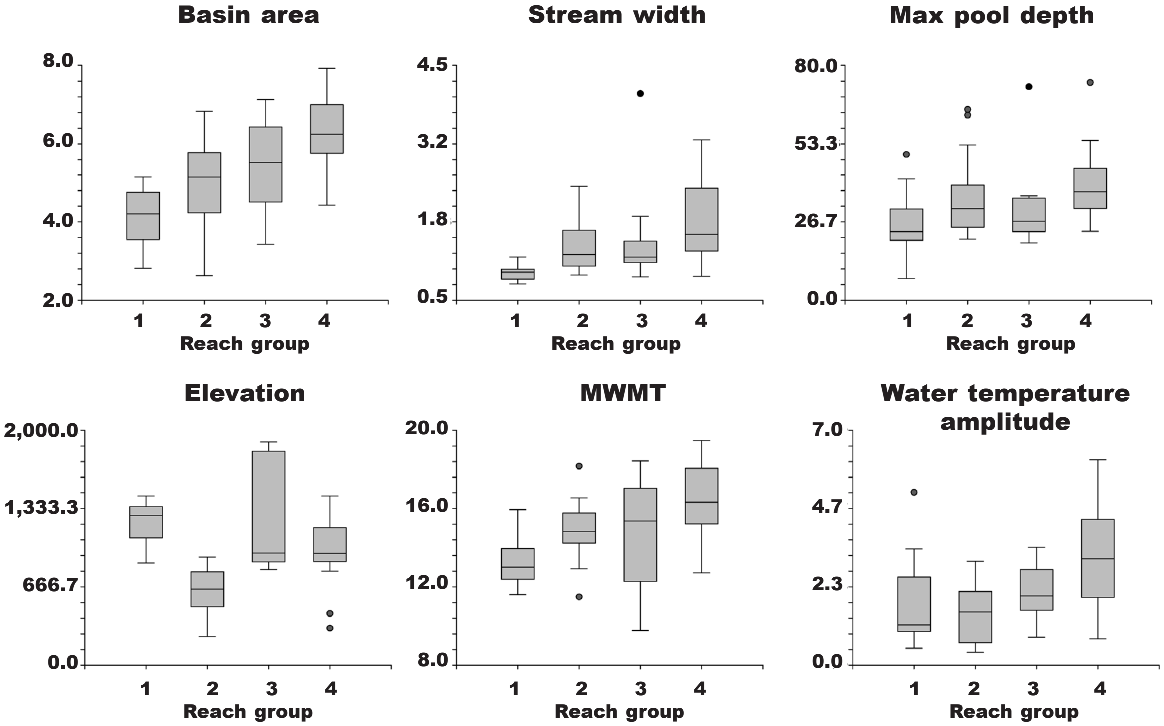

Fig. 4. Six key environmental attributes of the four reach groups illustrating the overlap in physical attributes consistent with a *continuum* (Vannote et al., 1980) or a hierarchical channel network (Benda et al., 2004). The boxes represent the middle 50% of the data, lines inside are the median, the T–shaped whiskers represent data 1.5 times past the middle 50%, and dots represent outliers.

Fig. 4. Seis atributos ambientales clave de los cuatro grupos de cursos que ilustran el solapamiento de los atributos físicos, lo que es consistente con un continuum *(Vannote et al., 1980) o con una red de canales jerarquizada (Benda et al., 2004). Los cuadrados representan el 50% medio de los datos, las líneas en su interior son las medianas, los signos en forma de T representan los datos que se hallan a 1,5 veces la media del 50%, y los puntos representan los valores atípicos.*

The composite multi–scale model greatly improved on the cluster analysis by using just 10 variables compared to 69, and demonstrating greatly improved separation (compare figures 2 and 3). This model distinguished the four tributary groups along informative environmental gradients based on five sub–basin scale variables (50%), three from land–surrounding–the–reach (30%), and two at the within–reach scale (20%). Four of the 10 variables represented processes or attributes that respond directly to both anthropogenic modifications and/or natural disturbances within the landscape (conifer and hardwood counts, riparian width, stream temperature [MWMT] and percent fine substrates). The composite models at each of the scales also contained informative attributes that respond directly to land management practices such as forestry and road–building (Tang et al., 1997; Hemstad & Newman, 2006).

Several attributes distinguishing the reach groups overlapped in values (fig. 4) indicating that these sets likely represent different positions along a continuum (Vannote et al., 1980), or gradient, within the dendritic network (Benda et al., 2004). Tributaries of Group 1 were the lowest order tributaries, at the highest elevation, with the narrowest riparian zones, lowest water temperatures, lowest daily water temperature fluctuations (amplitudes), highest fine sediment loads, and the fewest road crossings, and represented the highest end of the continuum (tables 2–4). Tributaries of Group 2 were the western– and northernmost streams, received the most precipitation, and with the highest mean annual air temperatures. Although the slopes of these reaches were just slightly greater than those of Group 1, they were the lowest in elevation, and transected the most mafic volcanic rock and chert, parent material that appeared to support more hardwood compared to coniferous forest types. These tributaries also had the highest upland and over–stream canopy, with riparian areas being the highest in mesic and hydric plants (tables 2–4). Tributaries of Group 3 were the eastern– and southernmost, with the lowest winter

Table 5. ANOVA tests of faunal assemblages and individual amphibian and reptile species, steelhead trout, and crayfish abundances among four stream groups. Data used for individual species were the sums of VES, seeps, and 10 m^2 of belts (see text), (n = 60) or electrofished reaches (n = 55). For assemblages, we used numbers of species detected per tributary, richness including incidentals. Several riparian and upland taxa were sampled by VES (see text), n = 40: * n = 40 (11, 9, 10, 10); ** n = 55 (12, 14, 10, 19); º Includes incidental observations; † Natural log transformed; †† Square root transformed; Ensatina. *Ensatina eschscholtzii*; Western fence lizard. *Sceloporus occidentalis*; Sagebrush lizard. *S. graciosus*; Northern alligator lizard. *Elgaria coerulea*.

*Tabla 5. Test ANOVA de las abundancias de las comunidades faunísticas y las especies individuales de anfibios y reptiles, la trucha cabeza de acero y el cangrejo señal, entre cuatro grupos de cursos. Los datos utilizados para las especies individuales fueron las sumas de VES, charcos sin drenaje y 10 m^2 de cinturones de muestreo (ver el texto), (n = 60) o cursos en los que se había utilizado la pesca con electricidad (n = 55). Para las comunidades, utilizamos los números de especies detectados por afluente, la riqueza incluyendo los imprevistos. Se recogieron varios taxones de tierras altas y de zona riparia mediante VES (ver el texto), n = 40: * n = 40 (11, 9, 10, 10); ** n = 55 (12, 14, 10, 19); º Incluye observaciones accidentales; † Log natural transformado; †† Raíz cuadrada transformada; Ensatina,* Ensatina eschscholtzii*; Lagarto de vientre azul del oeste,* Sceloporus occidentalis*; lagarto de Sagebrush,* S. graciosus*; lagarto aligator del norte,* Elgaria coerulea.

Dependent variable	*df*	MSE	*F*	*P*	Multiple comparisons	Groups–mean (standard error) I	II	III	IV
Richnessº									
Amphibians	3	1.65	4.06	0.0111	2 > 1, 2 > 3, 2 > 4	2.38	3.37	1.91	2.05
						(0.357)	(0.322)	(0.388)	(0.288)
Reptiles	3	3.24	0.35	0.7926		3.64	4.00	3.80	4.40
						(0.542)	(0.600)	(0.569)	(0.569)
Evenness									
Amphibians	3	0.15	2.14	0.1052		0.61	0.60	0.43	0.33
						(0.106)	(0.095)	(0.115)	(0.85)
Reptiles	3	0.16	0.46	0.7126		0.51	0.59	0.63	0.71
						(0.120)	(0.133)	(0.126)	(0.126)
Amphibians									
Coast giant salamander ††									
	3	2.05	1.14	0.3425		7.92	10.25	5.00	6.10
						(2.181)	(1.966)	(2.371)	(1.759)
*Ensatina ††	3	0.40	1.22	0.3158		0.91	0.55	0.10	0.70
						(0.302)	(0.334)	(0.317)	(0.317)
Foothill yellow–legged frog †									
	3	9.70	2.59	0.0615	2 > 1	0.46	9.06	4.82	3.75
						(2.767)	(2.494)	(3.007)	(2.201)
Coast tailed frog ††									
	3	0.46	7.55	0.0002	1 > 2, 1 > 3, 1 > 4	2.31	0.69	0.54	0.05
						(0.445)	(0.401)	(0.483)	(0.358)
Reptiles									
*Western fence lizard									
	3	6.08	4.53	0.0085	4 > 1, 4 > 2, 4 > 3	1.36	1.00	2.60	4.70
						(0.744)	(0.822)	(0.780)	(0.780)

Table 5. (Cont.)

Dependent variable	*df*	MSE	*F*	*P*	Multiple comparisons	Groups–mean (standard error) I	II	III	IV
*Sagebrush lizard ††									
	3	0.92	2.20	0.1053		1.36	0.33	1.30	3.30
						(0.799)	(0.883)	(0.838)	(0.838)
*North. alligator lizard									
	3	2.40	1.60	0.2056		1.54	2.33	1.30	0.80
						(0.467)	(0.516)	(0.490)	(0.490)
*Snakes	3	1.02	1.29	0.2919		0.82	0.22	1.10	0.90
						(0.306)	(0.338)	(0.320)	(0.320)
*Lizards	3	38.05	2.50	0.0750	4 > 2	6.82	4.78	8.10	12.2
						(1.860)	(2.056)	(1.951)	(1.951)
Fish abundances									
**Steelhead trout †									
	3	1.63	8.50	0.0001	4 > 1, 4 > 2, 4 > 3	0.00	0.85	0.95	2.27
						(0.000)	(0.341)	(0.403)	(0.293)

Non–parametric ANOVAs (Kruskal–Wallis)

Dependent variable	df	X^2	*P*	Multiple comparisons	Groups–mean (standard error) I	II	III	IV
Species abundances								
Signal crayfish	3	7.14	0.0675	2 > 1, 4 > 1	0.00	4.06	0.82	11.85
					(0.000)	(2.507)	(0.818)	(5.962)

exposure, highest minimum air temperatures, and lowest annual precipitation; they also had the greatest riparian widths and the most in–stream pebble. Sub–basins containing these tributaries appeared to support the most coniferous forest with the highest counts of trees in the two largest conifer size classes (tables 2–4). Tributaries of Group 4 were the second lowest in elevation, had the second highest annual precipitation, and the lowest minimum annual air temperatures. These tributaries also had the lowest gradients, highest percent boulder substrates, lowest amounts of gravel, lowest fine sediment loads (tied with Group 3), the least over–stream canopy, highest water temperatures, and highest number of road crossings (tables 2–4).

Responses of the bio–indicators

The coastal tailed frog was the only relatively common amphibian associated with tributaries of Group 1. However, the best predictive model (table 6) was relatively weak and uninformative (*cf*. Welsh & Lind, 2002). This poor performance likely resulted from the uneven distribution and low abundances we found for this species, despite evidence (Bury, 1968) of a once wider distribution throughout this and surrounding major watersheds, including to the east. Such patchy distributions have been observed elsewhere in recent studies, and are likely artifacts of past timber harvesting altering the requisite niche of this ancient frog, a species specifically adapted to conditions that occur most reliably in late succession forests (Welsh, 1990; Welsh & Lind, 2002; Welsh et al., 2005; Spear & Storfer, 2008). Consequently, the tailed frog is an excellent bio–indicator for the more structurally diverse, micro–climatically ameliorated, conditions typical of late seral forests (Welsh, 1990) which also support the highest levels of terrestrial salamander biodiversity (*e.g.*, Davic & Welsh, 2004). Furthermore, the presence of this frog can indicate the potential of streams to support coho salmon (see Welsh & Hodgson, 2008), a threatened salmonid once common in SFTR but that has not been detected in recent times.

Table 6. Non–parametric multiplicative regression (NPMR) models for five bio–indicators whose distributions varied significantly among stream groups. The data used in the modeling were those from just the reach groups where each metric was observed. Tolerance is in the units of the response variable and refers to the niche width along that variable; ecological neighborhood size refers to that portion of the data used to determine tolerances for each variable in the model: xR^2. Leave–one–out cross–validation R^2; *Ns. N*eighborhood size. (See methods for more details.)

Tabla 6. Modelos de regresión multiplicativa no paramétrica (NPRM) para cinco bioindicadores, cuyas distribuciones variaban significativamente entre los grupos de cauces. Los datos utilizados en la modelización fueron los de los grupos de tramos, en los que se observó todo parámetro métrico. La tolerancia está en las unidades de la variable respuesta y se refiere a la anchura del nicho a lo largo de dicha variable; el tamaño de la vecindad ecológica se refiere a la porción de los datos usados para determinar las tolerancias para cada variable del modelo: xR^2. R^2 *por validación cruzada dejando uno afuera; Ns. Anchura de nicho. (Para más detalles, ver los métodos.)*

Models (tolerance)	xR^2	Ns
Amphibian richness		
Northing (10.3 km)	0.226	20.0
Northing (13.7 km), Moss (1.5%)	0.381	5.8
Northing (17.1 km), Moss (1.5%), Stumps (4.8)	0.536	3.6
Northing (20.5 km), Moss (1.5%), Stumps (4.8), Hardwood seedlings (3.1%)	0.552	3.2
Northing (20.5 km), Moss (1.5%), Stumps (4.8), Hardwood seedlings (3.1%), Elevation (1159.2 m)	0.559	3.1
Northing (20.5 km), Moss (1.5%), Stumps (4.8), Hardwood seedlings (4.8%), Elevation (1159.2 m), Shrub (27.2%)	0.556	3.0
Foothill yellow–legged frog		
Soil temperature (2.2ºC)	0.243	16.5
Soil temperature (1.5ºC), Elevation (82.8 m)	0.453	3.0
Plantation (20.7%), Elevation (165.6 m), Soil temperature (1.5ºC)	0.470	3.5
Plantation (20.7%), Elevation (165.6 m), Soil temperature (2.2ºC), Watershed area (1.8 ha)	0.494	2.8
Plantation (14.8%), Elevation (165.6 m), Soil temperature (2.2ºC), Watershed area (1.8 ha), Hardwood (55.2%)	0.514	2.4
Tailed frog		
Conifer 15–27 cm DBH (9.2)	0.099	18.5
Conifer 15–27 cm DBH (6.9), Debris (0.9%)	0.209	2.3
Conifer 15–27 cm DBH (9.2 cm), Debris (0.9%), Gravel (13.2%)	0.255	2.1
Conifer 15–27 cm DBH (11.5), Debris (0.9%), Gravel (13.2%), Leaf (30.8%)	0.348	2.0
Conifer 15–27 cm DBH (13.8), Debris (0.9%), Gravel (13.2%), Soil (17.7%), Leaf (30.8%)	0.366	2.0
Steelhead		
Watershed area (0.7 ha)	0.510	13.7
Watershed area (0.7 ha), Road crossings (0.8)	0.591	5.2
Watershed area (0.7 ha), Road crossings (0.8), Rock (13.3%)	0.650	3.1
Watershed area (0.7 ha), Road crossings (1.1), Rock (13.3%), Soil (3.4%)	0.714	2.8
Watershed area (0.7 ha), Road crossings (1.1), Rock (13.3%), Soil (4.6%), Gravel (13.2%)	0.719	2.5

Table 6. (Cont.)

Models (tolerance)	xR^2	Ns
Crayfish		
Mesohabitat width (0.1 m)	0.303	14.8
Mesohabitat width (0.1 m), RCM geology (34.6%)	0.362	8.1
Mesohabitat width (0.1 m), RCM geology (27.3%), Fern (0.6%)	0.511	3.9
Mesohabitat width (0.1 m), RCM geology (34.6%), Fern (0.6%), Hardwood 15–27 cm DBH (10.2)	0.540	3.1
Mesohabitat width (0.1 m), RCM geology (42.2%), Fern (0.6%), Hardwood 15–27 cm DBH (10.2), Embeddedness (19.6 %)	0.557	2.4

The tributaries of Group 2 supported the highest numbers of foothill yellow–legged frogs (table 5), a species that was best predicted by increased soil temperatures (table 6). While showing a western distribution bias in the SFTR, they differ from the other amphibians by showing a preference for open stream reaches where they can bask (Lind, 2005). Differences in the predictive models between this frog and amphibian richness (despite the high values may for both, in this tributary group), is best explained by the comparatively high habitat heterogeneity among these streams, along with the specific and unique behavioral adaptations of the yellow–legged frog**.** Presence of the southern torrent salamander, the black salamander, the rough–skinned newt, and the Pacific chorus frog, along with the yellow–legged frog, combined to establish the highest amphibian richness among the tributary types in Group 2. This high amphibian richness is likely indicative of conditions that also support higher richness of other aquatic taxa associated with the aquatic and riparian habitats. High amphibian richness can function as an easily measured bio–indicator, where greater values indicate enhanced resilience and an improved likelihood that reaches can provide and sustain critical ecological services (Dobson et al., 2006).

None of the fauna in tributaries of Group 3 differed significantly in value from the other groups (table 5). These reaches were the most eastern, had lower winter sun exposures, lower precipitation, lower hardwoods 28–60 cm DBH, and lacked mafic volcanic rock and chert, compared to the other groups. This outcome indicates that for the fauna we assessed, the tributaries of Group 3 appear to be relatively impoverished compared to the other groups.

The tributaries of Group 4 supported more steelhead than other groups and more crayfish than Group 1. Crayfish abundance was associated with greater width and less channel embeddedness. Higher steelhead numbers were associated with greater basin area and higher temperatures (both MWMT and MWMT amplitude). The higher abundance in streams with higher temperatures occurred despite potential bioenergetic costs. Employing a subset of streams from each of our three fish–bearing groups (three per group) sampled in 2003, McCarthy et al. (2009) showed that individuals in higher temperature streams had lower growth efficiency, with some fish losing weight during the summer months. Bioenergetic models suggested that these fish were feeding at lower rate, 25% (or less) of the maximum consumption rate, and that projected future increases in stream temperatures could further exacerbate low growth rates and perhaps have population level effects. The streams of Group 4 also had more road crossings and exposed soil cover in the adjacent upland, a condition which can negatively affect salmonids (*e.g.*, Cederholm et al., 1981).

Influences on the fluvial network are hierarchical, with regional controls such as climate, physiography, and geology shaping sub–basin conditions, and both sets of attributes acting to shape each sub–basin tributary and its within–reach conditions (Knighton, 1984; Poole, 2002). Given the overlaps in the predictive environmental attributes and the distributions of our bio–indicators, we emphasize that these fauna are not associated just with the particular tributary type where they are most common. Rather the faunal elements generally have peak abundances in particular tributary types, but also occur in lower numbers in adjacent types reflecting the continuous nature of the fluvial network (fig. 4) (see Pringle, 2003). It is the collective influences on the greater sub–basin which shape available habitats within tributary types and determine where particular fauna are favored (Gomi et al., 2002; Benda et al., 2004). This conceptualization is supported by the outcome of our predictive modeling where a variety of significant models were derived for co–occurring species. We interpret this outcome as evidence that our set of independent variables represent numerous informative environmental gradients within this watershed. Further, because the NPMR models consisted of sets of variables acting at different spatial scales, we consider this evidence of the influence of cross–scale interactions (Peters et al., 2007), with attributes acting in unique combinations to influence each bio–indicator depending upon its evolved niche. The multi–scale analysis was informative because it combined variables affecting natural variability (Landres et al., 1999) and land–use history (Foster et al., 2003), and substantiating their combined influence on headwaters. This analysis illuminated variables that can be managed to improved ecological conditions and enhance headwater health, and recognizing that organisms are integrators of all that happens in a watershed (Karr, 2006), the NPMR models indicated several bio–indicators that could be used to track their improving trajectories (Tabor & Aguirre, 2004; Nichols & Williams, 2006).

Future papers will address metacommunity dynamics (*e.g.*, Welsh & Hodgson, 2010) and fine scale (i.e., microscale) responses of faunal assemblages, which may allow us to elucidate additional factors that affect the spatial patterns of stream–dwelling organisms in this watershed.

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Appendix 1. Hierarchical arrangement, by spatial scale and ecological components, of 69 independent variables used to characterize the headwater tributary reaches (300 m) in the South Fork Trinity River Watershed (fig. 1): g. GIS variable derived from ARCInfo or ARCView; p. PRISM data (Daly et al., 1994); t. Count (c) of trees: small trees = 12–60 cm diameter at breast height (DBH) were counted in a 1/10th–ha circle and large trees > 61 cm DBH were counted in a 1/5th–ha circle; u. Percent of 1/10th–ha plot; s. Collected 25 m upslope on both sides of the stream; d. From dataloggers deployed from June to October, 2002; a. Within 1 m aquatic search areas; b. Percent estimates from aquatic search areas; m. Meters; [1] Considered in amphibian richness NMPR models; [2] Considered in foothill yellow–legged frog (*Rana boylii*) NMPR models; [3] Considered in tailed frog (*Ascaphus truei*) NMPR models; [4] Considered in signal crayfish NMPR models; [5] Considered in steelhead NMPR models.

Apéndice 1. Disposición jerárquica, en cuanto a escala espacial y components ecológicos, de las 69 variables independientes utilizadas para caracterizar los tramos de las cabeceras de los afluentes (300 m), en la cuenca del río South Fork Trinity (fig. 1): g. Variable SIG derivada de ARCInfo o ARCView; p. Datos PRISM (Daly et al., 1994); t. Recuento (c) de árboles: árboles pequeños = 12–60 cm de diámetro a la altura del pecho (DBH) que se contaron en un círculo de 1/10 de ha, y árboles pequeños > 61 cm de DBH contados en un círculo de 1/5 de ha; u. Porcentaje de registros de 1/10 de ha; s. Recogidos en los 25 m de ladera a ambos lados de la corriente; d. De dataloggers dispuestos de junio a octubre, 2002; a. Dentro de areas de búsqueda acuática de 1 m; b. Porcentaje de estimas de las areas de investigación acuática; m. Metros; [1] Considerados en modelos NMPR de la riqueza de anfibios; [2] Consideredos en modelos NMPR de Rana boylii*; [3] Consideredos en modelos NMPR de Ascaphus truei; [4] Considerados en los modelos NMPR del cangrejo señal; [5] Considerados en los modelos NMPR de la trucha arco iris.*

Sub–basin attributes

Geographic relations

Easting[1], Northing[1,3], Sub–basin aspect_g[3], Sub–basin area_g[2,3,4,5], Reach slope[3,4,5], Reach elevation[1,2,5], Illumination at December 21st_g[1], Day of sample[1]

Climate

Precipitation_ p[2], Mean air temperature_p[1], Minimum air temperature_p

Disturbance regimes

Sub–basin road density_g, Sub–basin road crossings_g[2,3,4,5], Sub–basin in plantation (%)_g[2], Sub–basin in young conifer (%)_g, Sub–basin in young hardwood (%)_g[2,3,4,5], Sub–basin in late seral trees (%)_g[3,5], Sub–basin in other vegetation (%)_g[1], Sub–basin with recent fire history (%)_g, Stump count[1]

Parent geology

Sub–basin in geology types: HF (pre–Cretaceous metamorphic rocks) (%)_g[3]; RCM (mafic volcanic rock and chert) (%)_g[1,3,4]

Land surrounding the reach

Trees

Age of dominant cohort, Age of oldest cohort[1], Conifer 15–27 cm_t[2,3], Conifer 28–60 cm_t[2,4], Conifer 61–120 cm_t[4,5], Conifer > 120 cm _t, Hardwood 15–27 cm_t[4], Hardwood 28–60 cm_t[1,4], Hardwood 61–120 cm_t1, log_c[5], Riparian forest width (m) [3,4,5]

Shrub and understory vegetation

Shrub_u[1], Conifer seedling_u[3], Hardwood seedling_u[1,3]

Ground level vegetation

Fern_u[3,4,5], Grass_u, Herb_u

Ground cover

Soil_u[1,3,5], Leaf_u, Moss_u[1,2], Log_u, Rock_u[2,5], Debris_u3, Litter depth[1,3,4]

Forest climate

Soil temperature_s[2], 1 cm air temperature_s, Canopy_s[1,5], Canopy variation_s[1]

Appendix 1. (Cont.)

Within the reach

Aquatic conditions

Reach aspect, Canopy closure above the stream, Habitat width[2,3,4,5], S* pool sediment measures[1,5], Percent fines from S* pools[2,3,5], Maximum depth in S* pools[2,3,4,5], Mean weekly maximum water temperature (MWMT)_d[2,3,4,5], Water temperature daily amplitude_d[3,4,5], Stream flow_a[4], Embeddedness (from slow mesohabitats)_a[4]

Aquatic substrates

Bedrock_b, Boulder_b[3,4,5], Cobble_b[2,3,5], Pebble_b, Gravel_b[2,3,5], Sand_b, Fines_b[5], Organic fines_b[2], Large woody debris_b[1,2,4,5]