

Environmental correlates of species richness for native freshwater fish in Oregon, U.S.A.

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Abstract

Aim To better understand how environmental factors affect fish species richness across the state of Oregon.

Location Oregon, U.S.A.

Methods A database showing collection locations of 4911 fish specimens in the Oregon State University museum was modified by the Oregon Natural Heritage Program to include probable occurrences, and mapped within a grid of 375 hexagons that cover the state. The individual species maps of freshwater fish in Oregon were reviewed and revised by thirty regional fish biologists and then synthesized into a single map of native species richness. We used regression tree analysis (RTA) and multiple linear regression (MLR) to assess patterns of fish species richness with twenty environmental, three anthropogenic, and two historical variables.

Results RTA explained 66% of the variation in native species richness, associating richness with annual air temperature range, minimum January temperature, introduced species richness, and stream density. MLR explained 68% of native species richness variation and associated richness with maximum July temperature, air temperature range, standard deviation of monthly temperature, stream density, introduced species richness, and basin connectivity.

Main conclusions We conclude that for these data and at this scale, native fish species richness in Oregon is associated with annual climatic extremes, spatial variability of climate, stream density, basin connectivity, and introduced fishes.

Keywords

Biodiversity, climate, stream density, basin connectivity, alien fishes, Oregon.

INTRODUCTION

Species richness patterns are important biodiversity indicators. Biodiversity losses associated with human actions, and the extent of human alterations globally (Vitousek *et al.*, 1986), make understanding and conserving biodiversity fundamental concerns of scientists, managers, and concerned citizens (Wilson, 1985; Cairns & Lackey, 1992; Allan & Flecker, 1993).

Discussions of biodiversity often centre on terrestrial species, but in the U.S. aquatic organisms are the most imperilled of any biotic group (The Nature Conservancy, 1996). During the last 100 years, three genera, twenty-seven species, and thirteen

sub-species of fish were extirpated in North America (Miller, Williams & Williams, 1989). Currently 296 North American fish taxa are considered endangered, threatened, or of special concern (Williams *et al.*, 1989; Nehlsen, Williams & Lichatowich, 1991; Mayden *et al.*, 1992). In the state of Oregon, nine native freshwater fish species or sub-species are formally listed as endangered or threatened under the U.S. Endangered Species Act (several others are candidates or warranted) and thirty-six taxa are listed by the state of Oregon as sensitive, threatened, or endangered (Marshall, Chilcote & Weeks, 1996; National Marine Fisheries Service, 1996; U.S. Fish and Wildlife Service, 1996).

Controlling anthropogenic risks to biodiversity requires knowledge of the natural characteristics and processes that create, support, or limit diversity. Contemporary species diversity patterns are thought to result from a hierarchy of

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natural and anthropogenic processes and conditions acting across multiple scales; global factors set the context for continents and regions which, in turn, set the context for locales (Ricklefs, 1987; Tonn, 1990; Bohning-Gaese, 1997). The issue of local versus regional drivers in aquatic systems has also been discussed by Legendre & Legendre (1984), Jackson & Harvey (1989), and Mandrak (1995). Ricklefs (1987) gave a thorough treatment of scale issues as they relate to the diversity of biota in general, while Brown & Maurer (1989) and Brown (1995) discussed ecological relationships as a function of scale. Levin (1992) explained how analytical scale and the observed patterns are related, emphasizing that changing focus to larger spatial scales often means a loss in detail but a gain in predictability.

Different explanatory variables operate at different scales. At the global scale, Oberdorff, Guegan & Huguény (1995) reported that drainage basin area, mean annual discharge, and net primary production accounted for most variation in fish species richness in large river basins. At continental and regional scales, river basin area (Welcomme, 1979; Livingstone, Rowland & Bailey, 1982; Huguény, 1989), river surface area (Eadie *et al.*, 1986), basin discharge (Livingstone *et al.*, 1982; Oberdorff, Huguény & Guegan, 1997), energy availability (Oberdorff *et al.*, 1995, 1997), and climate (McAllister *et al.*, 1986; Oberdorff *et al.*, 1997), as well as historical factors such as dispersal history (Huguény, 1989) and glaciation (Oberdorff *et al.*, 1997), were used to explain patterns in species richness. At the local scale, species richness was correlated with elevation, stream gradient, stream order, drainage area, and the fish species richness of the basin in western Washington (Beecher, Dott & Fernau, 1988), but with regional, versus local, factors in impaired nearshore locales of the Great Lakes (Kelso & Minns, 1996). Water chemistry, habitat structure, channel morphology, food base, hydrologic regime, competition, and predation are also considered important local characteristics (Karr & Dudley, 1981; Oberdorff *et al.*, 1995; Mandrak, 1995).

To further the understanding of aquatic biodiversity we undertook an exploratory study of the regional pattern of species richness in Oregon native freshwater fish. We investigated both proximal and distal factors by relating species richness to selected climatic, geographic, historical, and anthropogenic variables. Existing biodiversity theories were used to select variables and to interpret results.

DATA AND METHODS

Geographic grid

Since Terentev (1963), many biogeographic analyses of species richness have used an approach known as gross geographic lumping (Pianka, 1966), grid analysis (McAllister *et al.*, 1986), or quadrat analysis (Kiestler, 1971). This method overlays a geometric grid on a map, and for each cell the number of species with some part of their known ranges falling within the cell is summed. The cumulative patterns formed within the grid are then assessed. This approach has been applied to birds (Cook, 1969; Bohning-Gaese, 1997), mammals (Simpson, 1964;

Wilson, 1973), amphibians and reptiles (Kiestler, 1971; Rogers, 1976), and fish (McAllister *et al.*, 1986; Mandrak, 1995).

We implemented an equal-area regular grid of 441 contiguous hexagons covering Oregon. Each grid cell was 640 km² with centres of neighbouring cells 27 km apart. Each cell had a unique identifier and known spatial position (White, Kimerling & Overton, 1992). A grid of this kind minimizes inconsistency in sampling unit shape and area which can confound statistical analyses (Mandrak, 1995). Further, the grid is an unbiased sampling structure imposing no initial assumptions of meaningful geographic barriers (e.g. drainage divides, Legendre & Legendre, 1984).

The original set of 441 grid cells was reduced to 375 by exclusion of all border cells that either fell over the Columbia and Snake Rivers or had greater than half their areas outside the state. The Columbia and Snake Rivers were excluded because they are minimally represented in Oregon and so are not comparable to other drainages in the state for which most, if not all, of the basin is represented. The remaining border cells contained >50% of their total area within Oregon. Explanatory variables in these cells were measured consistently on their reduced size so weighting was not used in final analyses. We did check to see if weighting by area made a difference in the choice of explanatory variables or in the percent of variance explained by the statistical models and found only minor differences.

Fish species richness data

We counted sixty-two native freshwater fish species in Oregon (Table 1) and richness ranged from 0–23 species per cell (Fig. 1). Our fish data were supplied by The Nature Conservancy's Oregon Natural Heritage Program. This database was initially constructed from data for 4911 specimens and over 1300 localities in the Fish Museum of the Department of Fisheries and Wildlife at Oregon State University, the Oregon Department of Fish and Wildlife's Oregon Rivers Information System, and Lee *et al.* (1980).

Species distribution maps developed from these data were reviewed by thirty regional fish biologists from throughout Oregon and supplemented with their knowledge of species distributions. These biologists added locations of confirmed and probable (>80% probability based on extrapolating from known locations and expert opinion) species occurrence (Master, 1996). The final database contained 4381 records of confirmed or probable occurrences of native and introduced fishes in Oregon.

The original database was constructed from a variety of sources (see Hughes, Rexstad & Bond, 1987 and Bond, Rexstad & Hughes, 1988 for more complete descriptions of the Oregon State University database). Consequently, data collection was unevenly distributed across the state and through time, with disparate collection methods. We acknowledge these imperfections but believe the data are appropriate for this region at a scale of study important to current fisheries research (Hinch, 1991). The data are also limited to presence of species within a cell at some time during a year and provide no information on population sizes, temporal use, or species

Table 1 Native species of Oregon freshwater fish.

<i>Lampetra ayresi</i> (Gunther, 1870)	<i>Gila coerulea</i> (Girard, 1856)	<i>Chasmistes brevirostris</i> Cope, 1879
<i>Lampetra lethophaga</i> Hubbs, 1971	<i>Hesperoleucus symmetricus</i> (Baird & Girard, 1854)	<i>Deltistes luxatus</i> (Cope, 1879)
<i>Lampetra minima</i> Bond & Kan, 1973	<i>Mylocheilus caurinus</i> (Richardson, 1836)	<i>Percopsis transmontana</i> (Eigenmann & Eigenmann, 1892)
<i>Lampetra richardsoni</i> Vladykov & Follet, 1965	<i>Ptychocheilus oregonensis</i> (Richardson, 1836)	<i>Lota lota</i> (Linnaeus, 1758)
<i>Lampetra similis</i> (Vladykov & Kott, 1979)	<i>Ptychocheilus umpqua</i> Snyder, 1908	<i>Gasterosteus aculeatus</i> Linnaeus, 1758
<i>Lampetra tridentata</i> (Gairdner, 1836)	<i>Rhinichthys cataractae</i> (Valenciennes, 1842)	<i>Cymatogaster aggregata</i> Gibbons, 1854
<i>Acipenser medirostris</i> Ayres, 1854	<i>Rhinichthys evermanni</i> Snyder, 1908	<i>Cottus aleuticus</i> Gilbert, 1896
<i>Acipenser transmontanus</i> Richardson, 1836	<i>Rhinichthys falcatus</i> (Eigenmann & Eigenmann, 1893)	<i>Cottus asper</i> Richardson, 1836
<i>Oncorhynchus clarki</i> (Richardson, 1836)	<i>Rhinichthys osculus</i> (Girard, 1856)	<i>Cottus bairdi</i> Girard, 1850
<i>Oncorhynchus gorbusha</i> (Walbaum, 1792)	<i>Richardsonius balteatus</i> (Richardson, 1836)	<i>Cottus beldingi</i> Eigenmann & Eigenmann, 1891
<i>Oncorhynchus keta</i> (Walbaum, 1792)	<i>Richardsonius egregius</i> (Girard, 1858)	<i>Cottus confusus</i> Bailey & Bond, 1963
<i>Oncorhynchus kisutch</i> (Walbaum, 1792)	<i>Oregonichthys crameri</i> (Snyder, 1908)	<i>Cottus gulosus</i> (Girard, 1854)
<i>Oncorhynchus mykiss</i> (Walbaum, 1792)	<i>Oregonichthys kalawatseti</i> (Markle <i>et al.</i> , 1991)	<i>Cottus klamathensis</i> Gilbert, 1898
<i>Oncorhynchus nerka</i> (Walbaum, 1792)	<i>Catostomus columbianus</i> (Eigenmann & Eigenmann, 1893)	<i>Cottus marginatus</i> (Bean, 1881)
<i>Oncorhynchus tshawytscha</i> (Walbaum, 1792)	<i>Catostomus macrocheilus</i> Girard, 1856	<i>Cottus perplexus</i> Gilbert & Evermann, 1894
<i>Prosopium williamsoni</i> (Girard, 1856)	<i>Catostomus occidentalis</i> Ayres, 1854	<i>Cottus pitensis</i> Bailey & Bond, 1963
<i>Salvelinus confluentus</i> (Suckley, 1858)	<i>Catostomus platyrhynchus</i> (Cope, 1874)	<i>Cottus princeps</i> Gilbert, 1898
<i>Thaleichthys pacificus</i> (Richardson, 1836)	<i>Catostomus rimiculus</i> Gilbert & Snyder, 1898	<i>Cottus rhotheus</i> (Smith, 1882)
<i>Thaleichthys pacificus</i> (Richardson, 1836)	<i>Catostomus snyderi</i> Gilbert, 1898	<i>Cottus tenuis</i> (Evermann & Meek, 1898)
<i>Acrocheilus alutaceus</i> Agassiz & Pickering, 1855	<i>Catostomus tahoensis</i> Gill & Jordan, 1878	<i>Platichthys stellatus</i> (Pallas, 1787)
<i>Gila alvordensis</i> Hubbs & Miller, 1972	<i>Catostomus warnerensis</i> Snyder, 1908	
<i>Gila bicolor</i> (Girard, 1856)		
<i>Gila boraxobius</i> Williams & Bond, 1980		

assemblages. A statistical sampling design, frequent seasonal collections, use of multiple sampling gear, and quantitative estimates of proportionate abundances would offer a more definitive database—but only at considerable expense.

Explanatory variables

We selected a set of climatic, hydrographic, historical, and anthropogenic variables and examined them for correlations with fish species richness. Variables were selected based on reported correlation with fish species richness as well as their availability in a digital database.

Climatic data

Statistical measures of climate were selected to represent within-cell stability, extremes, and spatial heterogeneity of air temperature and precipitation across Oregon. Stable environments change little with seasons (Owen, 1989) and have been generally hypothesized to produce higher species richness (Pianka, 1966; Sanders, 1968; Currie, 1991). Variables encompassing the annual range of air temperature and precipitation within each cell were used to evaluate climatic stability; large within-cell ranges were considered unstable while narrow ranges were more stable.

Maximum and minimum climatic metrics were interpreted as environmental thresholds that may impose limits on species

diversity (McAllister *et al.*, 1986). Mean precipitation is included here as a simple measure of the relative abundance of precipitation.

Lacking consistent direct measures of habitat complexity, two indirect estimates were used instead to represent several elements of habitat complexity or spatial heterogeneity within each cell. One estimate of heterogeneity was the standard deviation of air temperature extremes. This is an indirect measure of habitat heterogeneity, but it is an excellent integrator of elevation, aspect, and slope differences at that scale. These variables, in turn, represent complexity in stream productivity, stream temperature, and stream gradient. A second indirect measure of habitat diversity is higher-order stream density, defined as the kilometres of stream in the hexagons divided by their areas (640 km²). The theory of island biogeography (MacArthur & Wilson, 1967) hypothesizes that larger areas (rivers in this case) contain a wider array of habitats and food resources. More heterogeneous physical and biological conditions have been hypothesized to provide more available niches and so allow greater species richness (Sanders, 1968; Rogers, 1976; Currie, 1991). However, river size influences richness through effects on immigration and colonization (see below), as well as through effects on habitat diversity.

All climate variables were based on 1948–1988 climate station records from throughout Oregon. The data were modelled and interpolated to continuous digital surfaces at 1 km² resolution,

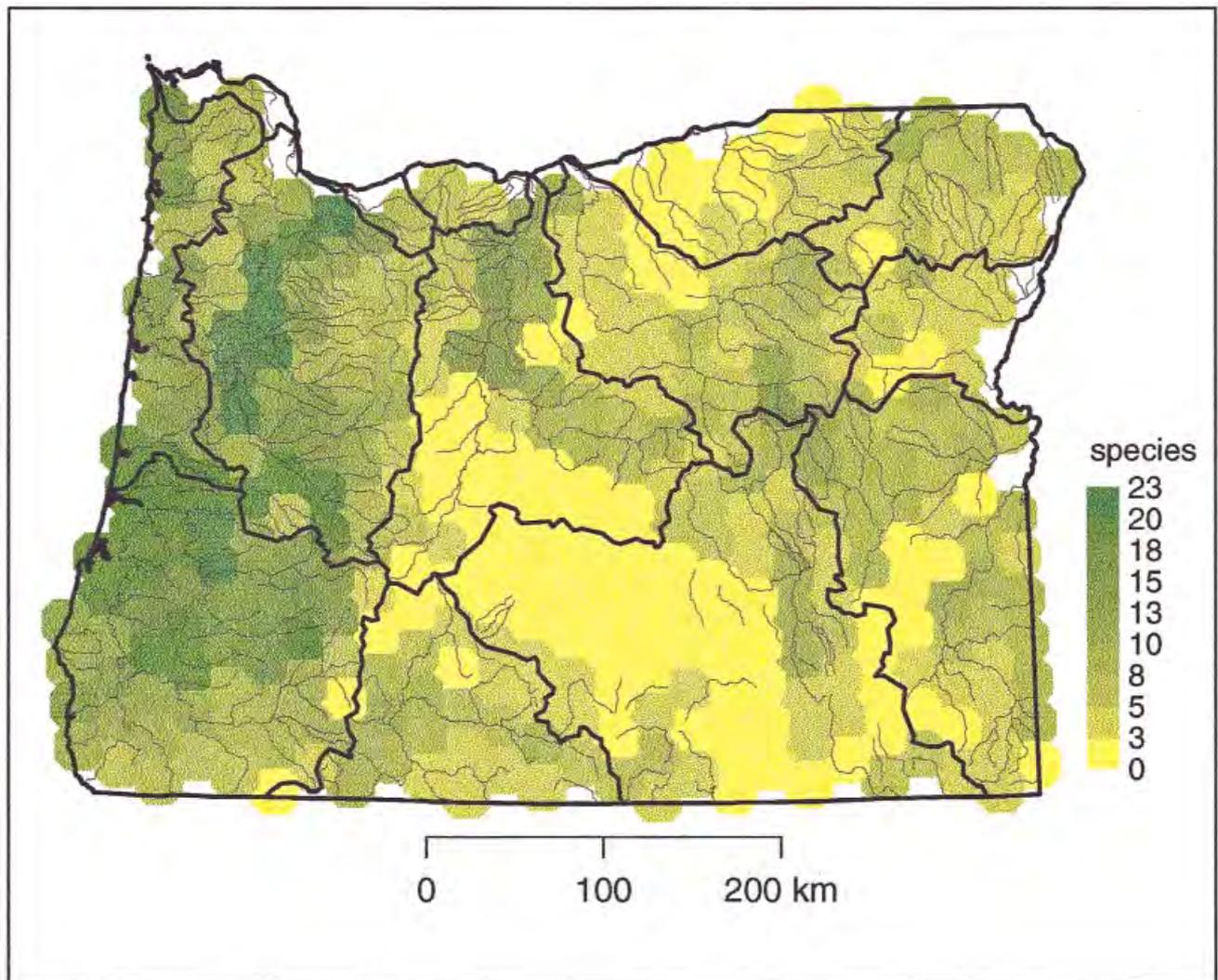


Figure 1 Spatial distribution of the species richness of native freshwater fish in Oregon. Major hydrographic regions and rivers are also shown.

and these surfaces were statistically aggregated to the sampling grid. Each pixel was 1 km^2 , so 640 modelled data points were included in each 640 km^2 grid cell.

January and July mean air temperature data were modelled and compiled using the method of Marks (1990). Initial values were the means of the monthly means calculated from daily mean temperatures at recording stations. These values were first corrected to potential temperatures at a reference air pressure of 1000 millibars using the station elevations and assuming a normal adiabatic lapse rate. The potential temperatures were then interpolated to the 1 km^2 pixel using a linear model. Finally, the interpolated values were converted to estimated actual temperatures from the adiabatic lapse rate correction and the elevation at each pixel.

Additional metrics were calculated from mean January and July air temperatures of each pixel. Minimum January and maximum July temperatures were the temperatures of the pixels in each grid cell with the lowest 40-year January mean

and the highest 40-year July mean, respectively. Since January and July standard deviations were highly correlated they were combined by taking the mean of the two values for each cell. This metric was called the monthly temperature standard deviation. Annual temperature range was the mean of the difference between mean July and January temperatures for each pixel; standard deviation in annual temperature range was the within-cell standard deviation of these differences.

Annual precipitation data were compiled from the dataset prepared by Daly, Neilson & Phillips (1994). They used a locally adaptive regression model to estimate annual precipitation values for unknown locations from known stations and elevation. Their 10 km^2 resolution data were linearly interpolated to 1 km^2 . Precipitation metrics were calculated from the mean annual precipitation of each pixel in each cell. Minimum and maximum precipitation were the precipitation values of the pixels in each cell with the lowest and highest 40-year means, respectively, and precipitation range

was the difference of these two. Mean precipitation was calculated from the pixel values for the period of record.

Hydrographic data

Species-area theory is a component of the theory of island biogeography, in which species richness results from the opposing processes of immigration and extinction. Generally, large areas are colonized by more dispersing organisms, and support larger populations, reducing the likelihood of extinction (MacArthur & Wilson, 1967; Wright, 1983). Because basin discharge, basin area, and river surface area are all measures of river size or area, they can be expected to correlate with species richness, with the relationships attributed to species-area theory (MacArthur & Wilson, 1967; Eadie *et al.*, 1986; Oberdorff *et al.*, 1995). However, larger water bodies are also expected to provide greater spatial heterogeneity or habitat complexity than smaller waters (Guegan, Lek & Oberdorff, 1998). The species-area relationship, therefore, incorporates a species-habitat complexity relationship, making it difficult to determine whether increased species richness in larger waters results from greater area, greater heterogeneity, or both.

For aquatic organisms, water bodies are islands in a sea of land. Since terrestrial area was constant among grid cells, we used stream density to measure potential colonization area, or island size; discharge data were not consistently available.

Densities of intermittent, first, second, third, and higher-order streams (> third), as well as total perennial stream densities, were examined (Strahler, 1957). Data were taken from the U.S. Geological Survey's Pacific Northwest River Reach Files, a 1:100,000 scale digital hydrographic database. Total lake and reservoir surface area per grid cell was included as a separate variable. Lake area has been used at local (Jackson & Harvey, 1989) and regional (Matusek & Beggs, 1988; Mandrak, 1995) scales to explain species richness.

Basin connectivity

River basin boundaries are not constant. Geological evidence of lake overflow and headwater capture (Legendre & Legendre, 1984; Minckley, Hendrickson & Bond, 1986; Orr, Orr & Baldwin, 1992), as well as the widespread distribution of some primary species (Hughes *et al.*, 1987), imply that over long times fish move across apparently impassable contemporary barriers. Smith (1981) proposed that barriers to dispersal into a basin can have a positive effect on speciation by promoting genetic isolation and subsequent evolution. But barriers also can promote extinction by reducing gene flow within a metapopulation and into the basin (Smith, 1981; Li *et al.*, 1995). The particular outcome depends on additional characteristics such as climatic history and stability.

A variable representing connectivity of major basins since the Pleistocene was developed. We used Minckley *et al.* (1986) to categorize the major basins of Oregon into one of three groups: currently connected to the Columbia River, historically connected to the Columbia or Sacramento Rivers, and exclusively coastal drainages. Each grid cell was assigned the category of the basin in which the majority of its area fell.

The most direct river distance of each grid cell to the sea

was calculated. Proximity to the Pacific Ocean may have affected dispersal history and, since the fish richness metric included fishes of marine and freshwater origin, as well as currently anadromous and euryhaline species, this characteristic could help explain species richness. For currently endorheic basins, we used the distance to the sea via historical inter-basin connections (Minckley *et al.*, 1986).

Anthropogenic data

Three anthropogenic variables (human population, roads, introduced fish) were included to evaluate whether direct and indirect measures of human environmental alterations were associated with fish species richness. These characteristics have all been implicated in biodiversity degradation (Soulé, 1991; Forester & Machlis, 1996); however, it is also possible for moderate levels of disturbance to increase native species richness (Leidy & Fiedler, 1985; Hughes & Gammon, 1987; Lyons, Wang & Simonson, 1996). Human population was used as a measure of potential human impacts on stream systems. Where population is high, more environmental alteration is likely.

Roads are often associated with degraded riparian condition (Thomas, Maser & Rodiek, 1979), changes in hydrology and stream geomorphology (Booth & Reinelt, 1994), and alteration of sediment levels (Reid & Dunne, 1984), each of which can influence fish in streams (Fausch, Hawkes & Parsons, 1988).

Introduced species were defined as species non-indigenous to Oregon (aliens) or fish that have been transplanted outside their native ranges. The forty-one introduced species (Table 2) ranged from 0 to 14 species per cell (Fig. 2). Introduced fish are believed to have a negative effect on native fishes at the local scale (Fausch, 1988; Ross, 1991; Baltz & Moyle, 1993). While there are few documented cases of introduced fish, alone, causing native species extinction in the American West, local extinctions, population declines, and shrinking native fish ranges commonly occur when species are introduced (Krueger & May, 1991). For example, Miller *et al.* (1989) associated alien species with 68% of fish extinctions in North America; in several cases they were the primary factor. Leidy & Fiedler (1985) found that non-native fishes dominated in highly disturbed waters; however, the greatest numbers of alien and native species co-occurred in streams experiencing intermediate levels of disturbance. We evaluated whether introduced species had widespread effects on native fishes, such as those reported by Whittier, Halliwell & Paulsen (1997), rather than simply local effects.

Seven of the original twenty-one explanatory variables (Table 3) were included in the final models; these are displayed in Fig. 2.

Statistical methods

Associations between native species richness and the set of explanatory variables were evaluated using regression tree analysis (RTA) and multiple linear regression (MLR). In RTA all explanatory variables were included. However, in the MLR the collinear and highly correlated variables were deleted to avoid computational complications (Table 3). Although the response (species richness, Fig. 1) is spatially correlated, our

<i>Acipenser transmontanus</i> Richardson, 1836*	<i>Ictalurus punctatus</i> (Rafinesque, 1818)
<i>Alosa sapidissima</i> (Wilson, 1811)	<i>Noturus gyrinus</i> (Mitchill, 1817)
<i>Oncorhynchus aguabonita</i> (Jordan, 1893)	<i>Pylodictis olivaris</i> (Rafinesque, 1818)
<i>Oncorhynchus clarki</i> (Richardson, 1836)*	<i>Fundulus diaphanus</i> (Lesueur, 1819)
<i>Oncorhynchus mykiss</i> (Walbaum, 1792)*	<i>Lucania parva</i> (Baird & Girard, 1855)
<i>Oncorhynchus nerka</i> (Walbaum, 1792)*	<i>Gambusia affinis</i> (Baird & Girard, 1853)
<i>Salmo salar</i> Linnaeus, 1758	<i>Morone saxatilis</i> (Walbaum, 1792)
<i>Salmo trutta</i> Linnaeus, 1758	<i>Archoplites interruptus</i> (Girard, 1854)
<i>Salvelinus fontinalis</i> (Mitchill, 1814)	<i>Lepomis cyanellus</i> Rafinesque, 1819
<i>Salvelinus namaycush</i> (Walbaum, 1792)	<i>Lepomis gibbosus</i> (Linnaeus, 1758)
<i>Carassius auratus</i> (Linnaeus, 1758)	<i>Lepomis gulosus</i> (Cuvier, 1829)
<i>Ctenopharyngodon idella</i> (Valenciennes, 1844)	<i>Lepomis macrochirus</i> Rafinesque, 1819
<i>Cyprinus carpio</i> Linnaeus, 1758	<i>Lepomis microlophus</i> (Gunther, 1859)
<i>Notemigonus crysoleucas</i> (Mitchill, 1814)	<i>Micropterus dolomieu</i> Lacepede, 1802
<i>Pimephales promelas</i> (Rafinesque, 1820)	<i>Micropterus salmoides</i> (Lacepede, 1802)
<i>Tinca tinca</i> (Linnaeus, 1758)	<i>Pomoxis annularis</i> Rafinesque, 1818
<i>Misgurnus anguillicaudatus</i> (Cantor, 1842)	<i>Pomoxis nigromaculatus</i> (Lesueur, 1829)
<i>Ameiurus catus</i> (Linnaeus, 1758)	<i>Piaractus brachypomus</i> (Cuvier, 1818)
<i>Ameiurus melas</i> (Rafinesque, 1820)	<i>Perca flavescens</i> (Mitchill, 1814)
<i>Ameiurus natalis</i> (Lesueur, 1819)	<i>Stizostedion vitreum</i> (Mitchill, 1818)
<i>Ameiurus nebulosus</i> (Lesueur, 1819)	

Table 2 Introduced species of Oregon fish. Includes aliens (species non-native to Oregon) and transplants* (species native to Oregon but transplanted outside their ranges).

objective was to seek explanations for the spatial correlation. Since the spatial trends essentially disappear in the residual plot (see results), we believe our regression model is valid. Explanatory variables were initially rounded to a level judged appropriate for the accuracy of each data source (temperature to nearest °C, precipitation to nearest cm, stream and road length to 10 m, lake area to 0.1 km², population to nearest integer).

Regression tree analysis

Regression tree analysis is a binary partitioning technique (Breiman *et al.*, 1984). Input to RTA consisted of a matrix 375 rows (the grid cells) by 22 columns (one response variable, twenty-one explanatory variables) and output was a decision tree grouping the grid cells according to a sequence of explanatory variables. To choose the first partition, RTA began with the 375 grid cells and systematically moved through the possible divisions of this set into two sub-groups. For each partition, RTA picked the variable that minimized the residual sum of squares (RSS) of the two sub-groups, relative to the parent group. The values of the selected explanatory variable over each subset defined a splitting threshold, and the mean of the native richness values in each sub-group was the predicted richness value for this sub-group. This process was recursively and independently continued on each sub-group, checking all divisions and all variables, until subset size was too small to continue or additional splits provided minor further reduction in the RSS.

Through this process, RTA successively split the whole dataset into increasingly homogeneous subsets using the most explanatory variable at each level. Contingent or hierarchical relationships were uncovered by this partitioning as each successive split was done within the context of all previous splits (Efron & Tibshirani, 1991; Michaelson *et al.*, 1994; Venables & Ripley, 1994). Since each cell was a spatial unit,

the method examined increasingly smaller, and ecologically structured, spatial scales of the data as subset size was reduced with each partition.

RTA could explain nearly all variation within a particular dataset by over-fitting the data and partitioning cells into too many sub-groups if some sort of pruning method were not used. We used a cross-validation procedure to decide where to prune. Cross-validation divided the data into ten randomly-chosen, approximately equal-sized blocks and then systematically reserved one block at a time to test the predictive ability of different-sized trees grown with the remaining data. To determine the optimal-size tree, we took the mode of many repeated cross-validations using the one standard error rule (Breiman *et al.*, 1984). Once size was determined the over-fitted tree was 'pruned' to the suggested size (Clark & Pregibon, 1992).

Multiple linear regression

Multiple linear regression (MLR) was used to complement RTA. Preliminary analyses showed that native richness responded differently depending on whether an observation was west or east of the Cascade Mountains crest. The RTA handled different relationships within groups as sub-groups. In MLR, however, observations are treated as a single unit, so interaction terms are necessary to account for conditional relationships. We considered including interaction terms but instead conducted separate analyses for the west and east. Some interactions within the east and west were still marginally significant. For example, when we included the interaction of degree of isolation with monthly standard deviation there was a small gain in the R^2 of 0.51 to 0.53, but the main effect, degree of isolation, was no longer significant. Rather than use the less interpretable model and because we were less interested in modelling sub-regions than in creating a broadly applicable model, the interactions were not included in the separate regression models.

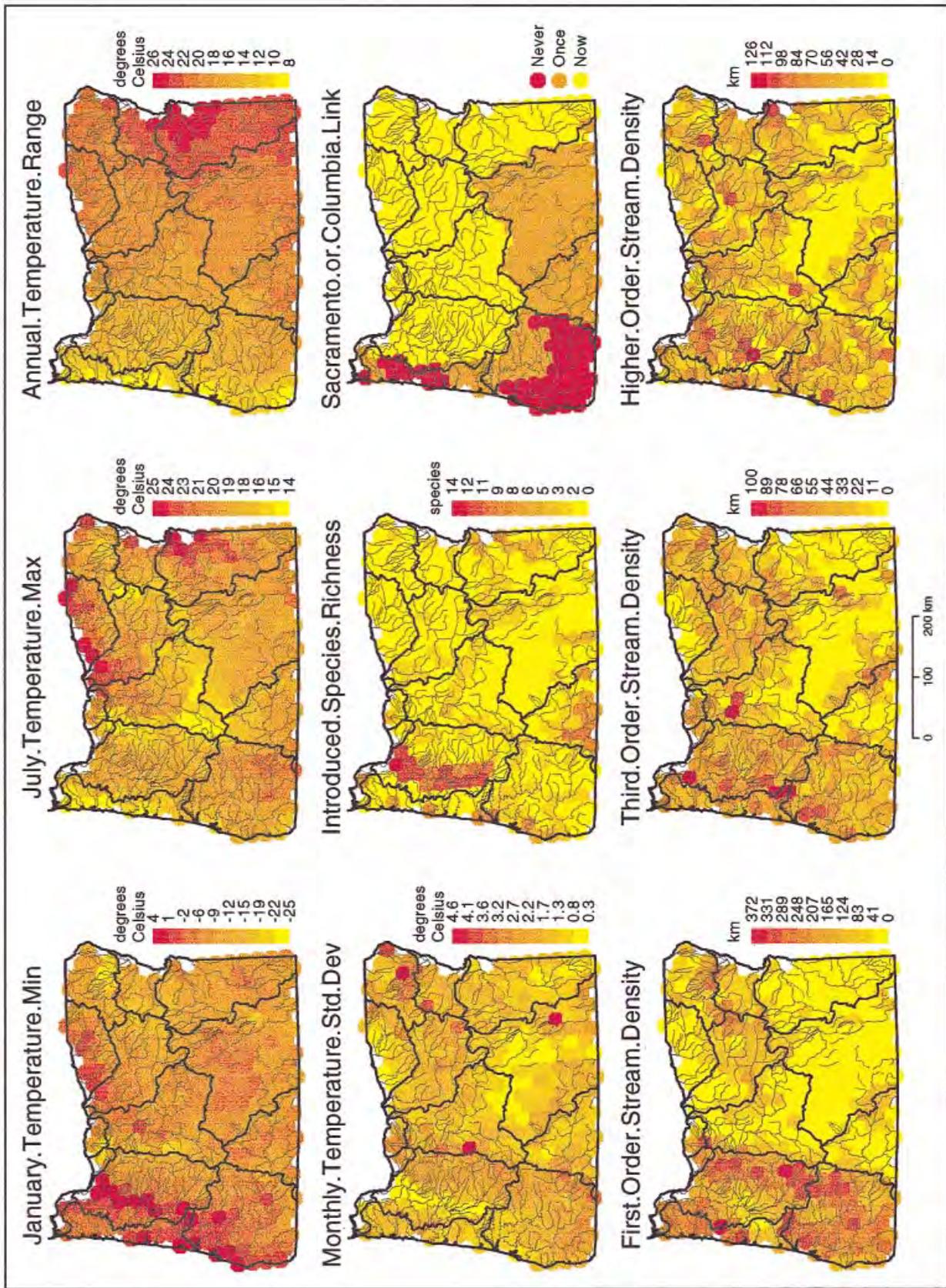


Figure 2 Spatial distribution of significant explanatory variables from regression tree analysis and multiple linear regression.

Variables	Theory tested	RTA	MLR
Climatic			
January temperature minimum	Environmental threshold	X	X
July temperature maximum	Environmental threshold	X	X
Annual temperature range	Climatic stability	X	X
Annual temperature range standard deviation	Spatial heterogeneity	X	X
Monthly temperature range standard deviation	Spatial heterogeneity	X	X
Annual precipitation minimum	Environmental threshold	X	X
Annual precipitation maximum	Environmental threshold	X	X
Annual precipitation range	Climatic stability	X	
Annual precipitation mean	Environmental threshold	X	X
Hydrographic			
Intermittent stream density	Species-area	X	X
First order stream density	Species-area	X	X
Second order stream density	Species-area	X	X
Third order stream density	Species-area	X	X
Higher order stream density	Species-area	X	X
	Spatial heterogeneity	X	X
Perennial stream density	Species-area	X	
Lake and reservoir area	Species-area	X	X
Historical			
Sacramento or Columbia Link	Historical context	X	X
River distance to the Pacific Ocean	Historical context	X	X
Anthropogenic			
Road density	Environmental alteration	X	X
Human population density (1990)	Environmental alteration	X	Ln
Introduced species richness	Environmental alteration	X	X

Table 3 Explanatory variables examined in each statistical analysis and the theory tested by each variable. The variables were reduced from the full set for the multiple linear regression analysis (MLR) because of strong correlation among some variables and exact collinearity. These conditions do not limit the application of regression tree analysis (RTA). Ln = natural log.

For both the west and east data we assessed the significance and explanatory power of all possible regression models with two to seven variables. From these potential models the Bayesian Information Criterion (BIC, Schwartz 1978) was used to choose the final models, where $BIC = n \log \hat{\sigma}^2 + p \log n$. The BIC considers sample size (n), estimated variance ($\hat{\sigma}^2$), and the number of coefficients in a model (p); smaller values of $\hat{\sigma}^2$ are rewarded in BIC while there is a penalty for increasing p as variables are added to the model. The best models are those with the smallest BIC, which means those with small $\hat{\sigma}^2$ and small p (Ramsey & Schafer, 1997). A BIC analysis suggests the number of variables the final model should contain, then the regression model with the highest R^2 of that size is chosen. We also investigated model fit using stepwise variable selection to see if the BIC and stepwise results were similar (in variables selected, number of variables selected, and R^2). The stepwise and BIC models were similar, differing slightly in the variables chosen and the R^2 . For example, for the east side the stepwise model included the same variables as the BIC model plus the standard deviation of annual temperature range.

RESULTS

Regression tree analysis

The RTA divided the observations into five groups according to four variables and explained 66% of the variation in native

species richness (Figs 3 and 4). The first partition of the data accounted for 49% of the total variation while subsequent partitions explained 3–8%. In this application, RTA's partitioning capability was well matched to the hierarchical nature of richness patterns. Despite the fact that RTA does not consider spatial proximity, most of the groups appear as contiguous regions versus scattered cells (Fig. 4a). The spatial distribution of residuals (Fig. 4b) showed a region in the upper Deschutes basin (upper left-centre) where there was a distinct boundary between substantial over- and under-prediction. This occurred in the vicinity of Lake Billy Chinook (a large dam and reservoir in a semi-arid environment). Although there was some overlap in observed species richness within sub-groups (Fig. 5), the sub-group medians were distinctly different.

Western Branch

According to the RTA model, fish species richness was initially split according to annual temperature range greater than and less than 16.5°C (Fig. 3). Cells with temperature ranges below 16.5°C occurred throughout most of western Oregon, had a mean richness of fourteen species, and were further split into two groups for which minimum January temperature was greater than and less than -7.5°C. Mean richness in these groups was fifteen and eight species respectively. Where minimum January temperature was > -7.5°C the next partition occurred according to the number of introduced species. With >1.5 introduced species, mean richness was seventeen native

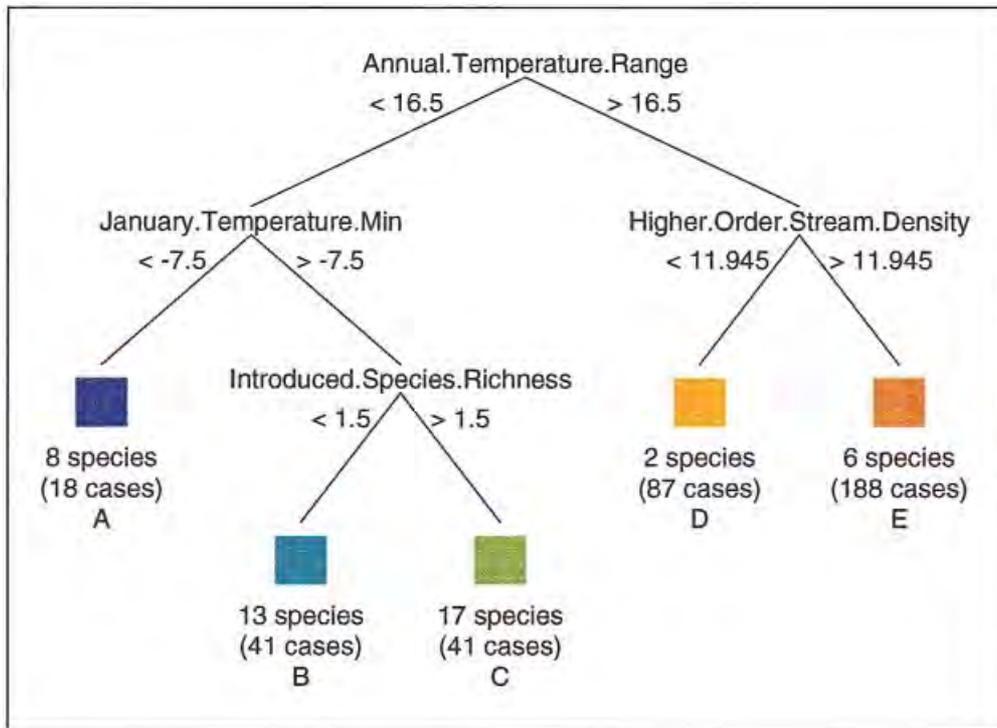


Figure 3 Structure of the regression tree analysis model. Each terminal node of the tree is symbolized with a different colour and coordinated with the spatial distribution of the observations within each final sub-group shown in Fig. 4(a), and with the boxplots in Fig. 5.

fish species, and where < 1.5 introduced species occurred, mean richness was thirteen native fish species. Except for an area in the southwest (upper Rogue River basin, Fig. 4a), the initial grouping was virtually contiguous throughout the wet west.

Succeeding subdivisions in western Oregon first distinguished the high elevation Cascades, where January minimum temperatures and species richness were low. Although the cold was limiting, richness was greater than the state average of seven species, possibly due to relatively abundant moisture. Elsewhere in western Oregon, where minimum January temperature was higher, cold temperature was not limiting and species richness was greater. The highest-predicted mean species richness (17) was associated with lower annual temperature range, warmer minimum January temperature, and the presence of more introduced species.

Eastern Branch

Cells with annual temperature range $> 16.5^{\circ}\text{C}$ had a mean richness of five species and formed a contiguous region over eastern Oregon and the upper Rogue basin. This region was divided once more according to the density of higher-order streams. Cells with > 11.945 kilometres had a mean richness of six species and those with fewer supported two species.

Multiple linear regression

Both MLR models and all variables within them were highly significant ($P \leq 0.02$) and the overall R^2 for the state was 0.68

(Table 4). It was calculated by subtracting the residual sum of squares for the east and west models from the total sum of squares (TSS), then dividing by the TSS. In the following paragraphs, when we talk about a variable's relationship with native fish species richness, we are assuming that the other variables in the model remain constant. The fit of the MLR model showed no outliers (Fig. 6). Predicted species richness indicated fairly contiguous cell patterns (Fig. 7a), and the only anomalous spatial pattern in residuals occurred in the vicinity of Lake Billy Chinook (Fig. 7b), as was also the case with RTA.

West model

The MLR model for western Oregon had an R^2 of 0.51 and associated native species richness with standard deviation of monthly temperature, degree of basin isolation, maximum July temperature, annual temperature range, and density of first-order streams (Table 4a). Maximum July temperature had a positive coefficient, indicating that warmer summer temperatures in the west generally resulted in more species (or that cooler summer temperatures resulted in fewer species). Standard deviation of monthly temperature, one of our estimates of spatial heterogeneity, had a negative relationship with species richness. Similar to the RTA results, annual temperature range was negatively associated with species richness. The MLR analyses also showed that grid cells with drainages currently or recently connected to the Columbia or Sacramento basins were associated positively with species

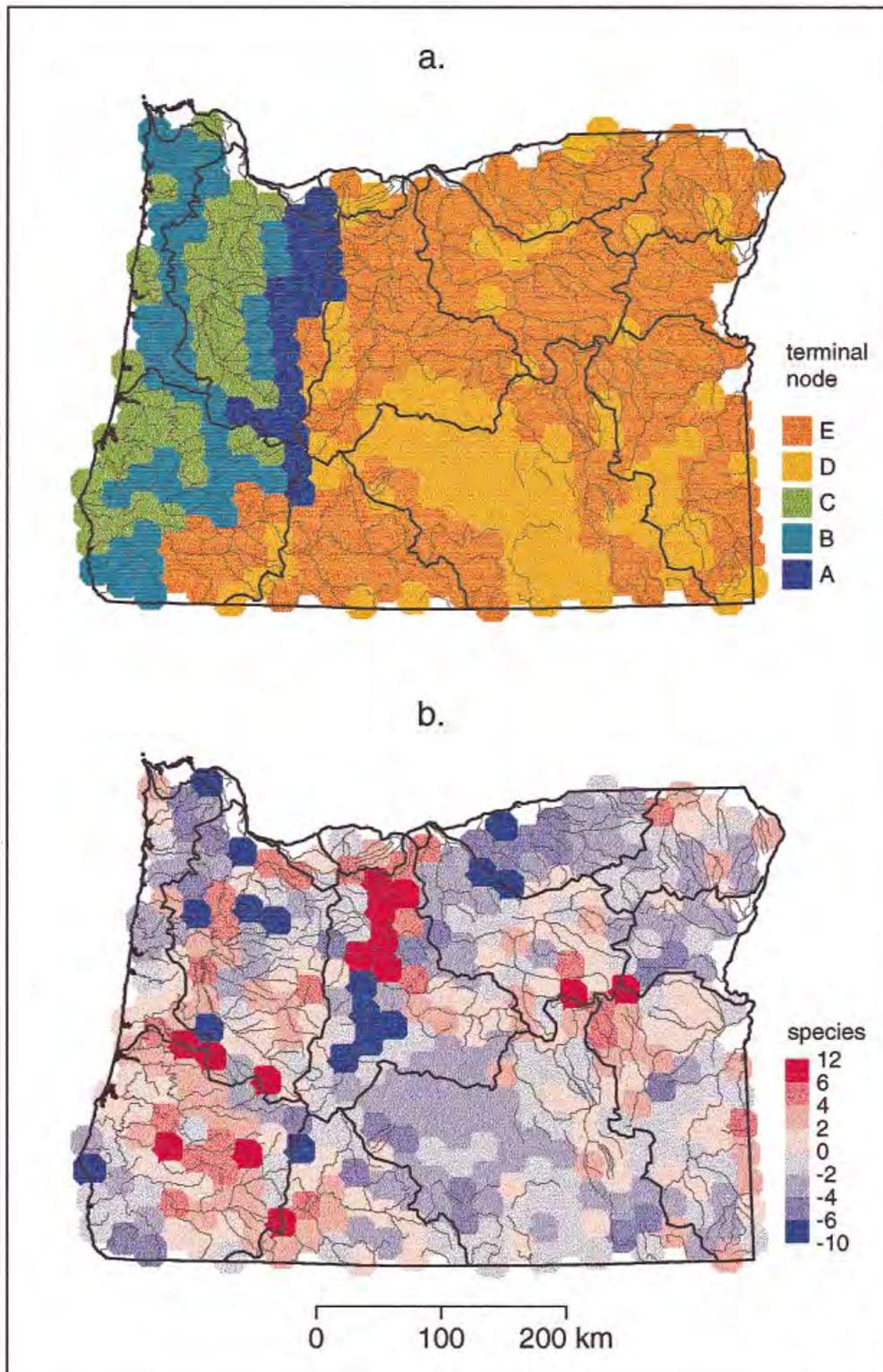


Figure 4 (a) Spatial distribution of each terminal node from the regression tree analysis model. (b) Spatial distribution of the residuals of the regression tree analysis model. Note, residuals are greater here than for MLR because RTA estimates means, which are distinctly different, while MLR estimates species richness as a continuous distribution.

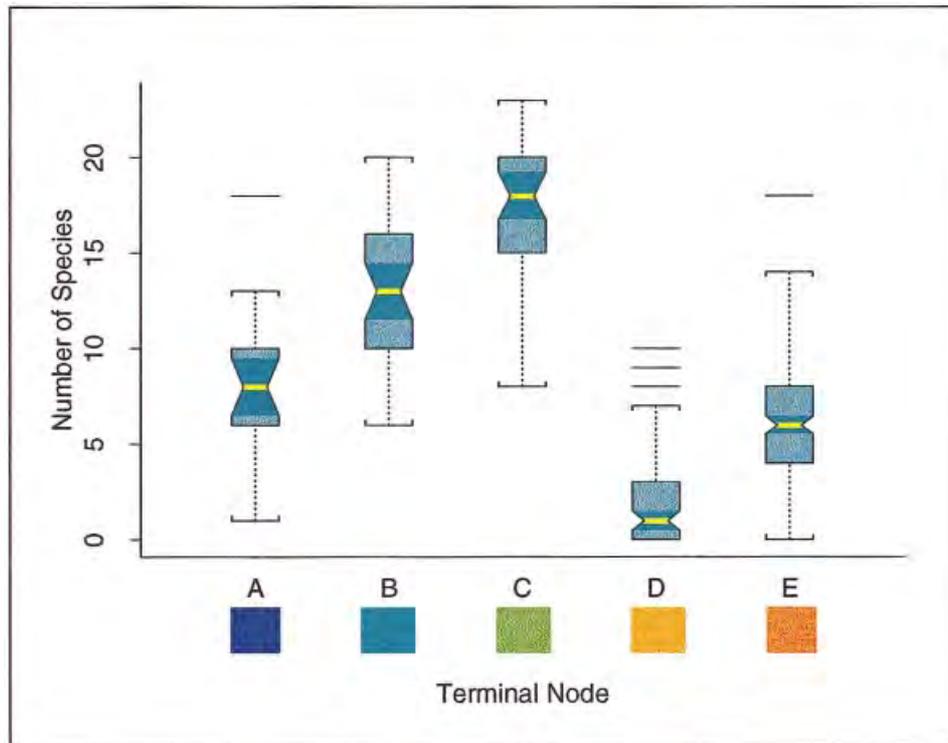


Figure 5 Species richness variability at terminal nodes of the regression tree. Unconnected horizontal lines are outliers. Brackets are at the nearest data point not >1.5 times the interquartile distance from the nearest quartile. Shaded areas are the 25th–75th percentiles. Non-overlapping notches represent distributions differing at an approximately 5% confidence level. The yellow line in the middle of the notch is the median value of richness for each node.

Variable	Coefficient	P-value	Partial-R
(a) West model (variance explained = 51%):			
July temperature maximum	0.240	<0.001	0.529
Annual temperature range	-0.174	<0.001	-0.443
Monthly temperature standard deviation	-0.409	<0.001	-0.382
First order stream density	0.002	0.020	0.222
Sacramento or Columbia Link	0.525	<0.001	0.385
(b) East model (variance explained = 45%):			
Annual temperature range	0.071	0.001	0.201
Third order stream density	0.018	<0.001	0.436
Higher order stream density	0.013	<0.001	0.376
Introduced species richness	0.153	<0.001	0.330

Table 4 Results of multiple linear regression (MLR) analysis: multiple R -squared values (variance explained), regression coefficients, P -values, and partial correlations between significant explanatory variables and native species richness in (a) western Oregon and (b) eastern Oregon. Combined variance explained = 68%.

richness of freshwater fish, compared with cells that were exclusively coastal in recent geological time. First-order stream density was also associated with greater richness of freshwater fish species.

East model

The east analysis explained 45% of the initial richness variation and significantly correlated richness with four variables: the lengths of third-order and higher-order streams, annual temperature range, and introduced species richness (Table 4b).

As seen in the RTA and in the west MLR analysis, annual temperature range was a significant variable in the east. This coefficient was positive in this case, suggesting that climatic stability may limit species richness in some regions (such as arid southeast Oregon), which is an opposite relationship from that found in the west. As with the western branch of RTA, the richness of introduced and native species were positively associated. Finally, the importance of larger streams in the arid and semi-arid east indicates the critical role of permanent rivers in this region.

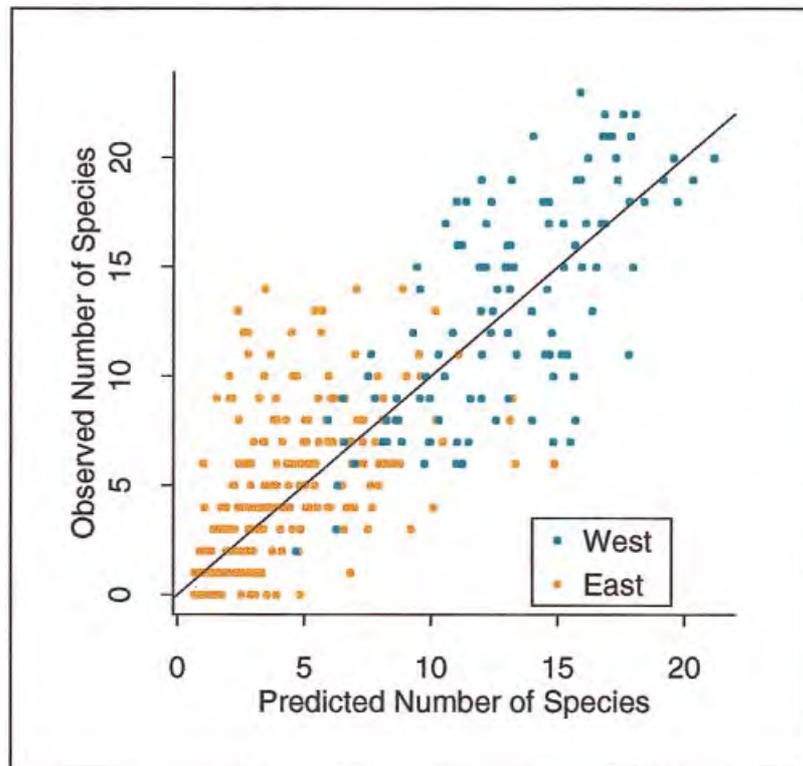


Figure 6 The number of native fish species observed and those predicted by the multiple linear regression model for western Oregon (blue dots) and eastern Oregon (orange dots). The straight line represents points where observed and predicted species are equivalent.

DISCUSSION

The regression tree and multiple linear analyses show that native fish species richness in Oregon is correlated with climatic, hydrographic, historical, and anthropogenic variables. The meaningful climatic variables were all related to temperature and included metrics of spatial heterogeneity, climatic stability, and environmental thresholds, or temperatures at which species peaked or declined markedly. The history of inter-basin connections in western Oregon was found meaningful, with the exclusively coastal basins showing a negative relationship to richness of freshwater fish.

The context of RTA is important to recognize. If Figs 3 and 4 display a hierarchical structure representative of some meaningful associations within Oregon, then conceptually each sub-group, or even the entire tree, may be a sub-group of a larger tree extending beyond Oregon. In other words, the study area is part of larger richness patterns (e.g. O'Connor *et al.*, 1996).

The decision to split the MLR analyses into western and eastern components was substantiated by MLR when an opposite relationship of annual temperature range to species richness was found on each side, and by RTA when the initial partition, according to annual temperature range, created subsets virtually identical to the presumed east/west dichotomy.

Several established biogeographic theories are both supported and contradicted by these results. Temperature stability was the most important correlate with species richness in the state,

supporting the theory that greater climatic stability often leads to greater species diversity (Pianka, 1966). Annual temperature range distinguished western (<16.5°C) from eastern (>16.5°C) Oregon, and within the west, broader ranges were associated with decreased richness. Climatic instability was associated with lower species richness in both analyses, but positively associated in the MLR for eastern Oregon. However, statewide, species richness was far lower in the more climatically variable eastern basins than in the more stable western basins.

The thermal limiting theory (McAllister *et al.*, 1986) was supported in both analyses for western Oregon. Low winter minimum temperatures (<-7.5°C) were associated with low species richness and high summer maximum temperatures with high species richness. McAllister *et al.* (1986) also found that species richness peaked at 'optimal' values of climatic variables and fell off sharply at suboptimal values.

The species-area theory (MacArthur & Wilson, 1967) was supported in eastern Oregon by both statistical analyses and in western Oregon by MLR, where greater density of first-order streams was associated with increased species richness. Both analytical approaches indicate that the consistently available habitat of larger perennial streams is a key to supporting high fish species diversity in eastern Oregon, while intermittent streams and playa lakes are less decisive. First-order stream density was also associated by MLR with greater richness of freshwater species in western Oregon. Angermeier & Schlosser (1989), working at the local scale, also found that

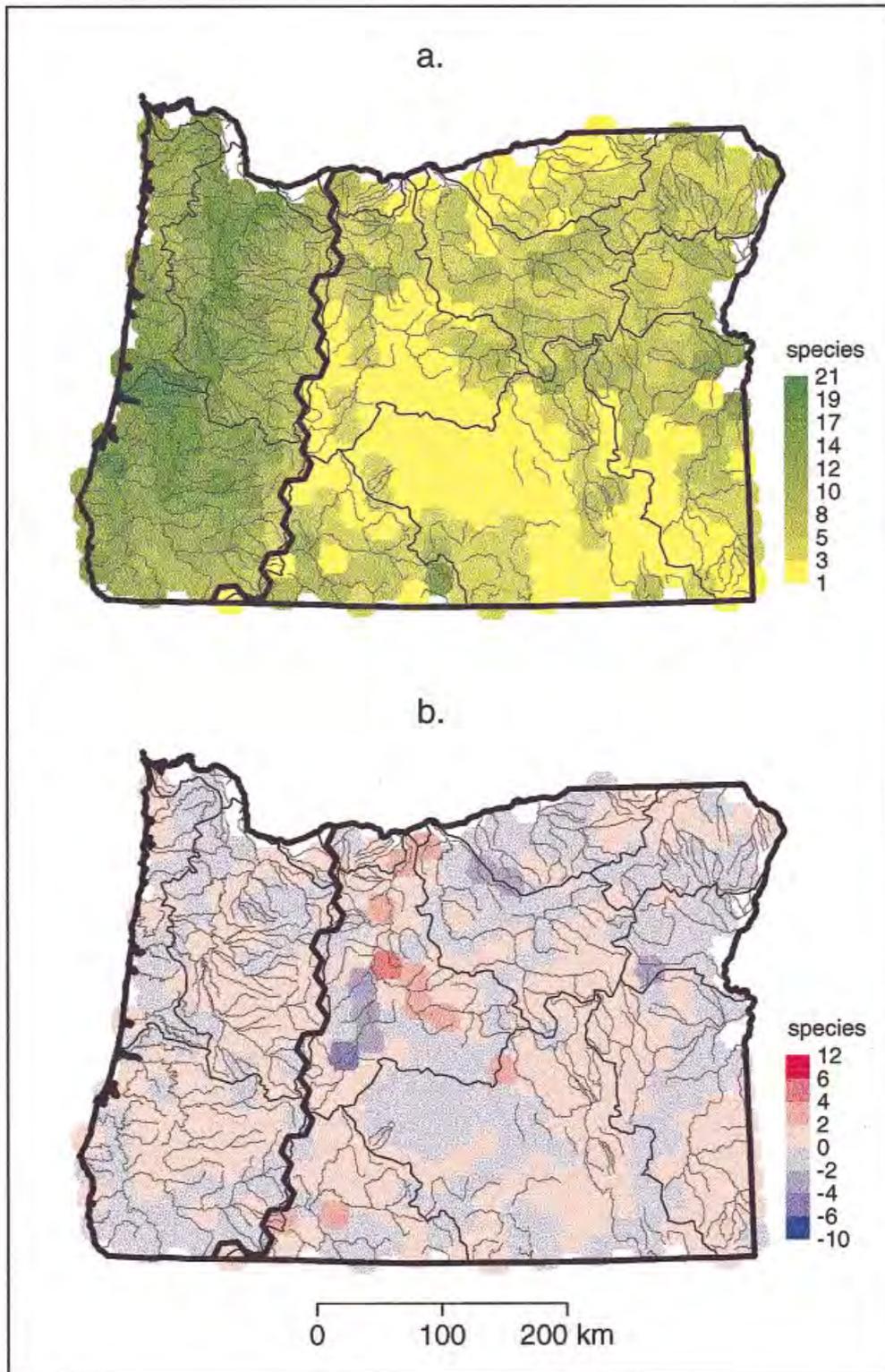


Figure 7 (a) Spatial distribution of predicted values for each western and eastern Oregon grid cell according to the multiple linear regression models. (b) Spatial distribution of the multiple linear regression model residuals for eastern and western Oregon. The heavy irregular north-south line separates largely eastern from largely western cells along the crest of the Cascade Mountains.

fish species richness was more strongly associated with habitat volume than with habitat complexity.

The spatial heterogeneity theory (Pianka, 1966), as measured by thermal heterogeneity, was contradicted by MLR when increased spatial heterogeneity of monthly temperature in western Oregon was associated with lower species richness. Spatial heterogeneity in temperature may be too coarse scaled an indicator of spatial heterogeneity, which is typically estimated at finer scales in streams by channel, discharge, or substrate heterogeneity. In other words, our landscape scale indicator of heterogeneity may have been an inadequate indicator if the critical scale of heterogeneity for fish species is at the site or local scale. The spatial heterogeneity theory was supported to the degree that increased river size (increased densities of third- and higher-order streams) also provided increased habitat complexity in eastern Oregon. This relationship was assumed by Guegan *et al.* (1998), who felt that increased river flows reflected greater fish species richness because of greater local habitat heterogeneity. However, the increased species richness they observed with greater flow was also associated with greater drainage area, making it difficult to separate assumed habitat heterogeneity from flow and area. They provided no direct measure of spatial or habitat heterogeneity.

Grid cells with current or historical stream connections to major river basins contained more species than those lacking such links, at least as demonstrated in the western Oregon portion of the MLR. These results support the theory that increased freshwater connectivity produces a greater species pool and greater local species richness of freshwater fish (Minckley *et al.*, 1986). No significant association between fish species richness and basin connective history or distance to the sea was found in the east, presumably because of the relative infrequency of past connections and the relatively lower vagility of many of the species. In western Oregon and regardless of basin size (Fig. 2), the exclusively coastal basins had decreased richness compared to those currently or once connected to the Columbia or Sacramento basins. One might assume that eastern Oregon fish assemblages are less dependent on anadromous species; however, north central and northeastern basins all contain several anadromous species. A second assumption might be that the coastal and eastern Oregon basins are smaller than the others, but rivers occur throughout the state that are large enough to navigate in small boats even during the dry season. Evidently greater connectivity with the fish faunas of major rivers like the Columbia and Sacramento has offered greater colonization potential for fishes just as proximity to major transportation corridors has for humans.

Within the broader spatial context of the Pacific Northwest or the Columbia River basin, other historical factors such as the absence of a Pleistocene continental ice sheet (McPhail & Lindsey, 1986), would likely be meaningful, as would long-term climatic fluctuations of the eastern basins. In other words, one would expect lower species richness in regions such as the state of Washington, which experienced extensive continental glaciation than in otherwise similar areas, such as the state of Oregon, which lacked continental glaciers (McAllister *et al.*, 1986). Similarly, pluvial periods interspersed with long dry periods, which are characteristic of the Basin and Range

Province that covers most of Nevada, western Utah, and southeastern Idaho, would support fewer native fish species than would the more predictably watered but still arid eastern regions of Oregon and Washington (Minckley *et al.*, 1986).

Moyle & Light (1996) proposed that invasions by alien fishes often occur without major assemblage effects in anthropogenically altered waters or in those with relatively benign habitat conditions (warm summers, mild winters, ample precipitation and river discharge, low channel gradients). Our inclusion of introduced species was founded on the idea that deleterious effects from the co-occurrence of native and introduced species might be detectable. We did not anticipate the positive relationships that occurred with both RTA and MLR, but we suggest three alternative explanations. First, our data on fish species at the hexagon scale (640 km²) may simply be too coarse for evaluating localized effects of species introductions. This hypothesis must be evaluated through more intensive sampling. Another possibility is that introduced fish may adversely affect native species where they coexist, but that the species have not co-occurred long enough to affect native richness at this broad scale. Confirmation of this hypothesis requires information on the relative abundance of the different species populations through time (Hughes & Noss, 1992). An alternative explanation is that the freshwater environments throughout the main stems of the large western rivers and most coastal basins were not saturated with native species, as Hugueny & Paugy (1995) concluded for West African rivers. The relatively depauperate condition of the North American fish fauna west of the 98th meridian (McAllister *et al.*, 1986) supports this contention. This might favour survival of some introduced fishes, and coexistence of introduced and native species, at least in benign habitats.

As proposed by Moyle & Light (1996), both alien and native species richness were highest in the more anthropogenically altered and benign waters of the Willamette Valley of western Oregon and the Klamath Basin of eastern Oregon. The fact that most fish species introductions to Oregon occurred in the past century may explain the positive relationship between alien and native species in Oregon; it may take more time for negative effects to become apparent. Increased research is needed on the effects of alien and native species in Oregon, particularly in the Willamette and Klamath Basins, both of which contain threatened fish species. No other indicator of disturbance that we used (road density, human population density) had a negative effect on fish species richness either. Available digital databases for Oregon land uses are at too coarse a level to distinguish anything but forest, agriculture, or urban categories—the extent and intensity of these activities, or of the predominant one in Oregon, grazing, are simply unavailable at the state scale. Thus, the land use data were at too coarse a scale to detect the local or site scale effects observed by other researchers working at smaller spatial scales. In a separate, more intensive study of fish assemblages in the Willamette Valley, species richness of native fishes was reduced and percent alien individuals was increased at sites highly disturbed by agriculture and urbanization (Hughes *et al.*, 1998).

Greatest species richness was predicted by RTA to occur throughout western Oregon, where annual temperature range

was <16.5°C and where minimum January temperature was >−7.5°C. Further, where the minimum January temperature was <−7.5°C, species richness was diminished, and in the MLR analysis a positive association between species richness and maximum July temperature in the west was found. These results all imply that species richness of native fishes in the west is limited where the coldest annual temperatures occur, i.e. in the high mountains.

In the east, increasing annual temperature range and aridity apparently limited species richness. Eastern Oregon is sheltered by the Cascade Mountains from marine influences (moderate temperatures and high precipitation) carried by prevailing west winds, so it is drier year round than western Oregon and experiences continental extremes in temperature. These extremes in precipitation and air temperature make hydrographic factors, or the availability of abundant surface water, critical to fish. In this region, stream density was consistently identified as important, most likely because eastern Oregon is also hydrologically variable with some well-watered mountains but large areas devoid of permanent surface water.

In conclusion, regression tree analysis and multiple linear regression analysis indicated that the species richness of native freshwater fish is positively correlated with low annual temperature extremes, warm summer air temperatures, low spatial variability in temperatures, high stream density, historical and present connectivity to great river basins, and high introduced fish species richness. Confirming conventional wisdom, these results offer support for the theories of environmental stability, environmental threshold, area, and connectivity as being important factors in fish species richness. The theories of spatial heterogeneity and disturbance were weakly supported or not supported, perhaps because they operate at different spatial and temporal scales than those we evaluated or because our indicators inadequately assessed them. Since warmer weather is associated with increased fish species richness, it is possible that continued climate warming and decreased shading as a result of riparian vegetation removal will result in more fish species in once cold waters as found by Lyons *et al.* (1996) in the state of Wisconsin. Of course, this result will require access to those warmer waters by warmwater fish species and sufficient time for colonization. Nevertheless, warmwater fish species are generally less valued in Oregon than the native salmonids that are disappearing (Nehlsen *et al.*, 1991; Marshall *et al.*, 1996), meaning that increased species richness of warmwater fish would not be viewed by Oregonians as a positive exchange for fewer salmon and trout. In other words, increased α species diversity is not always desirable.

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REFERENCES

- Allan, J.D. & Flecker, A.S. (1993) Biodiversity conservation in running waters. *BioScience*, **43**, 32–43.
- Angermeier, P.L. & Schlosser, I.J. (1989) Species-area relationships for stream fishes. *Ecology*, **70**, 1450–1462.
- Baltz, D.M. & Moyle, P.B. (1993) Invasion resistance to introduced species by a native assemblage of California stream fishes. *Ecol. Applications*, **3**, 246–255.
- Beecher, H.A., Dott, E.R. & Fernau, R.F. (1988) Fish species richness and stream order in Washington state streams. *Env. Biol. Fish.*, **22**, 193–209.
- Bohning-Gaese, K. (1997) Determinants of avian species richness at different spatial scales. *J. Biogeogr.*, **24**, 49–60.
- Bond, C.E., Rexstad, E. & Hughes, R.M. (1988) Habitat use of twenty-five common species of Oregon freshwater fish. *Northwest Sci.*, **62**, 223–232.
- Booth, D.B. & Reinelt, L.E. (1994) Consequences of urbanization on aquatic systems: measured effects, degradation thresholds, and corrective strategies. *Proceedings watershed '93 a national conference on watershed management*, 1994–300–781/12415, pp. 545–550. U.S. Govt Printing Office, Washington, DC.
- Breiman, L., Friedman, J.H., Olshen, R.A. & Stone, C.J. (1984) *Classification and regression trees*. Wadsworth, Pacific Grove, CA.
- Brown, J.H. (1995) *Macroecology*. University of Chicago Press, Chicago, IL.
- Brown, J.H. & Maurer, B.A. (1989) Macroecology: the division of food and space among species on continents. *Science*, **243**, 1145–1150.
- Cairns, M.A. & Lackey, R.T. (1992) Biodiversity and management of natural resources: the issues. *Fisheries*, **17**(3), 6–10.
- Clark, L. & Pregibon, D. (1992) Tree-based models. *Statistical models* (ed. by J.M. Chambers and T.J. Hastie), pp. 377–419. S. Wadsworth, Pacific Grove, CA.
- Cook, R.E. (1969) Variation in species density of North American birds. *Syst. Zool.*, **18**, 63–84.
- Currie, D.J. (1991) Energy and large-scale patterns of animal- and plant-species richness. *Am. Nat.*, **137**, 27–49.
- Daly, C., Neilson, R.P. & Phillips, D.L. (1994) A statistical-topographic model for mapping climatological precipitation over mountainous terrain. *J. appl. Meteor.*, **33**, 140–158.
- Eadie, J.M., Hurly, A., Montgomerie, R.D. & Teather, K.L. (1986) Lakes and rivers as islands: species-area relationships in the fish faunas of Ontario. *Env. Biol. Fish.*, **15**, 81–89.
- Efron, B. & Tibshirani, R. (1991) Statistical data analysis in the computer age. *Science*, **253**, 390–395.
- Fausch, K.D. (1988) Tests of competition between native and introduced salmonids in streams: what have we learned. *Can. J. Fish. Aquat. Sci.*, **45**, 2238–2246.
- Fausch, K.D., Hawkes, C.L. & Parsons, M.G. (1988) *Models that predict standing crop of stream fish from habitat variables: 1950–85*. PNW-GTR-213. USDA Forest Service, Portland, OR.
- Forester, D.J. & Machlis, G.E. (1996) Modeling human factors that affect the loss of biodiversity. *Conserv. Biol.*, **10**, 1253–1263.

- Guegan, J.F., Lek, S. & Oberdorff, T. (1998) Energy availability and habitat heterogeneity predict global riverine fish diversity. *Nature*, **391**, 382–384.
- Hinch, S.G. (1991) Small- and large-scale studies in fisheries ecology: the need for cooperation among researchers. *Fisheries*, **16**, 22–27.
- Hughes, R.M. & Gammon, J.R. (1987) Longitudinal changes in fish assemblages and water quality in the Willamette River, Oregon. *Trans. Am. Fish. Soc.* **116**, 196–209.
- Hughes, R.M., Kaufmann, P.R., Herlihy, A.T., Kincaid, T.M., Reynolds, L. & Larsen, D.P. (1998) A process for developing and evaluating indices of fish assemblage integrity: a case study for Wadeable streams in the Willamette Valley ecoregion, Oregon, USA. *Can. J. Fish. Aquat. Sci.* **55**, 1618–1631.
- Hughes, R.M. & Noss, R.F. (1992) Biological diversity and biological integrity: current concerns for lakes and streams. *Fisheries*, **17**(3), 11–19.
- Hughes, R.M., Rexstad, E. & Bond, C.E. (1987) The relationship of aquatic ecoregions, river basins, and physiographic provinces to the ichthyogeographic regions of Oregon. *Copeia*, **1987**, 423–432.
- Hugueny, B. (1989) West African rivers as biogeographic islands: species richness of fish communities. *Oecologia*, **79**, 235–243.
- Hugueny, B. & Paugy, D. (1995) Unsaturated fish communities in African rivers. *Am. Nat.* **146**, 162–169.
- Jackson, D.A. & Harvey, H.H. (1989) Biogeographic associations in fish assemblages: local vs. regional processes. *Ecology*, **70**, 1472–1484.
- Karr, J.R. & Dudley, D.R. (1981) Ecological perspective on water quality goals. *Environ. Mgmt*, **5**, 55–68.
- Kelso, R.M. & Minns, C.K. (1996) Is fish species richness at sites in the Canadian Great Lakes the result of local or regional factors? *Can. J. Fish. Aquat. Sci.* **53** (Suppl. 1), 175–193.
- Kiester, A.R. (1971) Species density of North American amphibians and reptiles. *Syst. Zool.* **20**, 127–137.
- Krueger, C.C. & May, B. (1991) Ecological and genetic effects of salmonid introductions in North America. *Can. J. Fish. Aquat. Sci.* **48** (Suppl. 1), 66–77.
- Lee, D.S., Gilbert, C.R., Hocutt, C.H., Jenkins, R.E., McAllister, D.E. & Stauffer, J.R., Jr (1980) *Atlas of North American freshwater fishes*. North Carolina State Museum of Natural History, Raleigh, N.C.
- Legendre, P. & Legendre, V. (1984) Postglacial dispersal of freshwater fishes in the Quebec Peninsula. *Can. J. Fish. Aquat. Sci.* **41**, 1781–1802.
- Leidy, R.A. & Fiedler, P.L. (1985) Human disturbance and patterns of fish species diversity in the San Francisco Bay drainage, California. *Biol. Conserv.* **33**, 247–267.
- Levin, S.A. (1992) The problem of pattern and scale in ecology. *Ecology*, **73**, 1943–1967.
- Li, H.W., Currens, C., Bottom, D., Clarke, S., Dambacher, J., Frissell, C., Harris, P., Hughes, R.M., McCullough, D., McGie, A., Moore, K., Nawa, R. & Thiele, S. (1995) Safe havens: refuges and evolutionarily significant units. *Am. Fish. Soc. Symp.* **17**, 371–380.
- Livingstone, D.A., Rowland, M. & Bailey, P.E. (1982) On the size of African riverine fish faunas. *Am. Zool.* **22**, 361–369.
- Lyons, J., Wang, L. & Simonson, T.D. (1996) Development and validation of an index of biotic integrity for coldwater streams in Wisconsin. *N. Am. J. Fish Mgmt*, **16**, 241–256.
- MacArthur, R.H. & Wilson, E.O. (1967) *The theory of island biogeography*. Princeton University Press, Princeton, N.J.
- Mandrak, N.E. (1995) Biogeographic patterns of fish species richness in Ontario lakes in relation to historical and environmental factors. *Can. J. Fish. Aquat. Sci.* **52**, 1462–1474.
- Marks, D. (1990) The sensitivity of potential evapotranspiration to climate change over the continental United States. *Biospheric feedbacks to climate change: the sensitivity of regional trace gas emissions, evapotranspiration, and energy balance to vegetation redistribution* (ed. by H. Gucinski, D. Marks and D.P. Turner), pp. IV-1–IV-31. EPA/600/3–90/078, U.S. Environmental Protection Agency, Corvallis, OR.
- Marshall, D.B., Chilcote, M.W. & Weeks, H. (1996) *Species at risk: sensitive, threatened and endangered vertebrates of Oregon*. Wildlife Diversity Program, Oregon Department of Fish and Wildlife, Portland, OR.
- Master, L. (1996) Predicting distributions for vertebrate species: some observations. *Gap analysis: a landscape approach to biodiversity planning* (ed. by J.M. Scott, T.H. Tear and F.W. Davis), pp. 171–176. American Society for Photogrammetry and Remote Sensing, Bethesda, MD.
- Matusek, J.E. & Beggs, G.L. (1988) Fish species richness in relation to lake area, pH, and other abiotic factors in Ontario lakes. *Can. J. Fish. Aquat. Sci.* **45**, 1931–1941.
- Mayden, R.L., Burr, B.M., Page, L.M. & Miller, R.R. (1992) The native freshwater fishes of North America. *Systematics, historical ecology, and North American freshwater fishes* (ed. by R.L. Mayden), pp. 827–863. Stanford University Press, Stanford, CA.
- McAllister, D.E., Platania, S.P., Schueler, F.W., Baldwin, M.E. & Lee, D.S. (1986) Ichthyofaunal patterns on a geographic grid. *The zoogeography of North American freshwater fishes* (ed. by C.H. Hocutt and E.O. Wiley), pp. 17–51. John Wiley and Sons, New York.
- McPhail, J.D. & Lindsey, C.C. (1986) Zoogeography of the freshwater fishes of Cascadia: the Columbia system and rivers north to the Stikine. *The zoogeography of North American freshwater fishes* (ed. by C.H. Hocutt and E.O. Wiley), pp. 615–637. John Wiley and Sons, New York.
- Michaelsen, J., Schimel, D.S., Friedl, M.A., Davis, F.W. & Dubayah, R.C. (1994) Regression tree analysis of satellite and terrain data to guide vegetation sampling and surveys. *J. Veg. Sci.* **5**, 673–686.
- Miller, R.R., Williams, J.D. & Williams, J.E. (1989) Extinctions of North American fishes during the past century. *Fisheries*, **14**(6), 22–38.
- Minckley, W.L., Hendrickson, D.A. & Bond, C.E. (1986) Geography of western North American freshwater fishes: description and relationships to intracontinental tectonism. *The zoogeography of North American freshwater fishes* (ed. by C.H. Hocutt and E.O. Wiley), pp. 519–613. John Wiley and Sons, New York.
- Moyle, P.B. & Light, T. (1996) Biological invasions of fresh water: empirical rules and assembly theory. *Biol. Conserv.* **78**, 149–161.
- National Marine Fisheries Service (1996) Office of Protected Resources. World wide web site: http://kingfish.ssp.nmfs.gov/tmcintyr/prt_res.html.
- The Nature Conservancy (1996) *Priorities for conservation: 1996 annual report card for U.S. plant and animal species*. Arlington, VA.
- Nehlsen, W., Williams, J.E. & Lichatowich, J.A. (1991) Pacific salmon at the crossroads: stocks at risk from California, Oregon, Idaho, and Washington. *Fisheries*, **16**(2), 4–21.
- Oberdorff, T., Guegan, J. & Hugueny, B. (1995) Global scale patterns of fish species richness in rivers. *Ecography*, **18**, 345–352.
- Oberdorff, T., Hugueny, B. & Guegan, J. (1997) Is there an influence of historical events on contemporary fish species richness in rivers? Comparisons between Western Europe and North America. *J. Biogeogr.* **24**, 461–467.
- O'Connor, R.J., Jones, M.T., White, D., Hunsaker, C., Loveland, T., Jones, B. & Preston, E. (1996) Spatial partitioning of environmental correlates of avian biodiversity in the conterminous United States. *Biodiv. Letts*, **3**, 97–110.
- Orr, E.L., Orr, W.N. & Baldwin, E.M. (1992) *Geology of Oregon*. Kendall/Hunt, Dubuque, IA.
- Owen, J.G. (1989) Patterns of herpetofaunal species richness: relation

- to temperature, precipitation, and variance in elevation. *J. Biogeogr.* **16**, 141–150.
- Pianka, E.R. (1966) Latitudinal gradients in species diversity: a review of concepts. *Am. Nat.* **100**, 33–46.
- Ramsey, F.L. & Schafer, D.W. (1997) *The statistical sleuth: a course in methods of data analysis*. Duxbury Press, Belmont, CA.
- Reid, L.M. & Dunne, T. (1984) Sediment production from forest road surfaces. *Water Resources Res.* **20**, 1753–1761.
- Ricklefs, R.E. (1987) Community diversity: relative roles of local and regional processes. *Science*, **235**, 167–171.
- Rogers, J.S. (1976) Species density and taxonomic diversity of Texas amphibians and reptiles. *Syst. Zool.* **25**, 26–40.
- Ross, S.T. (1991) Mechanisms structuring stream fish assemblages: are there lessons from introduced species. *Env. Biol. Fish.* **30**, 359–368.
- Sanders, H.L. (1968) Marine benthic diversity: a comparative study. *Am. Nat.* **102**, 243–282.
- Schwarz, G. (1978) Estimating the dimension of a model. *Annals Stat.* **6**, 461–464.
- Simpson, G.G. (1964) Species density of North American recent mammals. *Syst. Zool.* **13**, 57–73.
- Smith, G.R. (1981) Late Cenozoic freshwater fishes of North America. *Ann. Rev. Ecol. Syst.* **12**, 163–193.
- Soulé, M.E. (1991) Conservation: tactics for a constant crisis. *Science* **253**, 744–750.
- Strahler, A.N. (1957) Quantitative analysis of watershed geomorphology. *Trans. Am. Geophys. Union*, **38**, 913–920.
- Terentev, P.V. (1963) Attempt at application of analysis of variation to the qualitative richness of the fauna of terrestrial vertebrates of the U.S.S.R.. *Vestnik Leningradskovo Universiteta*, **21**, 19–26. (Translated by E.J. Maly and edited by E.R. Pianka, Smithsonian Herpetological Information Services.)
- Thomas, J.W., Maser, C. & Rodiek, J.E. (1979) Riparian zones. *Wildlife habitats in managed forest* (ed. by J.W. Thomas), pp. 41–47. USDA Agriculture Handbook Number 553.
- Tonn, W.M. (1990) Climate change and fish communities: a conceptual framework. *Trans. Am. Fish. Soc.* **119**, 337–352.
- U.S. Fish and Wildlife Service (1996) Endangered species program. World wide web site: <http://www.fws.gov/~r9endspp/endspp.html>.
- Venables, W.N. & Ripley, B.D. (1994) *Modern applied statistics in S-PLUS*. Springer-Verlag, New York.
- Vitousek, P.M., Ehrlich, P.R., Ehrlich, A.H. & Matson, P.A. (1986) Human appropriation of the products of photosynthesis. *BioScience*, **36**, 368–373.
- Welcomme, R.L. (1979) *Fisheries ecology of floodplain rivers*. Longman, New York.
- White, D., Kimerling, A.J. & Overton, W.S. (1992) Cartographic and geometric components of a global sampling design for environmental monitoring. *Cartogr. Geogr. Info. Syst.* **19**, 5–22.
- Whittier, T.R., Halliwell, D.B. & Paulsen, S.G. (1997) Cyprinid distributions in northeast USA lakes: evidence of regional-scale minnow biodiversity losses. *Can. J. Fish. Aquat. Sci.* **54**, 1593–1607.
- Williams, J.E., Johnson, J.E., Hendrickson, D.A., Contreras-Balderas, S., Williams, J.D., Navarro-Mendoza, M., McAllister, D.E. & Deacon, J.E. (1989) Fishes of North America endangered, threatened, or of special concern: 1989. *Fisheries*, **14**(6), 2–20.
- Wilson, E.O. (1985) The biological diversity crisis. *BioScience* **35**, 700–705.
- Wilson, J.W., III (1973) Analytical zoogeography of North American mammals. *Evolution*, **28**, 124–140.
- Wright, D.H. (1983) Species-energy theory: an extension of species-area theory. *Oikos*, **41**, 96–506.

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