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Species diversity gradients in relation to geological history in North American freshwater fishes

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ABSTRACT

Hypothesis: Geological events and their timing influence local climate, size and shape of fluvial habitats, isolating barriers, and different rates of speciation and extinction, which interact to create gradients of freshwater fish diversity at regional and continental scales.

Organisms: Recent freshwater fishes of North America south to southern Mexico and Cenozoic fossil species of the families Ictaluridae, Catostomidae, Cyprinidae, Salmonidae, Centrarchidae, and Cottidae.

Analytical methods: (1) Regression of species diversity in upper, middle, and lower reaches of five eastern and six western rivers against discharge and its variation, elevation, and gradient; (2) compilation of numbers of species native to quadrats of the Simpson Grid, a system of 150×150 mile units covering the continent; (3) estimation of the effects of nine environmental variables on species numbers in quadrats of the grid using spatial autoregression and regression trees; (4) estimation of origination and extinction rates from numbers of fossil and recent species contrasted between Atlantic drainage and Pacific drainage North America.

Results: (1) Fish species diversity responds positively to stream discharge and negatively to elevation, gradient, and discharge variation, except where these variables are overridden by proximity to a large source fauna. (2) Species diversity is high in the Mississippi Basin and low in the western mountains, far north, and Mexico. Spatial autoregression and regression trees reveal positive effects of precipitation, warm temperature, and fluvial connectedness on local fish diversity, followed by lesser effects of minimum temperature, elevation, run-off, frost-free days, drainage size, and temperature range. (3) Estimated origination and extinction rates are usually higher in the west where spatial units are small and temporal scales of the geological events that create them can be short. Extinction rates are usually much lower in the east where large-scale spatial and long-term geological processes interact to produce environmental stability.

Keywords: discharge variation, elevation, extinction rate, speciation rate, stability, tectonics.

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INTRODUCTION

Comparison of numbers of fish species in the Yukon, Illinois, and Alabama river drainages reveals a pronounced latitudinal gradient from depauperate northern to diverse southern faunas and suggests familiar explanatory hypotheses, such as climatic gradients and Pleistocene history (Pianka, 2000; Mittelbach *et al.*, 2007). But some dominant patterns contradict the latitudinal gradient and its associated hypotheses. For example, Tennessee has many more freshwater species than Florida and California (Etnier and Starnes, 1993), and cold-temperate, glaciated Michigan has more species than equivalent areas in unglaciated, subtropical Mexico (Hubbs and Lagler, 2004; Miller *et al.*, 2005).

Biogeographic explanations of complex freshwater fish patterns include species–area relationships (Oberdorff *et al.*, 1995; Rosenzweig, 1995), drainage-basin size (Gilbert, 1980; Robison, 1986; Hugueny, 1989; Brown, 1995; Matthews and Robison, 1998), river discharge (Livingstone *et al.*, 1982; Angermier and Schlosser, 1989; Hugueny, 1989; Oberdorff *et al.*, 1995; Taylor, 1997), habitat volume (Matthews, 1986; Oberdorff *et al.*, 1995), and habitat heterogeneity (Ross, 1986; Oberdorff *et al.*, 1995; Guégan *et al.*, 1998). Suggested ecological hypotheses include competition and predation (Ross *et al.*, 1985; Moyle and Vondracek, 1985). Proximal influences on the physiological ecology of fishes, including amount of aquatic habitat (Moyle and Herbold, 1987), temperature, current speed, food distribution and nutrition, predators, and fluctuations in these factors (Strange *et al.*, 1993; Grossman *et al.*, 1998), have been reviewed thoroughly by Matthews (1998). These studies represent an immense amount of work focused on diversity at local and regional scales, but do not explain mechanisms behind large regional or continental patterns, despite correlations that may indicate scale independence (Romanuk *et al.*, 2009). Diverse floodplain faunas in the Amazon and Mekong rivers (Rainboth, 1996; Lundberg *et al.*, 1998) lose diversity upstream towards the mountain headwaters, creating elevational diversity gradients that can span two orders of magnitude, with complete turnover of faunal composition, suggesting important effects of orogeny, elevation, and slope, factors that also work across smaller regions (Strange *et al.*, 1993; Robinson and Rand, 2005). These gradients also suggest a general pattern for stream networks that has been successfully modelled in the Mississippi–Missouri river system as the consequence of neutral metacommunity processes augmented with habitat capacity and dispersal (Muneepeerakul *et al.*, 2008). The success of a neutral metacommunity model with terms for habitat diversity and dispersal does not, however, imply the lack of deeper mechanistic causes of general patterns, in which species replace each other and adaptations depend on habitat properties. Fish diversity patterns studied here suggest that large-scale biogeographic phenomena may have tectonic and related hydrologic processes at their roots, consistent with the fact that the morphology and hydrology of river basins depend on interactions of plate tectonics and climate (Montgomery, 2000; Montgomery *et al.*, 2001). If so, it is important to investigate physical geologic history, on time scales longer than the ice ages, as a possible ultimate driver of myriad environmental factors that determine fish species diversity.

Much work has been directed at the best known event in recent geologic and climatic history – 2 million years of glacial advances and retreats repeated on a temporal scale of about 100,000 years. Climatic fluctuations repeatedly displaced plant and animal assemblages. These cycles might well have enhanced panmixia in central lowlands, possibly constraining most fish lineage originations to Appalachian and Ozark uplands (Mayden, 1987; Heckman *et al.*, 2009). Glacial cycles probably selected lineages for broader temperature tolerance and dispersal behaviours in eastern North America while causing extinctions of

populations in western North America (Smith, 1978), partly because of the different spatial–temporal interactions in the two provinces.

Freshwater fishes offer unique opportunities to examine effects of isolating barriers on the processes of dispersal, origination, and extinction, and their consequences for regional versus local species diversity patterns. Dispersal and gene flow in freshwater fishes differ from those processes in terrestrial organisms, because drainages on cratons (old, stable parts of continents) are hierarchic systems of provinces within- and among-which immigration contributes more frequently to diversity than does speciation. By contrast, drainages in isolated inter-mountain basins and those along sea coasts act as archipelagos within which speciation may generate more diversity than immigration depending on the height of barriers, whose strength (compare island distance) may fluctuate because of stream captures. Barriers that isolate drainage basins may cause isolation and lead to speciation (Hubbs and Miller, 1948) or extinction (Horwitz, 1978; Gorman, 1986; Hughes *et al.*, 1987; Matthews and Robison, 1998; Griffiths, 2006) depending on their temporal scale (but not spatial distance). For example, within the past 6000 years the Laurentian Great Lakes periodically changed from a large province of the Mississippi River drainage to a province of the St. Lawrence River. And 15,000 years ago the Bonneville Basin of Utah changed from an 18,000 square mile aquatic island to a province of the Columbia River basin, and back again after a mixing of fish species. Then, as Lake Bonneville evaporated, its tributaries became a biogeographic archipelago of rivers isolated by the Great Salt Lake. One-way barriers (i.e. falls) add another complication.

In this paper, we evaluate diversity patterns among North American freshwater fishes, especially at the continental scale. We test the effect of tectonic and climatic history on variables such as connectivity and topographic barriers, hydrology, and temperature (Grossman *et al.*, 1985; Heins and Matthews, 1987; Hugueny and Lévêque, 1994). We compare the effects of geological processes on the ultimate determinants of species density – relative rates of origination and extinction. The mid-domain effect (Dunn *et al.*, 2007) and neutral models (Muneepeerakul *et al.*, 2008) demonstrate emergent patterns in species numbers, but are not substitutes for tests of causal process hypotheses from which consistent predictions about biology can be made (Quinn and Dunham, 1983; Dunn *et al.*, 2007).

Horwitz (1978) proposed that local species diversity is enhanced by stable habitat volume (Gorman and Karr, 1978; Ross *et al.*, 1985; McAllister *et al.*, 1986; Ross, 1986; Matthews, 1998). This hypothesis predicts that fish species persistence should be reduced by variable in-stream flow and temperature. We test the effects of variability in stream volume as well as the effects of elevation and gradient on local species diversity with data from 11 western and eastern rivers. Species persistence is also predicted to increase with dispersal routes for immigration (Matthews and Robison, 1998; Griffiths, 2006). These hypotheses have two corollaries: (1) local extirpation is recurrent (Horwitz, 1978; Smith, 1978), and (2) the probability of recolonization following local extirpation depends on connectedness (Brown, 1978). We hypothesize that orogenic and volcanic processes on active continental margins create small geographic units isolated by barriers as well as aridity over short and long time scales; in turn, these geomorphic and climatic conditions affect both origination and extinction, with the latter dominating. By contrast, tectonically passive continental margins and stable cratons develop vast, low-elevation, stable, interconnected drainages, which reduce extinction rates and promote long-term accumulation of diversity. Tests of this hypothesis require comparisons with competing hypotheses that relate freshwater fish diversity to modern temperature and moisture variables, species interactions, and speciation. Models showing

circumstances in which certain variables repeatedly override others provide evidence to modify hypotheses, especially when an emergent phenomenon suggests a plausible mechanism to explain a pattern (Rosenzweig and Ziv, 1999).

Outline of the North American freshwater fish fauna

The North American native fauna as compiled here comprises 1116 species in 34 families (Fig. 1). Most of these families have inhabited the continent for at least 50 million years. Most families and many genera, but few species, have distribution patterns that cross the eastward-shifting continental divide (Spencer *et al.*, 2008). Ten families with the majority of species are Cyprinidae (minnows), Percidae (walleyes, perch, darters), Poeciliidae (live bearers), Catostomidae (suckers), Salmonidae (salmon, trout, whitefishes), Cichlidae (cichlids), Fundulidae (topminnows), Goodeidae (splitfins), Ictaluridae (North American catfishes), and Centrarchidae (sunfishes, basses, crappies) (Fig. 1).

The families can be classified by their latitudinal affinities (Mayden, 1992) and different responses to temperature. Notable Holarctic families include Petromyzontidae, Acipenseridae, Polyodontidae, Hiodontidae, Cyprinidae, Catostomidae, Salmonidae,

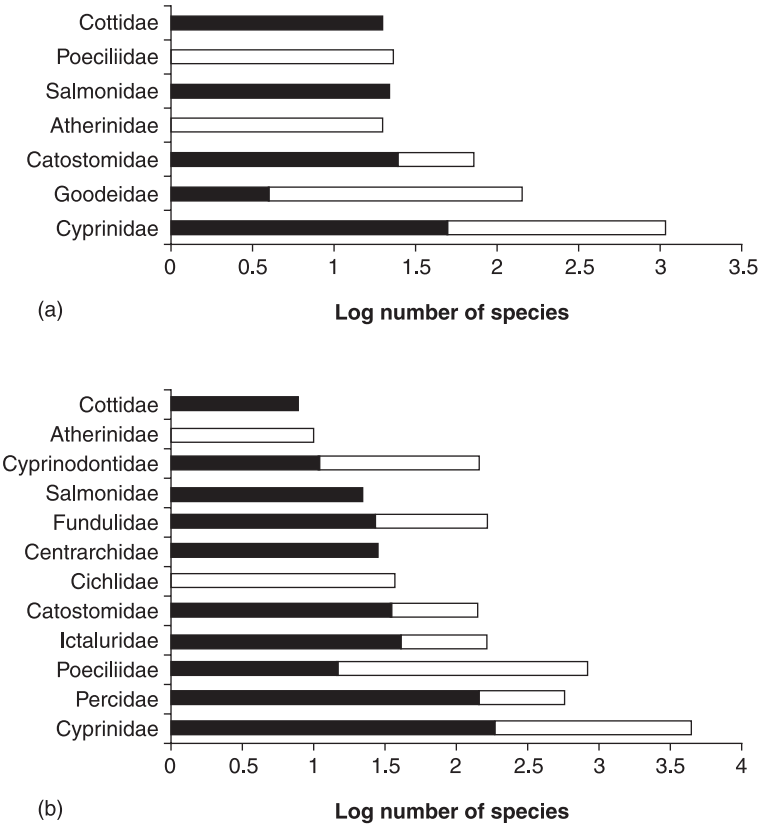


Fig. 1. Proportional species diversity (logarithms) of major families of North American freshwater fishes: (a) principal Pacific drainage families; (b) principal Atlantic drainage families. Solid bars: the number of species of northern or Holarctic origin. Open bars: the number of species of southern origin.

Osmeridae, Esocidae, Dalliidae, Umbridae, Percopsidae, Cottidae, Gasterosteidae, Enneacanthidae, and Percidae. Notable Neotropical and Mesoamerican families include Pimelodidae, Characidae, Atherinopsidae, Poeciliidae, Fundulidae, Goodeidae, Cyprinodontidae, and Cichlidae (Fig. 1). Lepisosteidae and Amiidae may be Pangaean in origin (Mayden, 1992). Fewer than two dozen species represent families with marine affinities (e.g. Clupeidae, Moronidae, Embiotocidae, Sciaenidae, Anguillidae, and Lotidae).

Longitudinally, two tectonic and faunal provinces can be recognized, at least at mid-latitudes. The eastern fauna extends from the Continental Divide to the Atlantic and Gulf coasts; the western fauna extends from the Continental Divide to the Pacific Ocean. Only about a dozen species cross the Continental Divide in the USA, where diversity is greatest, but more species cross the divide in northern and southern regions where it is lower in elevation.

METHODS

Using three analyses, we evaluate how tectonic construction of topography and drainages might influence evolution and assembly of freshwater fish species diversity in Atlantic- and Pacific-drainage North America. First, we evaluate the number of species inhabiting the upstream, middle, and downstream reaches of eastern and western rivers in the USA to test the influences of discharge, elevation, gradient, and flow variability on species diversity. Second, we use several spatial methods to test environmental hypotheses [following the cautionary suggestions of Rosenzweig (1995, p. 377)], by evaluating how modern ecological factors interact or act independently to influence species diversity patterns. Third, we estimate origination and extinction rates (Rosenzweig and Vetault, 1992; Etienne and Apol, 2009) of lineages in Atlantic and Pacific drainage provinces to compare causes at the regional scale.

Effects of elevation, gradient, stream discharge, and discharge variation

We analyse fish diversity gradients along the lengths of five eastern and six western rivers by regressing local species numbers against elevation, discharge, and coefficient of variation in discharge using long-term daily records from 129 United States Geological Survey (USGS) hydrologic gaging stations. These records are published annually for each state in USGS Water-Supply Papers. The gaging stations usually start upstream at agriculturally relevant elevations. We measured gradients within selected reaches from USGS topographic maps. We calculated means and coefficients of variation of discharge in 27 reaches, using older data averaged over periods that were least influenced by diversion dams. Coefficients of variation (CV, standard deviation divided by the mean) represent variability of each station's and each reach's daily flow records, usually covering a period of 40–80 years. We inspected histograms of gaging station discharge and CVs and divided each river into approximately homogeneous units separated by breaks. Table 1 presents mean elevation, discharge, and stream gradient for each segment, based on 2–12 station means for each stream's reach (Table 1, Fig. 2). We recorded native fish species inhabiting each reach from maps in the *Atlas of North American Freshwater Fishes* (Lee *et al.*, 1980) and state sources cited in the Appendix (evolutionary-ecology.com/data/2561-supplementary-refs.pdf).

Five eastern rivers, the Connecticut, Missouri, South Platte, Arkansas, and Rio Grande, represent the Atlantic drainages of the continent, and six rivers, the Columbia, Sacramento, Colorado, Gila, Humboldt, and Sevier, represent Pacific and interior (formerly Pacific)

drainages (Table 1, Fig. 2). Three Atlantic drainage rivers begin in the Rocky mountains and flow to the central lowlands: the South Platte River flows into the Missouri, the Missouri and Arkansas rivers flow into the Mississippi River. The Rio Grande flows from the Rocky Mountains to the Gulf of Mexico. The Connecticut River flows from northern New Hampshire and Vermont uplands to Long Island Sound. In the west, the Gila River flows into the lower Colorado River. The Humboldt and Sevier rivers terminate in dry lakebeds in Nevada and Utah but had Pliocene or Pleistocene connections to the Snake-Columbia drainage. We investigated other rivers – the Tennessee and Tombigbee rivers in the east and the Snake and Bear rivers in the west – but because of large effects of dams on their flow regimes, we did not use their data. The eastern and western groups of rivers were contrasted to investigate effects of geological processes on habitats and distributions. All Pacific drainages flow from tectonically active mountains, whereas Atlantic drainages in our sample flow either from the Rocky Mountains across the stable Great Plains or from the ancient eastern uplands.

Figure 2 presents bivariate scatter plots of species number on discharge, elevation, gradient, and coefficient of variation of discharge, following the approach of Horwitz (1978). We examine overall trends and unique outliers to suggest instances in which certain variables override others and suggest mechanisms (Table 1, Fig. 2).

Species density in relation to environmental variables

We document the presence or absence of 1116 native freshwater species in 389 equal-area quadrats selected from G.G. Simpson's study of North American mammal diversity (Simpson, 1964). This approach helps us to evaluate species density as well as environmental variables across a grid of quadrats 150×150 miles (241×241 km), on an equal-area projection of North America south to southern Mexico (Fig. 3). We selected those quadrats that included substantial land and fresh water (Rosenzweig, 1992; Badgley and Fox, 2000; Oberdorff *et al.*, 2001).

The grid method (McAllister *et al.*, 1986; Rosenzweig, 1992; Badgley and Fox, 2000) of displaying species densities allows us to examine fish density gradients independent of drainage sizes and without oversampling due to drainage hierarchy. Drainages are natural spatial units that ultimately govern species relationships and diversity in studies of fish biogeography (Gilbert, 1980; Romanuk *et al.*, 2009), but species densities over a grid have advantages when quantifying trends in species density patterns (Rosenzweig, 1992) and comparing spatial autocorrelation, topography, and climatic variables. Figure 3 illustrates the drainage areas and connectedness over the grid pattern.

We compiled numbers of native fish species per quadrat from museum records and primary literature up to about 2004. Coverage of North American fish records in United States and Canadian museums since 1930 is dense, with the possible exception of the Arctic. For example, the University of Michigan Museum of Zoology contains 2.9 million specimens in 151,890 catalogued lots from 55,199 North American localities, especially in the United States and Mexico. Total North American museum records provide documentation from over 200,000 fish localities (D.W. Nelson, personal communication). Species distributions are summarized in Hocutt and Wiley (1986) and records are available on spot distribution maps in three national monographs – *Freshwater Fishes of Canada* (Scott and Crossman, 1973), *Atlas of North American Freshwater Fishes* (Lee *et al.*, 1980), and *Freshwater Fishes of Mexico* (Miller *et al.*, 2005) – and more than 30 state and provincial books with species distribution data (see Appendix: evolutionary-ecology.com/data/2561-supplementary-refs.pdf). We prepared

transparent overlays of the Simpson grid, registered to the base maps in the state and provincial monographs that have spot distribution maps for native ranges of each fish species. By placing the appropriate grid overlay on each spot distribution map, we were able to tabulate the presence or absence of each species in each quadrat and count the number of native species originally present in each quadrat. We standardized species names and corrected distributions by checking synonymies in taxonomic revisions and notes in editions of the checklist of *Common and Scientific Names of Fishes from the United States, Canada, and Mexico* (Nelson *et al.*, 2004).

Environmental variables include annual temperature range, temperature of warmest month, temperature of coldest month, number of frost-free days, and annual precipitation (from atlases by Ward *et al.*, 1936), as well as actual evapotranspiration (AET, from USSR National Committee for the International Hydrographic Decade 1977). We estimated average elevation and topographic relief (difference between the lowest and highest point in each quadrat) from the *Times Atlas of the World* (Badgley and Fox, 2000), and run-off and drainage areas from US Geological Survey, Canadian, and Mexican drainage atlases. We enumerated fluvial connectedness as the number of each quadrat's four borders and four contiguous corners crossed by mapped rivers, as counted on the US and Mexico drainage maps published by the Museum of Zoology, University of Michigan, and the Canadian Drainage Map in *The Atlas of Canada* (Natural Resources Canada, 2009).

We use several spatially oriented methods to determine the ways in which environmental variables interact as well as function independently. We estimated the inter-correlation among variables with principal components analysis (Badgley and Fox, 2000), and level of spatial autocorrelation of fish diversity with Moran's I statistic (Sokal and Oden, 1978) and variograms fitted with the *gstat* package in R (Pebesma, 2003).

We used spatial simultaneous autoregression (SAR) in the R (CRAN, www.cran.org) package *spdep* (Bivand, 2006) to identify strengths of relationships and interdependencies among climatic variables (mean annual temperature, maximum temperature, minimum temperature, precipitation, and AET), as well as tectonic proxy variables (elevation, relief, and connectedness), and their ability to predict fish diversity. SAR is similar to ordinary, least-squares (OLS) multivariate regression but assumes that the response of groups of variables at a spatial unit is not independent of neighbouring areas, and adjusts degrees of freedom accordingly. We assessed a number of models accounting for linear and quadratic relationships and selected the best ones using the Akaike information criterion (AIC) to determine the optimal set of predictive covariates (Bivand, 2006). The *spdep* package provides several options for SAR modelling and we used an error-model estimation method, which assumes that all autoregressive effects occur in the error term of the regression model (Cressie, 1993; Lichstein, 2002; Kissling and Carl, 2008). We searched combinations and subsets of environmental variables to examine models balancing predictive power and number of variables (Burnham and Anderson, 2002). The method of choice used a backward-selection procedure, eliminating non-significant variables one-by-one, and applying a Bonferroni correction (Tables 3–5). We tested the hypothesis that Atlantic and Pacific drainage areas differ in their underlying predictor variables, first with analyses of the continent as a whole, and then separate Atlantic and Pacific drainage quadrats (Tables 4 and 5).

We constructed Ordinary Kriging maps to display distribution pattern of fish density and certain informative variables for comparison: actual evapotranspiration, mean annual precipitation, maximum temperature, annual temperature range, connectedness, relief, SAR-modelled fish species density, and residuals from the SAR model (Fig. 5). Kriging is

an interpolation procedure that uses the distance between points to estimate values for unknown intermediate points, taking into consideration error and uncertainty. Ordinary Kriging is a form that does not assume that local means are close to the population mean. We produced Kriging maps with ArcGIS version 9.3.

We used regression trees, constructed through binary recursive partitioning, to stratify the data to a hierarchy of predictor variables hypothesized to influence species density (Breiman *et al.*, 1984; Stanton and White, 1986) and represented the hierarchy as a tree diagram (Fig. 6). The method is an alternative to ordinary regression in that it does not compute a global model for the data set but partitions the data into nodes and branches; each branch has its separate, predictive model based on a single most-informative variable with its own set of quadrats. Thus, interactions are not considered. The method partitions (splits) the data into all possible sets to find sets that minimize the sum of squares around the mean of each part of each variable. Partitioning starts at the base of the tree and subdivides values of the most informative variable onto branches, analogous to coding and assigning characters to branches in parsimony cladistics. The first split in the regression tree starts with the most informative variable, based on the *P*-value of its association with species density. Then, the two categories of variable values that created the optimum split are split again, and so on down through other variables to the terminal branches on the tree. Single sets of partitioned variables diagnose their own branches. Variables that do not inform branches are recursively eliminated. This procedure creates branches of individual variables most associated with species density, selected according to their *P*-values.

As the preliminary heuristic step, we used the Random Forest procedure (Breiman, 2001) to rank the variables according to predictive strength (Table 2). The Random Forest is a computationally intensive, machine-learning ensemble of classification trees in which each tree depends on the values of an independently sampled vector with the same distribution across all trees. The method randomly permutes subsets of variables over numerous possible trees and calculates the increase in predictive strength given each possible tree after eliminating each variable. The measure of strength is an average decrease in mean squared error (MSE) among all possible permutations after omitting the variable in question. The second column in Table 2 is the residual sum of squares, which is a measure of decrease of node impurity (analogous to noise) from splitting the particular variable in question. The method calculates the mean value of fish species density in each node as well as the number of quadrats in that partition, and the change in R^2 with each level of branching. (In this algorithm, the terminal branches do not need to be 'pruned' to avoid interpreting noise.) The partitions may contribute to geographic interpretation by reference to the locations of quadrats included in the partitions.

Origination and extinction rates

Origination and extinction rates were estimated from the extant species diversity based on modern records, the number of known extinct species based on the fossil record, and the estimated time of origin of the living members of each monophyletic group for six family-level clades (Table 4). The six clades with the best fossil records for both Atlantic and Pacific drainages are Ictaluridae [catfishes (Lundberg, 1975)], Catostomidae [suckers (Smith, 1981; Cavender, 1986; Smith *et al.*, 2002)], Cyprinidae [minnows (Uyeno and Miller, 1963; Smith, 1981; Cavender, 1986; Smith *et al.*, 2002)], Salmoninae [Coregoninae excluded (Smith, 1981; Cavender, 1986; Wilson and Williams, 1992; Smith *et al.*, 2002; Eiting and Smith, 2007)], Centrarchidae (Cavender, 1986), and Cottidae (Smith, 1987). Additional

fossil records were obtained from Uyeno and Miller (1963), the collections of the University of Michigan Museum of Paleontology, the University of Oregon Museum of Natural History, the Los Angeles County Museum, and Grande (1984).

Analysis was restricted to the North American living monophyletic groups and their corresponding North American fossil members. We chose to compare portions of faunas separated by the Continental Divide [notwithstanding its large eastward migration (Spencer *et al.*, 2008)] rather than the alternative climatic partition at the 100th parallel, west longitude, or above and below the 1000 m line, because the first division minimizes species overlap and maximizes congruence between recent and fossil members of lineages through time. The latter two divisions would better divide eastern versus western climatic provinces, but would conflate many lineages of fishes that span those boundaries.

The fossil record of each group, except possibly Cottidae, extends back to the early Cenozoic and in some cases latest Cretaceous. We assumed that in all groups, the time of origin of the North American group is the late Cretaceous. The North America groups analysed here were unlikely to have descended from more than one Cenozoic ancestor in Eurasia. On the basis of the time of appearance of synapomorphies recorded in the fossil record, the time of origin of each group is assumed to be earliest Cenozoic, after the end-Cretaceous extinction. Thus, we assume that 65 Ma is the time of origin of the single species ancestry for each monophyletic group of living species. Except for Cottidae, which might be later, these dates are consistent with estimates based on density of the fossil record, using the method of Marshall (1990) in which the lower 95% confidence limit is taken as the estimated time of ancestry.

In families except the Cyprinidae, Ictaluridae, and Centrarchidae, it is possible that a few descendants of the species ancestral to the living North American clades also occur in Asia, but (rare) Asian fossils and their extinction and origination rates are not important to the question investigated here. Because these assumptions are not justified for three northern family groups with related Eurasian species – Coregoninae (whitefishes), Esocidae (pikes), and Percidae (perch) – we omitted them from this analysis.

The deterministic equations of Rosenzweig and Vetault (1992) use the number of living taxa, N_L, the number of known extinct taxa, N_E, and the estimated age, t, of the clade to estimate the rate of extinction, E, the rate of origination, S, and the resulting rate of diversification, D, for each group, assuming that $D = S - E$. The probabilistic methods of Etienne and Apol (2009) incorporate estimation of dependencies between numbers of living and extant species and allow estimation of speciation and extinction rates based on maximum likelihood, given the observed data, conditioned on the fact that the clade is extant.

RESULTS

Effects of elevation, gradient, stream discharge, and discharge variation

Analysis of species diversity in 11 United States rivers (Table 1) shows positive effects of stream discharge and negative effects of elevation, stream gradient, and coefficient of variation of discharge on number of species (Fig. 2). Mississippi drainage rivers show strong downstream gradients. Diversity increases downstream from 17 to 117 in the Arkansas River, from 7 to 31 in the South Platte River, and from 39 to 124 in the mainstream Missouri River. The Arkansas and Missouri rivers join the Mississippi River and the South Platte joins the Missouri River. Among Atlantic drainages, the low reaches on the

Table 1. Topographic and hydrological data for reaches of eastern and western rivers

River	No. of stations	Elevation (m)	Gradient ($m \cdot km^{-1}$)	Discharge ($m^3 \cdot s^{-1}$)	Discharge CV	No. of species
Arkansas	6	1849	6.8	15.9	1.1	17
	9	790	1.3	6.4	2.1	24
	4	265	3.0	295	2.2	117
Connecticut	7	290	3.2	57	0.7	35
	2	52	0.6	333	0.8	51
Missouri	9	836	0.8	213	0.6	39
	6	366	0.4	818	0.4	87
	4	192	0.2	1786	0.5	124
South Platte	5	2136	11.1	5.9	1.1	7
	3	1280	1.3	10.0	1.9	31
Rio Grande	12	2086	2.8	23.1	1.4	21
	5	697	0.9	61	1.0	57
Colorado	4	2433	2.6	9.5	1.4	6
	6	1549	1.1	117	1.1	11
	3	122	0.8	380	0.6	11
	2	15	0.8	264	1.2	7
Gila	8	969	1.5	8.8	1.7	11
	3	153	0.4	13.3	4.5	6
Sacramento	5	135	1.3	253	0.8	27
	5	13	0.2	429	0.6	25
Columbia	2	318	0.4	2912	0.6	23
	3	182	0.5	3178	0.5	21
	2	91	0.3	4332	0.7	29
Sevier	4	1895	1.7	4.0	1.0	9
	4	1500	1.4	6.0	1.3	9
Humboldt	3	1505	1.0	9.4	1.6	7
	3	1269	0.4	8.4	1.8	6

Note: Stream data from long records of US Geological Survey Water Supply Papers; fish data from sources for Figure 1.

Arkansas and South Platte rivers have the highest CVs, 2.2 and 1.9 respectively (Table 1). The upper reach of the Connecticut River has 35 species; its CV is similar to that of its lower reach, which has 51 species, but its gradient is five times higher (Table 1). The Rio Grande has 21 species at moderate to high elevations and gradients, and 54 species in the lower reach.

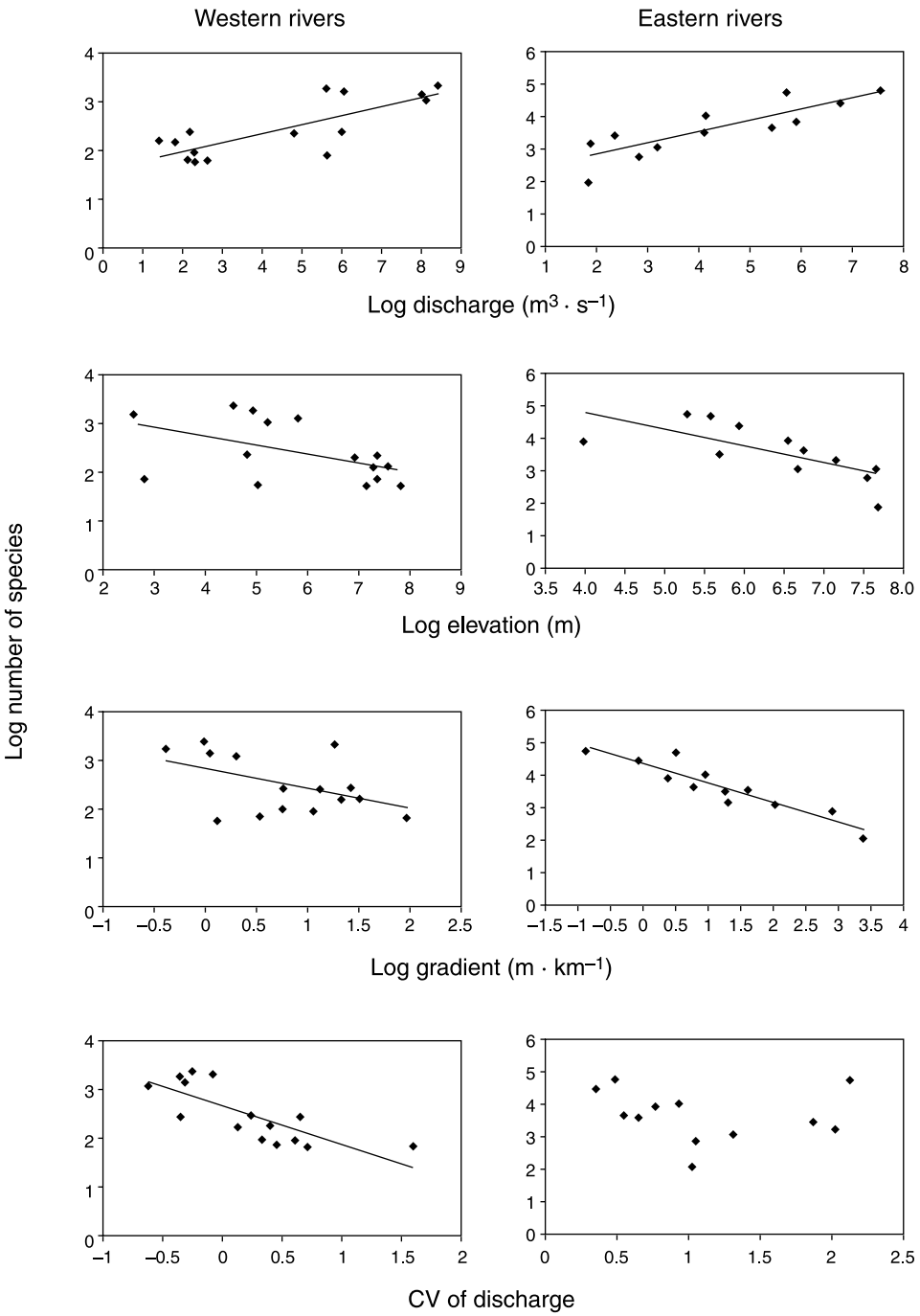


Fig. 2. Comparison of regressions of natural logarithm of number of species on logarithms of mean discharge, elevation above sea level, and stream gradient, and coefficient of variation of discharge at 15 reaches along six western rivers and 12 reaches along five eastern rivers. Informative outliers include: low diversity at all elevations and gradients on the Colorado River; low diversity at highest elevation and lowest discharge on the South Platte River above Denver; and low diversity at lowest elevation on the Connecticut River. The three eastern stations with highest coefficients of variation are interpreted to have higher than predicted species number – they are the lowest and middle stations on the Arkansas River and the lowest station on the South Platte River (Table 1).

High coefficients of variation and low species diversities characterize western desert streams, such as the small Gila and Humboldt rivers (CV = 1.6–4.5) and the large Colorado River (CV = 0.6–1.4). These rivers have only 6–11 species per reach. Species numbers often decline in relation to CV of discharge in desert rivers, but it is often the low rather than the headwater stretches that show variable discharge (Table 1). The highest species diversities in the west occur in the Columbia and Sacramento rivers with 21–29 species per reach, associated with generally high discharge and low coefficient of variation in discharge (Table 1, Fig. 2).

Species density in a grid of equal-area quadrats

The strongest species density gradient across the North American continent runs west to east just south of the glaciated area, at 35–38°N latitude, along which eastern quadrats contain an average of seven to nine times as many species as western quadrats (Fig. 3). In the far north, at about 55°N latitude, the diversity is low and the east–west gradient is weak and reversed: western quadrats contain 1.8 times as many species as eastern quadrats. The latitudinal gradient at mid continent (98°W longitude) is variable, but southern quadrats contain an average of 1.8 times as many species as far northern quadrats.

The highest species density in North American freshwater fishes is 155–233 species per quadrat, in the Tennessee River, Alabama River, and surrounding areas of the lower Mississippi Valley (Fig. 3). The Mississippi River and adjacent drainages are the centres of continental fish species diversity: 39 contiguous quadrats each contain more than 100 native species (Fig. 3). By contrast, the lowest species densities in the Mississippi drainage are in high-elevation headwaters, which have 15–31 species per quadrat, consistent with Table 1 and Fig. 2. The lowest densities on the continent occur in 87 glaciated northern and arid western quadrats, which have 1–10 species, and 159 cold northern and arid western quadrats, which have 11–24 species. Regions with intermediate diversity (50–149 species) occur in the Gulf Coast, Atlantic Coast, and Great Lakes drainages adjacent to the Mississippi Basin.

The most diverse Pacific-drainage quadrats occur in the Sacramento, Klamath, and Columbia drainages (Fig. 3), with 27–36 species, and in eastern and southern Mexico, with 25–63 species. Alaska and British Columbia, with up to 28 species per quadrat, are depauperate but more diverse than most basins in the inter-mountain western United States. The 10 highest diversity quadrats in Mexico, which have 50–63 species, are in the warm, humid south. In the United States, Atlantic coastal quadrats have lower species density than their latitudinal counterparts in the Mississippi River drainage, but 2–4 times as many species as western coastal streams (Fig. 3).

Species density exhibits a high spatial autocorrelation in the east, but a low spatial autocorrelation in the west; Moran's I declines from 1.0 to 0 in 2700 km in the east (not shown). Moran's I declines from only 0.4 to 0 in 1770 km in the west, documenting low autocorrelation. In the Atlantic drainages, variograms show a strong directional trend in autocorrelation from the southern Mississippi Basin northeastward to the Great Lakes Basin.

Species density in relation to environmental variables

Most species-density scatter plots on climatic variables (Fig. 4) peak over a maximum value for each variable and decay towards higher and lower values, but also many quadrats with

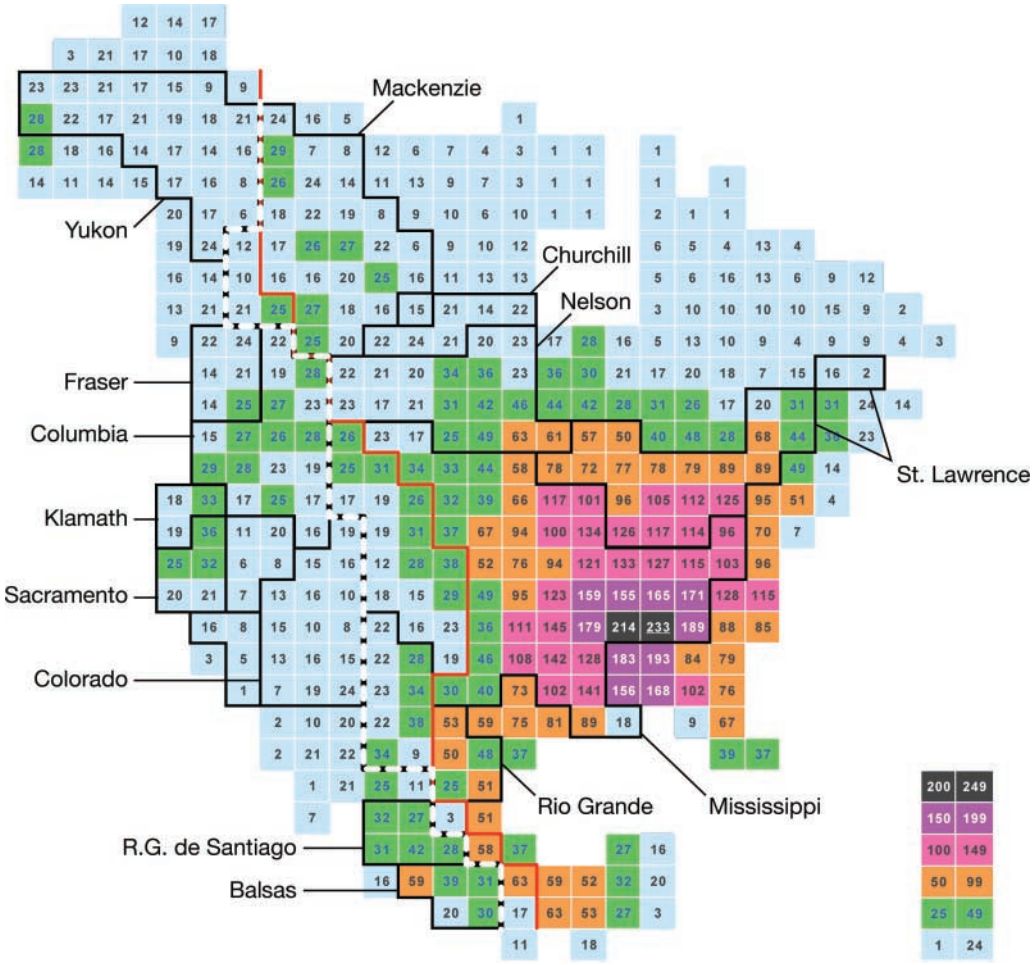


Fig. 3. Distribution of species density in quadrats of the Simpson grid. Quadrat numbers record the numbers of species counted in each quadrat. The major river basins of North America are approximately outlined by black borders. The Continental Divide is shown by black-white dashes, and the break point between quadrats with mean elevation above and below 1000 m is shown by a red line.

few species exist under the best environmental conditions. Principal components analysis of the environmental variables revealed two clusters, a combination of temperature-related factors explaining 71% of the variance and a weaker cluster reflecting moisture, which explained 16% of the variance. Potential and actual evapotranspiration loaded onto both components (Badgley and Fox, 2000, table 7). The variables with the highest positive correlation coefficient ($R > 0.50$) with species density are actual evapotranspiration, precipitation, drainage connectedness, and maximum temperature. Frost-free days and drainage size rank next highest, with positive correlation coefficients between 0.40 and 0.50. Actual evapotranspiration (AET) encompasses temperature, moisture, wind, and humidity; it is the best predictor of fish species density, with a high positive correlation coefficient and the most similar geographic pattern in the Krigged maps (Fig. 5). But the functional effect of

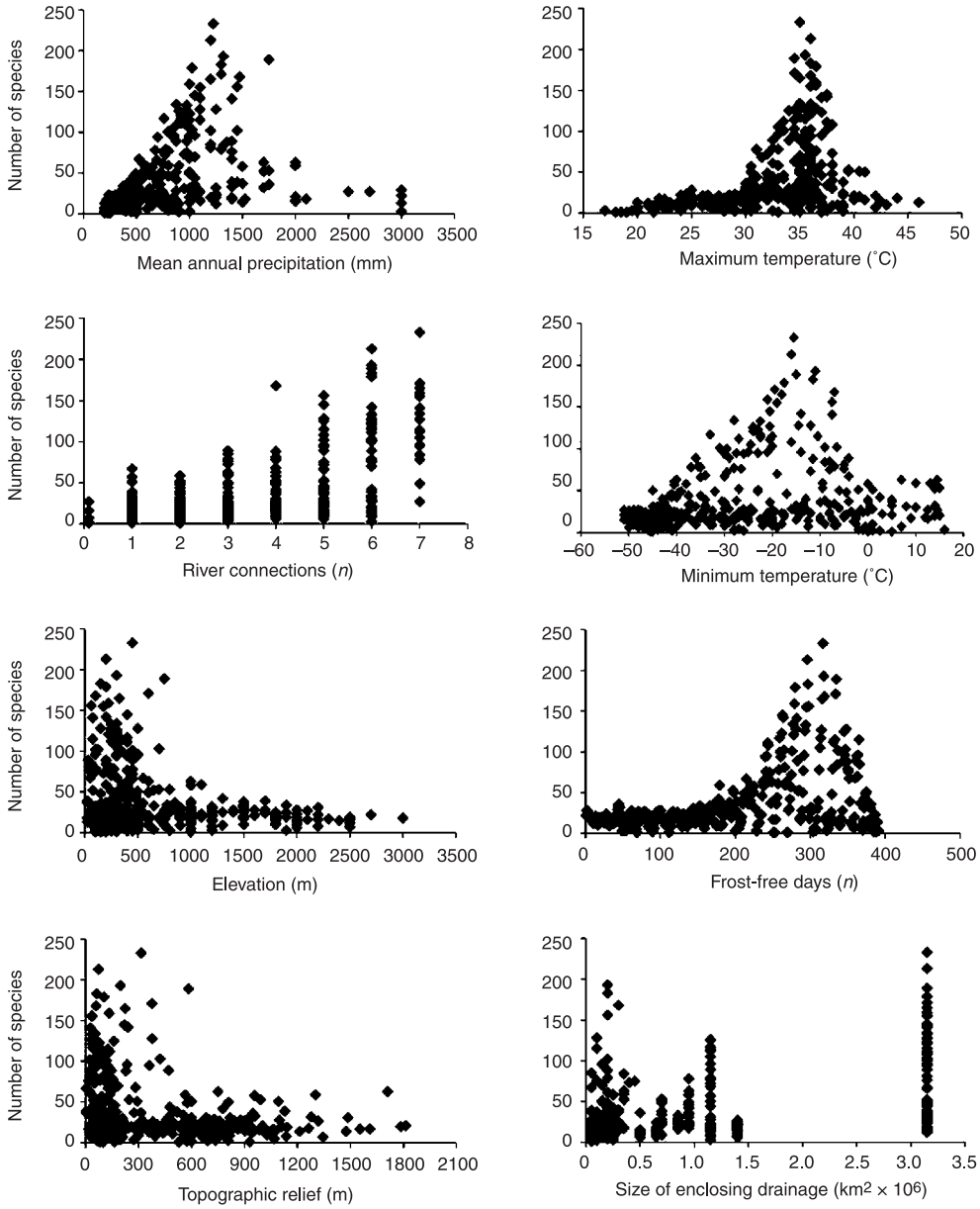


Fig. 4. Frequencies of species densities plotted against quadrat values of eight environmental variables. The outstanding column of values at the maximum in the drainage size panel is the range of quadrat species numbers in the Mississippi Basin.

AET on fish persistence in nature is mostly negative – high evapotranspiration removes water from surface fish habitats and groundwater (Weisman, 1977; Xenopoulos *et al.*, 2005). We therefore consider the positive statistical relationship between evapotranspiration and fish species density in this data set to be independently caused by the combination of warmth

Table 2. Ranking of variables' relative importance in predicting fish species density

Variable	% reduction MSE	Inc node purity
Precipitation	25.24	108877
Connectedness	24.16	106576
Frost-free days	19.97	91657
Maximum temperature	19.12	51530
Run-off	15.39	46630
Elevation	14.67	37021
Minimum temperature	12.90	39461
West/East	12.92	26354
Relief	12.66	26455
Drainage size	11.66	27566
Temperature range	11.60	25189

Note: The method, 'Random Forest', permutes all possible combinations of trees and computes the mean percent reduction in total mean squared error (MSE) achieved by inclusion of each variable. Node purity computes the resudual sum of squares to estimate the decrease in node impurity from splitting of the variable in question (see Fig. 6).

and precipitation and we omitted AET from the regression analyses. Because the correlation of AET and species diversity is frequently considered in the literature, we return to it in the Discussion.

Table 2 presents a ranking of environmental factors based on their mean square contributions to permutations of the independent variables in the 'Random Forest' method. Precipitation and connectedness rank highest, similar to the results of OLS regression analysis (not presented here), followed by frost-free days and maximum temperature, all of which have positive coefficients. Run-off (positive) and elevation (negative) are mid-level influences, followed by minimum temperature, and finally a categorical variable that separates Pacific and internal western drainages from Atlantic drainages, relief, drainage size, and temperature range.

Spatial autoregression of data for the whole continent produced a model with seven variables. Two variables, a quadratic term for maximum temperature (Fig. 4) and log precipitation, have high z-values, implying large and significant effects on fish density. Precipitation ranked high in the SAR model as well as in the OLS regression and Random Forest results. The effects of these variables on species density are positive (Table 3). Minimum temperature, elevation, and a quadratic term for minimum temperature have negative coefficients. Log drainage size and connectivity are last, with positive coefficients (Table 3). All seven variables are highly significant. The AIC-based selection method chose a model that also included maximum temperature, frost-free days, and run-off.

The influential variables in the best SAR analysis of Pacific-drainage quadrats emphasize the importance of drainage size, precipitation, maximum temperature (negative), and a quadratic term for maximum temperature (Fig. 4, Table 4). All four variables are highly significant. They emphasize the positive importance of precipitation on fish diversity and the negative effect of evaporation, caused by high temperatures. An AIC-based selection procedure chose a model in which connectedness, minimum temperature, and temperature range were recognized rather than drainage size.

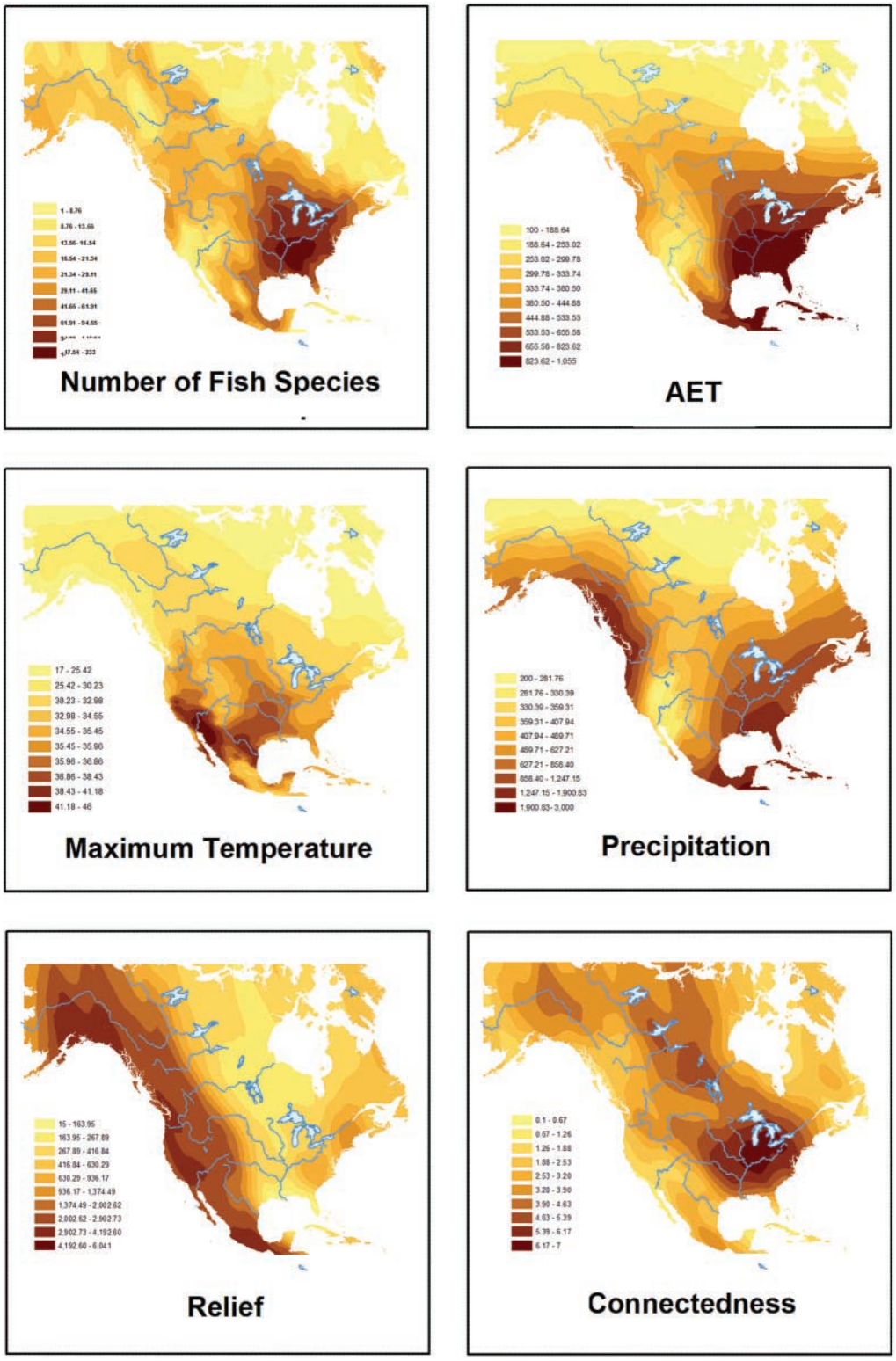
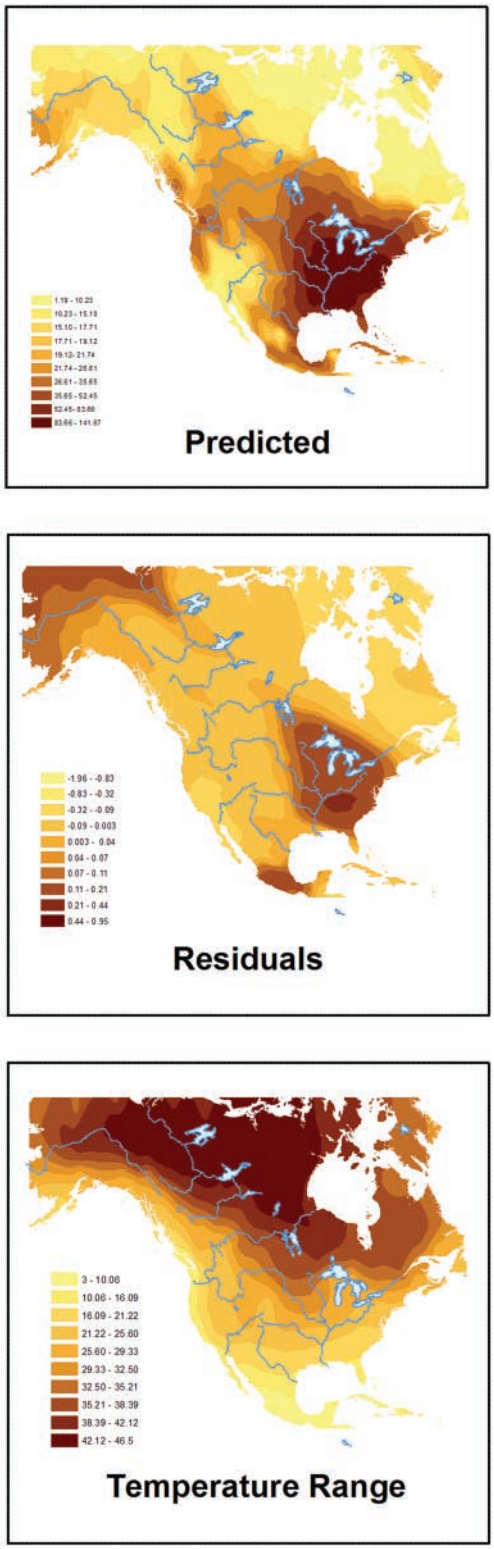


Fig. 5. Kriged maps of species density, six environmental variables, species density predicted by the



SAR model, and residuals from the predicted model. AET = actual evapotranspiration.

Table 3. Spatial autoregression model of fish species density and environmental variables over the North American continent

Variable	Estimate	Standard error	*z*-value	Pr(> | *z* |)
(Intercept)	−0.54	0.76	−0.71	0.48
Log precipitation	0.40	0.09	4.59	<0.001
Minimum temperature	−0.04	0.01	−4.42	<0.001
Log elevation	−0.16	0.05	−3.46	<0.001
Log drainage size	0.10	0.03	3.31	<0.001
Connectivity	0.05	0.02	2.92	<0.01
Maximum temperature^2	0.001	0.00	6.22	<0.001
Minimum temperature^2	−0.001	0.00	−3.87	<0.001

Note: *z* is the number of standard deviations that the slope estimate deviates from zero. Pr is the probability that the estimate is at least as large as *z*.

Lambda: 0.7469; LR test value: 144.2; *P*-value: $<2.22 \times e^{-16}$.
Log likelihood: −252.11.
ML residual variance (σ^2): 0.1816 (σ: 0.4261).
Number of observations: 388; number of parameters estimated: 10; AIC: 524.

Table 4. Spatial autoregression model of fish species density and environmental variables in western North America

Variable	Estimate	Standard error	*z*-value	Pr(> | *z* |)
(Intercept)	5.20	1.73	2.99	0.003
Log precipitation	0.31	0.09	3.40	<0.001
Log drainage size	0.17	0.05	3.75	<0.001
Maximum temperature	−0.33	0.10	−3.21	<0.001
Maximum temperature^2	0.01	0.00	3.57	<0.001

Note: *z* is the number of standard deviations that the slope estimate deviates from zero. Pr is the probability that the estimate is at least as large as *z*.

Lambda: 0.6731; LR test value: 44.26; *P*-value: $<2.88 \times e^{-11}$.
Log likelihood: −92.36.
ML residual variance (σ^2): 0.1809 (σ: 0.4254).
Number of observations: 147; number of parameters estimated: 7; AIC: 199.

Spatial autoregression of Atlantic-drainage quadrats produced a model with seven nearly equally important variables: temperature range, log frost-free days, connectedness, a quadratic term for temperature range (negative), a quadratic term for maximum temperature, maximum temperature (negative), and log run-off (Table 5). Model selection by the AIC-based procedure chose precipitation and minimum temperature rather than run-off.

Figure 5 shows Kriged maps of six of the most interesting variables as well as fitted species diversity and residual variations of the optimal SAR model (Table 3). The residuals show that the model fitted diversity fairly well, but underestimated the actual species density in the Mississippi basin (especially the Tennessee drainage), Great Lakes, east-Coastal United States except Florida, southeastern Canada, northwestern Alaska, and southern Mexico.

Table 5. Spatial autoregression model of fish species density and environmental variables in eastern North America

Variable	Estimate	Standard error	z-value	Pr(> | z |)
(Intercept)	−0.87	1.65	−0.52	0.60
Log frost-free days	0.86	0.19	4.48	<0.001
Log run-off	0.20	0.07	2.97	<0.01
Temperature range	0.16	0.04	4.62	<0.001
Connectivity	0.09	0.02	4.40	<0.001
Maximum temperature	−0.33	0.11	−3.13	<0.01
Maximum temperature^2	0.01	0.00	3.74	<0.001
Temperature range^2	−0.00	0.00	−4.16	<0.001

Note: z is the number of standard deviations that the slope estimate deviates from zero. Pr is the probability that the estimate is at least as large as z.

Lambda: 0.7736; LR test value: 85.01; P-value: $<2.22 \times e^{-16}$.
Log likelihood: −151.012.
ML residual variance (σ^2): 0.1686 (σ: 0.4106).
Number of observations: 243; number of parameters estimated: 10; AIC: 322.

Results of the recursive partitioning and regression tree (Fig. 6) split the 389 quadrats in the matrix first by precipitation, with species-poor quadrats in the branch characterized by mean annual rainfall below 513 mm, and diverse quadrats in the branch of wetter areas. The drier quadrats contain an average of only 14 species, whereas the wetter quadrats have an average of 41 species. Next, the method partitioned the 206 species-poor quadrats into a group of small-drainage quadrats with an average of six species and a group of larger-drainage quadrats with an average of 18 species. The cumulative explanatory power of each level of splits increases (lower half of Fig. 6). The partitioning continued (Fig. 6) through sets of quadrats based on warmer vs. cooler temperature, more vs. less precipitation, colder vs. warmer minimum temperatures, and a secondary group with colder vs. warmer maximum temperatures, until the partitioning in the low-precipitation branch was exhausted. The order of factors in Fig. 6 shows the relative and cumulative amount of variation explained by the variables. The high-precipitation and many-species branch at the top of the tree, covering 164 quadrats with an average of 41 species, was partitioned successively by high vs. low connectivity, warmer vs. cooler maximum temperature, west vs. east, elevations below vs. above 475 m, and low vs. high run-off. At the terminal level, the elevation partition split into branches with low vs. high relief. The rate of improvement of R^2-values at each level approached a plateau at nine splits, with little additional improvement. The most powerful explanatory variables are therefore precipitation, drainage size, connectedness, and maximum temperature, followed by elevation, run-off, and relief (Fig. 6).

Analysis of origination and extinction rates

Table 6 compares rates of origination and extinction in six families. The number of fossil occurrences in each region is similar: 270 in the west versus 280 species in the east. Estimates of extinction and origination rates are expressed as number of events per species per million years. Both rates are higher in the west than in the east for all families except Cyprinidae and Ictaluridae, for which origination rate is slightly higher in the east (Table 6). Diversification

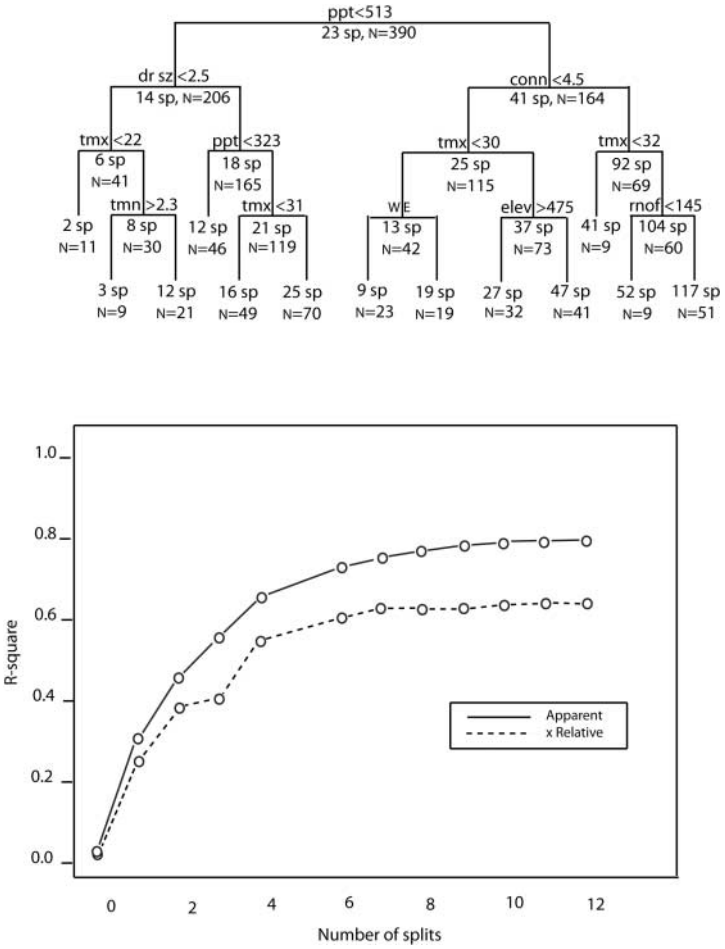


Fig. 6. (Top) Regression tree showing hierarchy of influence of environmental variables with split point for each environmental variable, number of quadrats (*N*), and average number of species in each branch (see Discussion). (Bottom) Cumulative increase in R^2 with each split.

rates (origination rate minus extinction rate) are slightly higher in the east, except for Cottidae (sculpins). Origination rates are estimated to be 0.05–0.12 originations per species per million years in the west and 0.03–0.09 per species per million years in the east. Extinction rates are estimated to be 0.01–0.12 extinctions per species per million years in the west and 0.0–0.02 per species per million years in the east (Table 6). The diversification rates are usually 0.04–0.05 per species per million years in the west and 0.03–0.09 per species per million years in the east.

DISCUSSION

Diverse fish assemblages occur in areas characterized by warmth, abundant precipitation and inferred high primary productivity, in waters connected to diverse source areas, south of glacial limits, in rivers with large catchment areas, high discharge and high habitat

Table 6. Estimated rates of originations (S) and extinctions (Ex) in six North American clades, based on numbers of living and extinct species known in western and eastern groups

	West originations		East originations		West extinctions		East extinctions	
N. Am. clade	Living spp. (*n*)	Orig. rate	Living spp. (*n*)	Orig. rate	Extinct spp. (*n*)	Ext. rate	Extinct spp. (*n*)	Ext. rate
Cottidae	20	$S = 0.06, 0.07$	8	$S = 0.03$	8	Ex = 0.02	0	Ex = 0
Centrarchidae	1	$S = 0.06, 0.12$	30	$S = 0.06$	8	Ex = 0.12	5	Ex = 0.01
Salmoninae	17	$S = 0.05$	5	$S = 0.03$	4	Ex = 0.01	0	Ex = 0
Catostomidae	28	$S = 0.07, 0.08$	39	$S = 0.06, 0.07$	14	Ex = 0.03	7	Ex = 0.01
Cyprinidae	49	$S = 0.08$	287	$S = ?, 0.09$	19	Ex = 0.02	1	Ex = ?, 0.0
Ictaluridae	1	$S = 0.05, 0.09$	39	$S = 0.07, 0.08$	6	Ex = ?, 0.09	14	Ex = 0.02
Sample totals	116 living spp.		408 living spp.		59 extinct spp.		27 extinct spp.	

Note: Time to each single species ancestor is assumed to be 65 million years. When two estimates are given, the first is based on the method of Etienne and Apo (2009), and the second on the method of Rosenzweig and Vetault (1992). Single values indicate converged estimates. Question marks indicate a lack of resolution.

diversity (Oberdorff *et al.*, 1995; Rosenzweig, 1995; Guégan *et al.*, 1998). Previous analyses have not considered the role of tectonic history, which is important because mountains of different ages differentially influence fish habitats, species ranges, and adaptation to swift-stream habitats. The time scale of importance is not the post-glacial 18,000 years, but the millions of years required for major landscape changes and evolution of significant hill-stream adaptations (Minckley *et al.*, 1986). Regional comparative studies in Oregon, which has a range of climatic conditions from the humid, coastal west to the high desert in the east, identified summer warmth, seasonal temperature extremes, river size, flow stability, potential basin connectivity, and diversity of source faunas as important determinants of native species diversity (Rathert *et al.*, 1999). High diversity has also been attributed to high speciation rates and low diversity to low speciation rates or high extinction rates, but without estimation of either. Historical causes that contribute to diversification have been considered (Hugueny, 1989; Hugueny and Lévêque, 1994; Oberdorff *et al.*, 1995; Hugueny *et al.*, 1997) but were often focused on effects of Pleistocene glaciation and deglaciation or discounted (Oberdorff *et al.*, 1997; Guégan *et al.*, 1998). A comparison based on rivers of only restricted parts of continents – western Europe and eastern North America – suggested the explanatory power of isolation, extirpation, and immigration, and demonstrated the importance of dispersal and regional species pools on species diversity at several scales (Oberdorff *et al.*, 1997) but missed the impact of orogeny because limited geographic units were examined. Similarly, the study of fish biogeography among ecoregions of Europe without Asia by Griffiths (2006) identified few long-term effects of mountains, but noted an influence of post-glacial dispersal on body size, migration, food habits, and life-history traits.

In contrast, our data on numbers of species along profiles of elevation, gradient, and discharge of rivers support the hypothesis that Late Cenozoic orogenic activity, acting through river elevations and slope, is a major determinant of freshwater fish species diversity gradients from local to continental scales. Spatial regression of environmental variables across the North American continent supports the hypothesis that species density is increased by high precipitation, temperature of the warmest month, and connectivity among adjacent drainages. Origination and extinction rates in six families of fishes support the hypothesis that geological history has determined species diversity primarily by its effect on extinction rates, not origination rates.

Variations in river profile and fish species diversity

High elevations and gradients are always sufficient to reduce severely the species numbers in upper reaches of actively emerging mountains. The nutritional energy available for these fish to remain in their small headwater home ranges is often insufficient to overcome the metabolic cost of maintaining station against the high kinetic energy of stream gradients greater than ~3 m per kilometre. Elevation also influences fish habitat through changes in substrate texture, erosion, and the lapse rate of temperature (Robinson and Rand, 2005). The age of mountains affects diversity – much of the longitudinal gradient in mid-continental North America is caused by the diversity of current-adapted darters in ancient Appalachian headwaters, especially in the Mississippi drainage. Darters do not occur in the young Rocky Mountain headwaters of the same drainage. Many high-elevation areas in the world have high terrestrial primary productivity, but any positive potential in this variable is usually overridden by high kinetic energy in high stream gradients. Hill-stream fishes south of the Tibetan Plateau, catfishes in the Andes, loaches in the Ponto-Caspian region, darters in the

Appalachians, and sculpins in North American high-gradient streams best exemplify the few fish groups that are morphologically and physiologically adapted to these conditions. The Columbia and Sacramento rivers have the highest diversity in the western United States, but fish faunas there are limited to three or fewer species of trout and sculpins found at higher elevations and stream gradients upstream of the gaging stations of Table 1.

Large Atlantic drainages east of the Great Plains often have less variable flow and more species in middle and downstream reaches, supporting the negative effect of variable flow documented by Horwitz (1978) and Schlosser (1990). Three exceptions suggest a strong effect of diverse faunal source areas. The lowest and middle stations on the Arkansas River and the low station on the South Platte River have the most variable discharges in the eastern rivers, yet have higher than predicted species numbers (Table 1, Fig. 2), suggesting that connection to a rich source fauna overrides variability in discharge. The lowest station on the Connecticut River, which has fewer freshwater species than predicted by its large discharge and low elevation, shows inverse expression of this trend (Oberdorff *et al.*, 1997). This river flows to the sea and is cut off from input from other drainages except by marine immigration and headwater stream captures on time scales of tens to hundreds of thousands of years. Similarly, the Rio Grande is depauperate among Atlantic-drainage rivers with only 54 species in low-gradient reaches near the Gulf of Mexico (Table 2), demonstrating the negative effects of both isolation by its marine terminus and by downstream volume depleted by aridity.

Within both the Pacific-drainage Colorado River and streams of the Great Basin, low elevation and gradient do not produce high species diversity, because lower reaches of streams in the desert are less stable (with higher CVs) than upper reaches (Smith, 1978). This pattern suggests that under conditions of low precipitation, the limiting effect of variable flow can override the positive effect of large mean discharge (Fig. 2). Small, steep headwaters of eastern rivers – the Missouri, South Platte, Arkansas, and Rio Grande – also support low species diversity. The Columbia and Sacramento rivers have high discharge and low flow variation and support regional species maxima, but their species diversity is only a fraction of that found in the much smaller streams east of the Appalachians, demonstrating the importance of diversity of source faunas in the long-term regional collective areas (Oberdorff *et al.*, 1997; Rathert *et al.*, 1999), as well as the differences in age, elevation, and slope of the mountains.

High-elevation headwaters are a feature of tectonically active continental margins where long-term topographic disturbance results from subduction of oceanic plates. The resulting orogenies create steep erosional slopes that fluctuate over thousands to millions of years and impose high barriers between basins, resulting in small geographic ranges. These montane conditions restrict the frequency of species carried across drainage divides by stream captures to rare events over millions of years, compared with the higher incidence of species transfer among flat prairie and plains streams (Cross *et al.*, 1986), probably common events over thousands of years.

Below thresholds of permanent in-stream flow, local extirpations are frequent (Ross *et al.*, 1985). In small streams isolated from source drainages for significant intervals of geological time, local extirpations are not replaced and low recolonization frequency following extirpations contributes to permanent extinctions. These historical processes characterized the past 30–40 million years in the west, during which time dynamic topography changed elevations dramatically, lowering the hundreds of valleys of the Basin and Range Province

while elevating the Colorado Plateau (Spencer *et al.*, 2008). The cumulative effect is extremely low fish diversity in both regions.

Effects of climatic variables across the grid

Estimates of Moran's *I* show high spatial autocorrelation of species diversity among quadrats in the east, oriented southwest to northeast. This direction coincides with the dominant trend in post-glacial immigration of fishes from the Mississippi drainage to the Great Lakes drainage. By contrast, Moran's *I* for the west indicates a short, steep decline of values, consistent with the many small, isolated drainages and prevailing low diversity. Although climatic variables occur in two correlated groups – temperature and moisture – across the landscape, individual variables may act independently on diversity in general as well as local circumstances. For example, minimum and maximum temperatures act as correlated aspects of the climate system, but they function to determine separately the southern and northern limits of fish species ranges. Furthermore, they do so differently, as when the same maximum temperature causes metabolic burnout in coldwater species and necessary growth in warmwater species. Similarly, the same minimum temperature may regulate a metabolic optimum in coldwater species and metabolic shutdown in warmwater species.

Fish diversity in relation to environmental variables shows central optima with sharp declines to extremes of precipitation, maximum temperature, minimum temperature, frost-free days, elevation, relief (Figs. 4, 5), and run-off (not shown, but similar to precipitation). Low species densities also occur under optimal and high rainfall values in quadrats with small drainage sizes and low connectedness, demonstrating the dominance of drainage size, connectedness, and geological history over even the most favourable of climatic conditions (Fig. 5). Low diversities in favourable climates demonstrate that optimal temperature and moisture are necessary but not sufficient to support high diversity.

Among climatic variables, actual evapotranspiration is the highest-ranked correlate and best predictor of species density (Fig. 5). Evaporation and transpiration are crucial parts of the water cycle, differentiating moist regions with stable water tables, where high precipitation and groundwater override high evapotranspiration, from arid regions where high evaporation and transpiration cause fluctuating water tables and intermittent streams (Weisman, 1977; Xenopoulos *et al.*, 2005). High actual evapotranspiration is a good proxy for high primary productivity (Rosenzweig, 1995), which is functionally beneficial to fish through riparian shade, decomposing leaf litter, and abundant insects as fish food. But high productivity and favourable climates do not necessarily support high diversity without geological stability, large drainages, and high aquatic connectivity.

Precipitation and run-off are important, though indirect, correlates with each other and with stable fish habitat. Maximum (monthly) temperature, a measure of seasonally available heat energy for ecosystem productivity, number of frost-free days, and length of the growing season represent another set of correlated variables especially important for ectotherms such as fishes. Seasonal temperature range and minimum (monthly) temperature represent some of the limiting physiological challenges to fish growth. High diversity occurs in cold, glaciated Great Lakes regions that benefitted from numerous post-glacial stream captures from the northwest and south (Hubbs and Lagler, 2004). Biogeographers often infer causes of fish species diversity patterns using regressions of species number on standard atmospheric environmental variables. But climatic data are only proxies for the variables that actually

influence fish survival and reproduction in aquatic habitats. Aquatic data associated with physiological mechanisms, for example temperature, current speed, and oxygen gradients, are not available at sufficient resolution on a continental scale; as these and other climate variables become available, they should offer better explanation of patterns.

Different analyses produced slightly different rankings of the 10 environmental variables suspected of interacting to create the pattern of species density seen in Fig. 3, because the analyses extract different information from the non-linear relationships (Fig. 4) and their interactions. Table 3 reinforces the importance of precipitation and shows the interacting sets of almost all variables across the continent. The important variables for eastern North America differ from those for the whole continent because the length of the growing season in the east dominates in the absence of western aridity. The most influential variables are consistent with expectations based on the effects of physiology, ecology, and dispersal as likely causes of the pattern of high species density in the Mississippi Basin and low density in the arid southwest and far north (Tables 3 and 5). The Pacific drainages show effects by fewer variables than other parts of the continent (precipitation, maximum temperature, and drainage size in Table 4, but also connectedness, minimum temperature, and temperature range in the AIC-based analysis). The ambiguity may be caused by the extreme heterogeneity of environments in the long narrow Pacific province, from the Arctic to the southwest desert, to the hot, humid tropics. Among all of the SARs, the AIC values are about an order of magnitude higher in the three models selected using the Bonferroni correction method.

Interpolated maps of the variables in Fig. 5 allow visual comparison of correlated groups. These analyses, along with the Random Forest procedure, ranked mean annual precipitation and connectedness substantially above other variables in predicting species density (Tables 3–5), supporting the importance of connected, high-volume aquatic habitats for high species density. Connectedness requires large drainages or geologically recent stream captures, but not all large drainages have high connectivity, especially in the west.

Residuals from the best SAR model (Fig. 5) indicate that having ideal environmental conditions is not sufficient to account for some extraordinarily high diversities, especially in the Tennessee drainage (but also in the Mississippi Basin and most contiguous drainages). Factors not in the spatial regression models, such as the conditions favouring speciation and low extinction during the late Cenozoic, may provide the explanation. The adjacent Great Lakes and other northern areas share post-glacial colonization from the Mississippi Basin during the past 14,000 years. Northwestern Alaska is richer than the SAR model predicts because its northern fauna is adapted to arctic climates and persisted in a large, unglaciated Alaskan refuge during the Pleistocene. The underestimated diversity in southern Mexico probably reflects positive effects of warm and large (although short) rivers. The model overestimates fish diversity in the southwestern United States, where the climate is warm, but arid and dissected by barriers.

The regression tree (Fig. 6) selected precipitation as the most influential variable, splitting low- and high-precipitation regions in the west and north. They were then split at the second level by drainage size, which separates the Mississippi drainage and its rich fauna from all others, and then by connectedness. The quadrats in small drainages were divided latitudinally by temperature of the warmest month. The third and fourth levels on the dry side identify causes of diversity differences in the west and far north. The branch identified with connectedness is partitioned by maximum temperature. These upper levels of the regression tree, containing six branch splits based on precipitation, connectedness, and

drainage size, account for about 75% of the gain in variance explained (R^2; Fig. 6, bottom), emphasizing the overwhelming importance of persistent water volume and connections among tributaries in large drainages.

Role of regional origination and extinction rates

The origination and extinction rates in six families with good fossil records indicate that all of the western samples have suffered higher extinction rates than eastern samples, consistent with predictions from the river-profile and environmental analyses (Tables 1–6). The variables most informative in the previous analyses suggest that extinction of western fishes is likely caused by two primary factors. First, low precipitation causes sparse and unstable aquatic habitats under the western mid-latitude atmospheric convergence zone with its subsidence of dry air, and the rain-shadow effect east of the Cordillera and Basin-and-Range mountains (Ernst, 2010). Second, the high Sierras, Cascades, Basin-and-Range, and Rocky Mountains pose barriers to fish dispersal and break the landscape into small isolated drainages with high rates of local extirpation (Strange *et al.*, 1993; Smith *et al.*, 2002). The consequence is an inter-mountain fish fauna exhibiting characteristics of an archipelago of basins, with the balance of immigration and speciation rates of isolated drainages determined by the strength and timing of barriers.

Cottidae and Salmoninae show higher origination rates in the west than in the east (Table 6). These fishes are abundant and diverse in cooler waters of the northwest. Their extinction rates are among the lowest in the west (0.01–0.02 species per million years), presumably because of the persistence of favourable habitats through the last 6 million years (Eiting and Smith, 2007). In contrast, warmwater fishes do not show significantly different origination rates between the west and east.

One consequence of high extinction rates is that many western species are relics, such as pupfish (Echelle, 2008), minnows, and lake suckers (Smith *et al.*, 2002), whose sister species have gone extinct over the past 1–3 million years. Survivors in western habitats are mostly localized minnows and suckers, supplemented by salmonids, sculpins, sturgeons, sticklebacks, lampreys, one sunfish, mudminnow, and troutperch in the north, and pupfishes, goodeids, cichlids, catfishes, and killifishes in the south. In the east, species with restricted ranges are small darters, suckers, and minnows endemic to headwater streams (Mayden, 1987). Local endemics are frequent in Appalachian and Ozark tributaries, where originations are less often cancelled by extinction, but range sizes are usually much larger for most eastern fishes (McAllister *et al.*, 1986). In the east, the positive relationship between endemism and diversity is strong, as found by Oberdorff *et al.* (1999), because many localized species of minnows and darters in the southeastern United States are young isolates in small headwaters. As a consequence of the tens of millions of years of tectonic disturbance and extinction in the west, however, endemic genera and species are often old relics (Barbour, 1973).

The interactions of processes from tectonic activity to local population dynamics are summarized in qualitative models (Fig. 7) that connect geological stability, climate, habitat, and population responses. Oceanic plates along the west coast are subducting under the continent, creating the long Cordilleran orogenic belts with steep, eroding slopes (Montgomery *et al.*, 2001; McElroy and Wilkinson, 2005), high ratios of riffle-to-pool habitats, and limited floodplains. By contrast, the passive eastern continental margins of North and South America have vast low-gradient floodplains, with high primary productivity and annual nutrient enrichment in large floodplain environments (Welcomme, 2008). Flow variations

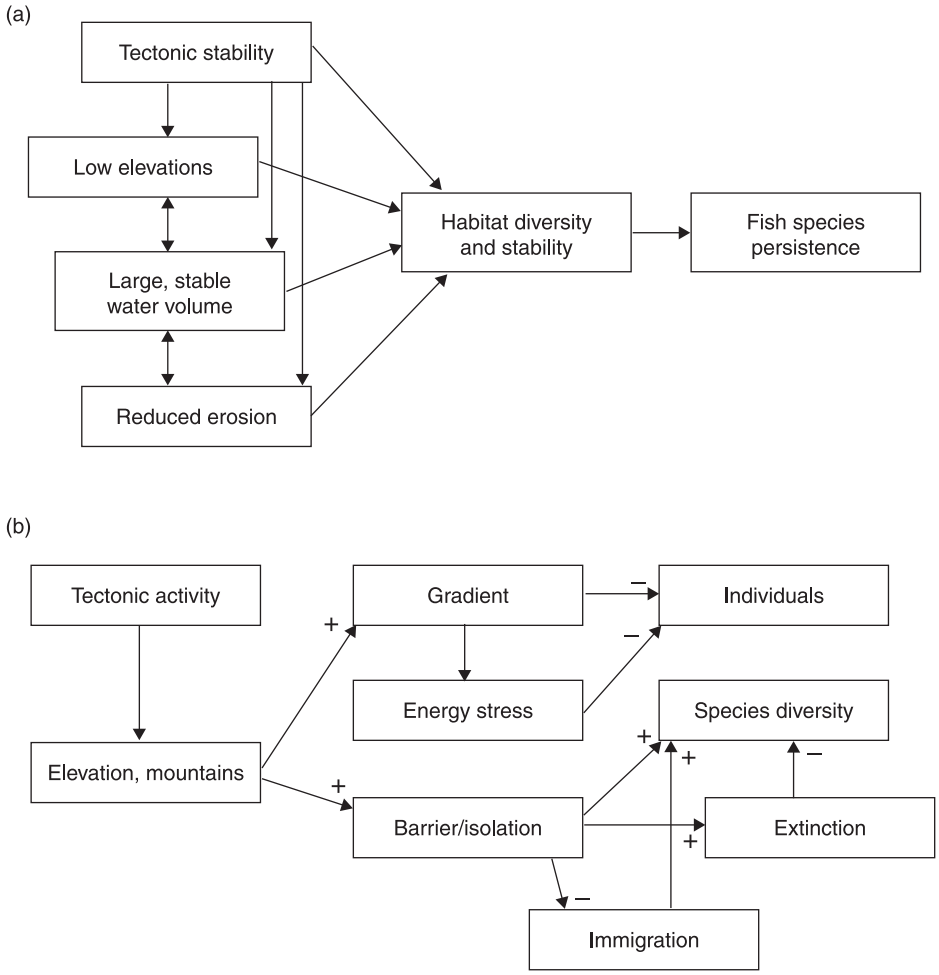


Fig. 7. (a) Diagram of hypothesized interactions influencing habitat stability and species persistence across the North American continent. (b) Diagram of hypothesized variables, effects, and feedbacks stemming from tectonic and elevation differences across North America.

on large floodplains transfer terrestrial primary productivity to aquatic systems, create thicker soils, high water tables, and more stable habitats, as well as providing dispersal opportunities.

Fish habitats on the North American stable craton and the ancient Appalachian Mountains appear to have been dominated by colonization and speciation over extinction in the late Cenozoic, suggested by our failure to discover significant extinction rates. Major drainages (Tennessee, Cumberland, Ohio, Missouri) act as subprovinces that have been connected near the centre of the Mississippi drainage province for millions of years. The abundant post-glacial recolonizations of the Ohio River and Great Lakes (Fig. 3) support the conclusion that extinctions by glacial advances have been surprisingly modest. The reverse is true of tectonically active regions. There, basins were rearranged by large tectonic changes, assembling the Columbia, Snake, Sacramento, Klamath, Green, and

Colorado rivers in the past 6 million years (Spencer *et al.*, 2008), with limited but recognizable fish colonization in pirated streams. A consequence is that in the tectonically active regions, the time scale for large topographic and hydrologic changes is much shorter than the time scale for evolutionary changes within fish lineages (Smith *et al.*, 2002).

Glacial and post-glacial colonization among drainages depended on the orientation of river systems. In north–south oriented systems (e.g. Mississippi, Alabama, Mackenzie rivers), fish populations could follow their temperature niches north and south during glacial–interglacial climatic cycles. The Great Lakes Basin has gained nearly 200 species via stream captures in the past 14,000 years of deglaciation (Hubbs and Lagler, 2004). The most diverse quadrats in North America, with over 200 species, benefitted from multiple late Cenozoic stream captures between the Tombigbee and Tennessee drainages (Starnes and Etnier, 1986). In contrast, species in both west- and east-flowing coastal rivers were trapped in small geographic units by topography, and subject to extinction with less recolonization during climatic shifts (Moyle and Herbold, 1987; Reyjol *et al.*, 2007).

The relationship of fish diversity to active versus passive continental margins may be general. In large, old rivers on passive margins, such as the Mississippi, Amazon, Congo, and lower Mekong, stable habitat diversity contributes to the accumulation of large numbers of species, which persist because of low extinction rates and high dispersal in large geographic units. Species diversity in large tropical river basins is two to three times that in the Mississippi Basin (Rainboth, 1996; Lundberg *et al.*, 1998), consistent with their large land masses (Rosenzweig, 1995). Speciation is widely thought to proceed at higher rates in tropical areas where trophic and reproductive interactions are not impeded by glaciation or seasonal dormancy (Mittelbach *et al.*, 2007), but paleontological evidence, so far, does not support this hypothesis for freshwater fishes (Lundberg *et al.*, 1986; Lundberg and Chernoff, 1992; Cione *et al.*, 2009). Our results suggest that in North America, highly diverse fish faunas are caused by low extinction rates, not high speciation rates.

Evidence for interspecific interactions is unusual in fishes, compared with other vertebrates (Begon *et al.*, 2005), and colonization appears little influenced by competition in the sense of Hugueny and Cornell (2000). But circumstantial evidence suggests that interactions caused changes in body size distributions. Large-bodied minnows in western North America, such as *Ptychocheilus*, *Pogonichthys*, *Mylopharodon*, and *Gila*, reaching more than a kilogram in weight, are related to several hundred species of small-bodied minnows in the east and south that rarely reach more than 50 g. These large, predaceous minnows exist in the absence of large esocid and centrarchid predators in the west, suggesting a role for competitive release. When large esocids were present in the western Pliocene, predaceous minnows in the assemblages were smaller (Smith *et al.*, 2000).

In summary, geological history establishes the landscapes over which fish create their habitats (Montgomery, 2000). The Atlantic-drainage fauna of North America exists in a system of hierarchical provinces or archipelagos, with patterns of diversity emerging between regional variations in speciation (Rosenzweig, 2004), but with low extinction rates over the late Cenozoic. Species diversity is high where the stable craton and passive continental margin created large, permanent, connected lowland rivers and a climate with mild or no winters. Here sub-provinces are connected drainages, among which diversity is maintained by dispersal from other drainages, but with some speciation in headwaters. In the west, species diversity is low in tectonically active regions with steep slopes, small basins isolated by mountains, short or geologically young rivers with limited floodplains, and precipitation plus groundwater often inadequate to maintain permanent in-stream flow. In this regard,

Pacific-drainage North America is a system of aquatic archipelagos (Rosenzweig, 2004), within which barriers restrict immigration and gene flow, promoting speciation, but also causing extinction to override speciation. Drainages such as the Great Basin, Colorado River, Columbia River, and Sacramento River are generally but inconsistently isolated, so that their faunas experience infrequent immigration and show relictual endemism. By evaluating diversity patterns in the context of geological history, we can integrate the evolutionary processes in time and space with the ecological processes operating over Holocene time scales.

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