Evaluating changes in stream fish species richness over a 50-year time-period within a landscape context

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Abstract Worldwide, streams and rivers are facing a suite of pressures that alter water quality and degrade physical habitat, both of which can lead to changes in the composition and richness of fish populations. These potential changes are of particular importance in the Southeast USA, home to one of the richest stream fish assemblages in North America. Using data from 83 stream sites in North Carolina sampled in the 1960's and the past decade, we used hierarchical Bayesian models to evaluate relationships between species richness and catchment land use and land cover (e.g., agriculture and forest cover). In addition, we examined how the rate of change in species richness over 50 years was related to catchment land use and land cover. We found a negative and positive correlation between forest land cover and agricultural land use and average species richness, respectively. After controlling for introduced species, most (66 %) stream sites showed an increase in native fish species richness, and the magnitude of the rate of increase was positively correlated to the amount of forested land cover in the catchment. Site-specific trends in species richness were not positive, on average, until the percentage forest cover in the network catchment exceeded about 55 %. These results suggest that streams with catchments that have moderate to high (>55 %) levels of forested land in upstream network catchments may be better able to increase the number of native species at a faster rate compared to less-forested catchments.

Keywords Stream fish · Species richness · Hierarchical Bayesian · Land use · Forest cover

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Introduction

Streams and their aquatic habitats are continually being altered, if not through immediate stressors such as point source pollution and dams, through long-term and often unnoticed effects, such as catchment deforestation (Foley et al. 2005; Dudgeon et al. 2006; Carpenter et al. 2011). In the US, recent estimates have suggested that 44 % (of over 3.5 million river miles assessed in 44 states) of sampled rivers and streams were impaired, meaning the water quality was

not high enough to meet the intended uses (USEPA 2009). Freshwater fish are particularly vulnerable to degradation of the surrounding landscape and changes in water quality and quantity. In North America the modern extinction rate (post-1950s) was estimated to be 877 times greater than background extinction rates for freshwater fishes, with 57 taxa going extinct from 1898 to 2006 (Burkhead 2012). Many of these extinctions were undoubtedly linked to anthropogenic activities (Burkhead 2012).

Changes in local (site-specific) stream fish species richness is of great concern from both a conservation and management perspective. Site-specific changes in richness could result from natural (e.g., forest fire; Dunham et al. 2003) and anthropogenic (development and agriculture) changes to the landscape. However, anthropogenic landscape alterations often have greater effects than natural changes, and the results are almost always a negative influence on native fish assemblages (Allan 2004). Such effects can lead to changes in fish species richness over time through local extinctions or range expansions of native or introduced species. Because there are a variety of mechanisms that can lead to site-specific changes in species richness (e.g., loss of physical habitat, changes in water quality, the encroachment of tolerant species, etc.) we would expect there to be substantial spatial heterogeneity in changes in richness over time, and we predict that much of this heterogeneity is related to the landscape context. For example, catchment deforestation has predictable outcomes on streams, including increased sediment load, homogenization of substrate, increased peak flows, stream channel widening, and increased water temperature (Allan 2004). Therefore, the amount of deforestation (or the percentage in forested land in a stream's catchment) should help predict changes in species richness.

Although the loss of species in altered systems is well documented (Argent and Carline 2004; Scott 2006; Jelks et al. 2008), recent evidence suggests that negative effects are perhaps more widespread and under-identified than originally thought. For example, Sutherland et al. (2002) reported significant increases in baseflow sediment in catchments with as little as 13 % deforestation. Additionally, Scott and Helfman (2001) brought to light the idea of native invasive species—species that are native to downstream habitats, but move into homogenized upstream habitat. These native invaders may signify habitat degradation, yet often go unnoticed based on their perceived native status. As loss of forested land continues in the US (Alig et al. 2004), efforts to conserve and manage native fish assemblages and their habitats are becoming increasingly urgent.

Streams in the Southeast US are home to some of the greatest freshwater fish biodiversity in North America and the world (Warren et al. 2000; Jelks et al. 2008), although the high degree of localization is likely what makes endemic species threatened (Brooks et al. 1992). Furthermore, many endemic species are small-bodied and frequently have characteristics that make them more vulnerable to habitat changes. For example, endemic darters (Family Percidae) and madtoms (Family Ictaluridae) are benthic species, while many endemic shiners (Family Cyprinidae) require clean substrates for feeding and spawning (Etnier and Starnes 1993; Jenkins and Burkhead 1994; Hewitt et al. 2009). Based on the habitat requirements of endemic species, and the fact that cumulative habitat degradation may be occurring even at baseflow conditions (Sutherland et al. 2002), benthic habitats and associated endemic species are often the first impacted (Angermeier 1995). Of additional concern is the repeated pattern of exotic species establishment and potential for biotic homogenization following the degradation of both native fish assemblages and their suitable habitats (Lapointe et al. 2012; Tracy et al. 2013).

One of the best ways to understand potential drivers of change, and thus to help manage biodiversity to minimize loss, is through a historic understanding of stream fish assemblages. Anderson et al. (1995) investigated fish assemblages in streams throughout much of Texas over 33 years and reported that, while diversity was very similar between time periods at the state-level, smaller scales (e.g., regional or basin scales) showed losses of habitat-specific species, such as darters and minnows, and increases of tolerant species, such as Inland Silverside, (*Menidia beryllina*), and Western Mosquitofish (*Gambusia affinis*)—both classified as having an opportunistic life-history strategy (Winemiller and Rose 1992). Similarly, Patton et al. (1998) examined historic fish data from Wyoming to report few large, statewide changes, but still reported several site-level assemblage changes—particularly decreases of native guilds where suitable habitat was lost.

Using fish assemblage data from 83 stream sites in North Carolina collected over a 52 year time-period, the objectives of this study were to 1) quantify spatial heterogeneity in changes in stream fish species richness from the early 1960s to mid-2000s, 2) examine any linkages between these changes and landscape-level covariates, and 3) evaluate the influence of introduced species on temporal changes in species richness.

Materials and methods

Sample collection

This investigation drew from two primary data sources, both from wadeable streams in North Carolina—a historic stream fish dataset and a contemporary dataset based on ongoing, long-term stream fish monitoring. The historic data set came from a large inventory and re-identification of vouchered stream fish samples collected between 1960 and 1964 by the North Carolina Wildlife Resources Commission (NCWRC) for which the vouchers now reside at the North Carolina Museum of Natural Sciences (NCSM). During these four years, state biologists sampled approximately 1937 streams throughout North Carolina. Sites were sampled once and sampling was done with rotenone or cresol, and covered between 61–123 m (200–400 ft.) stream reaches. The objective of all sampling was to "assess stream species composition and evaluate and classify the fisheries supported by them" (Starnes and Hogue 2011). At each site, all species present (along with total number) were recorded. Vouchering (fixation and preservation) of species ranged from nothing vouchered to vouchers completely matching the recorded data; however, vouchers for larger species were conspicuously absent due to a 1-gallon container constraint. From 2008–2011, the NCSM Fishes Unit undertook the task of verifying vouchered specimens and compiling a detailed report (Starnes and Hogue 2011) describing both basin and site-level historic species assemblages.

The second data set came from an ongoing stream sampling program conducted by the North Carolina Department of Environment and Natural Resources (NCDENR) Division of Water Resources Biological Assessment Branch. Since 1991, a standardized protocol has been used to sample 183-m (600-ft.)

stream reaches in over 900 wadeable streams throughout North Carolina. As part of the North Carolina basinwide assessment program, the sites are sampled approximately once every five years, mainly between April and June when environmental conditions (e.g., conductivity, turbidity) are comparable to previous samples. Backpack electrofishing units are used (most frequently two units), along with an appropriate number of dip netters based on the stream size. Reaches are sampled using two-pass depletion; the first pass is made moving upstream shocking along the banks, while the second pass returns downstream covering all available mid-channel habitats. All fish species are collected and identified; unidentifiable individuals of all sizes are preserved in formalin and identified upon return to the laboratory. Additional programmatic details can be found in the Standard Operating Procedures (NCDENR 2006).

Data manipulation

Due to the large number of sites in both surveys, spatially overlapping sites provided a unique opportunity to evaluate the possibility of any changes in stream fish richness and native communities over the past 50^+ years. We queried sites common to both the historic and contemporary data sets, where commonality was contingent on a shared ComID (a Common Identifier—defined as a 10-digit integer value that uniquely identifies the occurrence of each reach in the National Hydrography Dataset). This query resulted in 106 common sites. We then eliminated 23 historic sample sites based on lack of voucher specimens. In addition, we eliminated any historic samples that had recorded and voucher specimen lists that differed by more than one species (although frequently the recorded and vouchers specimen lists matched exactly). No sample sites were removed from the contemporary data set because consistent and reliable sampling and identification protocols were used. For the remaining 83 common sites we re-plotted both historic and current site coordinates (which were generally very close; e.g., governed by road access) to insure that comparisons were not only from the same reach, but comparable—e.g., not above and below a small dam.

Species richness modeling

To evaluate our primary question of heterogeneity and change in fish species richness over time (where richness = the number of species at a site during a sampling event), we used a Bayesian hierarchical modeling approach to explicitly consider both site-level changes, as well as second level to accommodate landscape covariates. The model we used can also be considered a varying intercepts and varying slopes model, with intercepts and slopes allowed to vary by site. The first level of the model included the covariate time as a predictor of species richness, and the second level incorporated the landscape covariates that we hypothesized would explain variation in site average richness (intercepts) and changes in richness over time (slopes). Our first model investigated only site-level species richness over time, and was considered unconditional (i.e., lacking covariates) at the second level. The first level of the model is expressed as

$$y_i \sim N\left(\alpha_{j(i)} + \beta_{j(i)} x_i, \sigma_y^2\right), \text{ for } i = 1, \ldots n \quad (1)$$

where y_i is species richness from sample i, of site j related to time x_i (a continuous variable) with intercept and slope coefficients α_j and β_j, and residual variance σ_y^2. The second level of the model (here unconditional) is expressed as

$$\binom{\alpha_j}{\beta_j} \sim N\left(\binom{\mu_\alpha}{\mu_\beta}, \binom{\sigma_\alpha^2 \quad \rho\sigma_\alpha\sigma_\beta}{\rho\sigma_\alpha\sigma_\beta \quad \sigma_\beta^2}\right), \quad (2)$$
$$\text{for } j = 1, \ldots J$$

where μ_α is the grand-mean intercept (the average species richness across all sites), μ_β is the grand-mean slope (average change in species richness across all sites), σ_α^2 and σ_β^2 are the variance estimates among the site-specific intercepts and slopes of species richness, and ρ is a between-group correlation parameter. Both μ_α and μ_β were given non-informative normal priors, while σ_y, σ_α, and σ_β were given non-informative uniform priors.

This model provided estimates of changes in species richness over time at the state-level; however, we were primarily interested in the trend hetero-geneity among sites and wanted to examine models with landscape covariates in an effort to identify landscape-level drivers of changes in stream fish richness. Landscape-based covariates were quantified for each site at the upstream network catchment level (i.e., the entire upstream catchment of the reach, as opposed

to the local catchment) and included percentage agricultural land, (human) population density, percentage forested land, and US Environmental Protection Agency Level III ecoregion. Percentage agricultural and forested land data were from the 2001 National Land Cover Database (Homer et al. 2007), population density was expressed as number of people per km² (NOAA 2010), and Level III Ecoregions follow those in Bailey et al. (1994). We also considered percentage developed land, number of road crossings, and mean elevation; however, these covariates were moderately or strongly correlated (Spearman's $\rho > 0.5$) to our existing covariates, and were excluded from further modeling.

When covariates were included, the second level of the model was modified so that

$$\binom{\alpha_j}{\beta_j} \sim N\left(\binom{\gamma_0^\alpha + \gamma_1^\alpha \cdot covariate}{\gamma_0^\beta + \gamma_1^\beta \cdot covariate}\right),$$
$$\times \binom{\sigma_\alpha^2 \quad \rho\sigma_\alpha\sigma_\beta}{\rho\sigma_\alpha\sigma_\beta \quad \sigma_\beta^2}\right), \text{ for } j = 1, \ldots J \quad (3)$$

where γ_0^α, γ_0^β, γ_1^α, and γ_1^β are coefficients for the intercept, effect of time and a covariate. σ_α^2 and σ_β^2 are conditional variances, the regional variance in α_j and β_j after controlling for the effect of the covariate. γ_0^α, γ_0^β, γ_1^α, and γ_1^β were given non-informative normal priors, while priors for σ_α^2 and σ_β^2 remained non-informative uniform. We fit each covariate model with both a full data set that included all sampled species (native and introduced), as well as with a data set from which introduced species were removed at the basin-scale. Any differences between the results may provide information regarding the contribution of introduced species to overall trends.

Prior to model fitting, the covariate year was grand-mean centered by subtracting each value from the overall mean to improve model convergence (Gelman 2004). To reduce skewness, percent agricultural land use was logit transformed and population density was $\log_e$ transformed (percent forest cover was not transformed). We ran three concurrent Markov chains beginning each chain with randomly generated values. The first 10000 iterations of each chain were discarded as burn-in, and the remaining 24000 values were assessed for convergence both visually, as well as with the Brooks-Gelman-Rubin statistic, $\widehat{R}$, with values <1.1 indicating convergence (although no values >1.02 were recorded). Analyses were run using JAGS

Fig. 1 Map of North Carolina highlighting the 83 sample sites investigated in this study and the Level III ecoregions in which they were found. All sites were sampled a minimum of two times (several with three or four sample visits), once between 1960–1964 and a second time after 1990
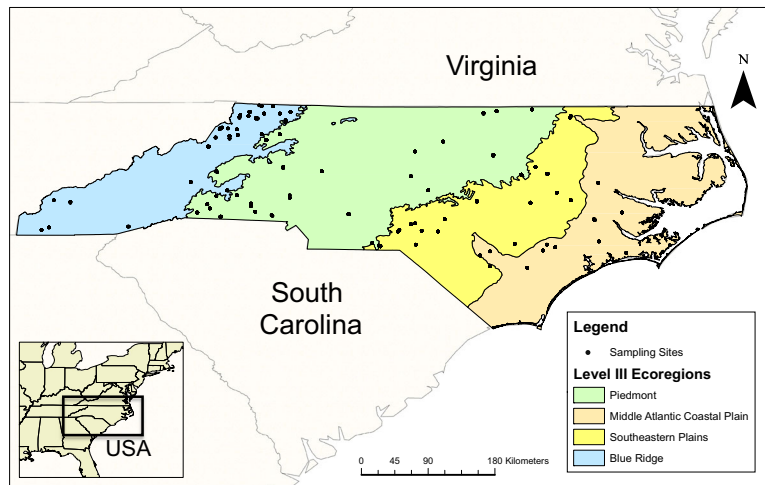
in the rjags package (Plummer 2013), run from within R (R Core Team 2013).

Native vs. introduced species

A second factor we wanted to evaluate was the effect of introduced stream fish species throughout the state. At the basin level, NCDENR has documented all introduced fish species in North Carolina.[1] Based on this list, we removed all introduced species, basin-by-basin, from our data (both historic and current samples). Species identification was generally not an issue while modeling richness, because the richness response depends only on the number of unique entities present, not the particular species involved. However, species did matter for examination of introduced species, and thus we pooled species by family to avoid any misidentification issues, such as endemic darters and shiners. Next, we standardized occurrence of family to work with percentages, because effort was unequal throughout the sampling (however, the relatively large amount of effort associated with both sampling programs supported standardization of percent occurrence; similar to the methods used in Anderson et al. 1995). From these occurrence data, we were able to examine changes in native and introduced species (by family), primarily through considering how frequently different families were encountered over time.
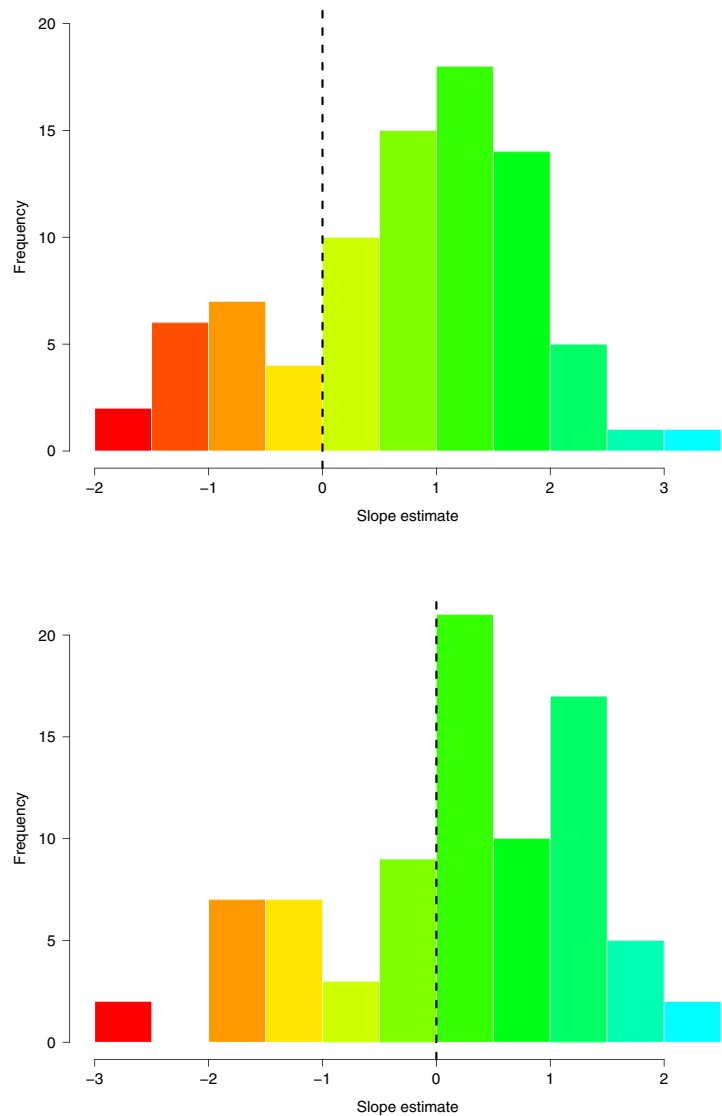
Results

Species richness modeling

Our site-matching criteria produced 83 sites in which the historic data could be matched to the current data (Fig. 1). Although the 83 sites were not uniformly distributed throughout the state, physiographic provinces were relatively well represented. While some eastern portions of the state were less represented than western portions, this is likely a reflection of the fact that the eastern portion of the Middle Atlantic Coastal Plain in the state contains fewer wadeable streams. Overall, at least one site was represented in each of 15 basins, 14 sites was the maximum in one basin (Cape Fear), and the mean number of sites per basin was 5.5. The Blue Ridge and Piedmont ecoregions contained 28 and 27 sites, respectively, while the Southeastern Plains and Middle Atlantic Coastal Plain ecoregions contained 16 and 12 sites, respectively. Combined, the historic and contemporary samples for all species included $n = 3318$ species observations, while the native only data that we examined included $n = 3038$ species observations.

Primarily, we were interested in slope estimates, which we initially considered a description of a site that has improved over time (positive slope) or one that has degraded over time (negative slope). Considering all species found, 64 of 83 (77 %) sites had a positive slope, while the remaining 19 sites had negative slopes (top panel of Fig. 2). The grand-mean number of species per site for the statewide regression was 14 (95 % credible interval [CI] =

13 − 15; range = 7[3, 11] − 22[20, 25]), with a slope of 0.74 (95 % CI = 0.14 − 1.33). On average, the number of species per site in the state increased over time. The correlation between varying intercepts and slopes was negligible ($\rho = -0.21$; 95 % CI: −0.73 − 0.21). The same unconditional model for native species showed that species richness at individual sites increased at a slower rate compared to when introduced species were included in the analysis (bottom panel Fig. 2), though positive trends in species richness remained at 55 (66 %) sites. In addition to an expected decrease in the grand-mean number of species ($\mu_\alpha = 13$; 95 % CI = 12 − 14), the statewide slope estimate also decreased to the point

where it was no longer different from zero ($\mu_\beta = 0.22$; 95 % CI = −0.32 − 0.76).

The next set of models we examined included landscape-level covariates to explain variation in the site-specific slopes and intercepts. The effect of percentage forest cover on the mean number of species at each site was negative and significant, while the effect of logit(percentage agriculture) was positive and significant (Table 1); there was no significant effect of $\log_e$(population density) on mean richness. We detected only weak negative effects of $\log_e$(population density) and logit(percentage agriculture) on site-specific trends in species richness (Table 1; Figs. 3 and 4). Percentage forest cover, however, had a
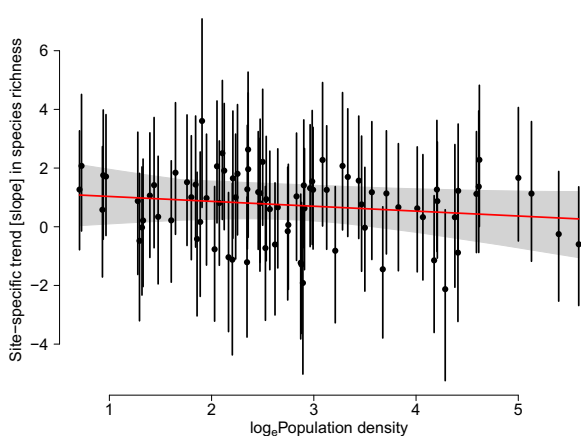
Table 1 Posterior means and 95 % credible intervals (in parentheses) for parameters of models examining the effects of landscape covariates on stream fish species richness

| Parameter	Forest	Agriculture	Population density
γ_0^{α}	17.27	16.34	13.09
	(14.89, 19.70)	(14.80, 17.90)	(10.56, 15.70)
γ_0^{β}	−2.32	0.39	1.19
	(−3.74,0.86)	(−0.66,1.42)	(−0.37, 2.76)
γ_1^{α}	-0.06	1.54	0.29
	(−0.10, −0.02)	(0.75, 2.35)	(−0.59, 1.13)
γ_1^{β}	0.06	−0.22	−0.17
	(0.03, 0.08)	(−0.76, 0.32)	(−0.70, 0.35)
σ_{α}	3.63	3.52	3.93
	(2.87, 4.48)	(2.78, 4.36)	(3.16, 4.78)
σ_{β}	1.19	1.70	1.74
	(0.09, 2.16)	(0.44, 2.61)	(0.36, 2.65)
σ_y	3.39	3.39	3.38
	(2.18, 3.99)	(2.81, 4.08)	(2.80, 4.08)
ρ	0.11	−0.16	−0.19

The agriculture covariate is a logit transform of percentage agriculture and population density was transformed by the natural logarithm. γ_0^{α} = intercept; γ_0^{β} = year effect; γ_1 = covariate intercept (α) and slope (β) effect; σ = standard deviations; ρ = correlation. See text for complete explanation of model terms

strongly significant positive relationship with the site-specific trends in species richness, clearly showing that increases in species richness tended to occur in catchments with greater proportions of forested land (Fig. 5). Site-specific trends in species richness were not positive, on average, until the percentage forest cover in the network catchment exceeded about 55 %.

Slopes of site-specific trends in species richness by ecoregion presented a clear pattern of increasing richness in upland ecoregions (Blue Ridge and Piedmont) and decreasing species richness in the Southeastern Plain and Middle Atlantic Coastal Plain ecoregions (Fig. 6). Based on 95 % CIs, all ecoregion-specific slopes were significantly different from zero (Table 2).

Fig. 3 Site-specific posterior mean slope estimates (*solid circles*) of changes in fish species richness as they relate to the $\log_e$(population density) for their network catchment. *Vertical lines* are 90 % credible intervals on the slope estimates and the *solid regression line* is shaded with the 95 % credible interval
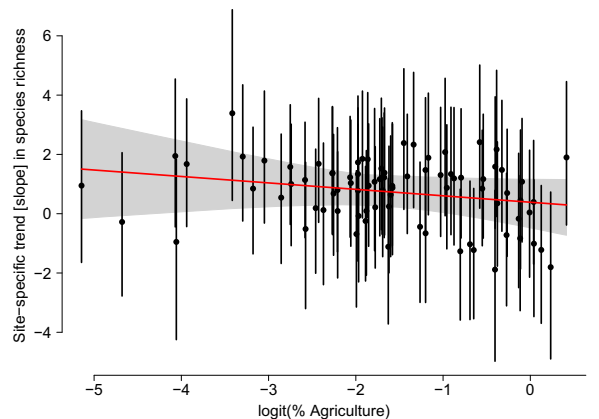
Fig. 4 Site-specific posterior mean slope estimates (*solid circles*) of changes in fish species richness as they relate to the logit(Percentage agriculture) for their network catchment. *Vertical lines* are 90 % credible intervals on the slope estimates and the *solid regression line* is shaded with the 95 % credible interval
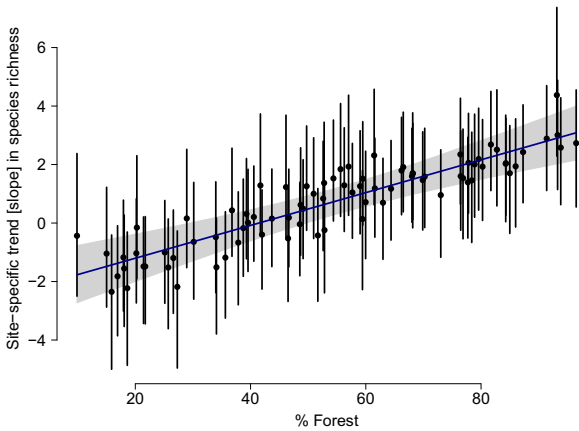
Fig. 5 Site-specific posterior mean slope estimates (*solid circles*) of changes in fish species richness as they relate to the percentage forest for their network catchment. *Vertical lines* are 90 % credible intervals on the slope estimates and the *solid regression line* is shaded with the 95 % credible interval

Similar results for the four covariate models were obtained when considering only native species. Intercept estimates for the catchment covariates did not change in direction or significance. When modeling site-specific trends, percentage forest cover remained a significant positive effect ($\mu_\beta = 0.04$; 95 % CI $= 0.02 - 0.07$), while the effects of logit (percentage agriculture) and $\log_e$(population density) remained

weak and uncertain ($\mu_\beta = -0.22$; 95 % CI $= -0.76 - 0.32$ for population density and $\mu_\beta = 0.04$; 95 % CI $= -0.43 - 0.51$ for agriculture). The effect of population density did become positive in the native species analysis; however, the estimate was near zero and non-significant. For the ecoregion model, slope estimates showed substantial decreases in magnitudes in the Blue Ridge and Piedmont ecoregions, and were virtually identical in the Southeastern and Middle Atlantic Coastal Plain ecoregions (Table 2). Despite these different estimates from the native species ecoregion model, all slopes remained significantly different from zero.

Native vs. introduced species

For examination of changes in introduced and native species by family, we combined the Southeastern and Middle Atlantic Coastal Plain Ecoregions as they historically contain many similar species and share several large river basins (e.g., Cape Fear, Neuse, Tar–Pamlico). In all three ecoregions, native cyprinids demonstrated some of the greatest reductions in percent occurrence, with the greatest decline in the Blue Ridge ecoregion (Fig. 7). Ictalurids also showed losses, but only in the Piedmont and Middle Atlantic Coastal Plains ecoregions. Native percids showed

Fig. 6 Hierarchical ecoregion posterior mean slope estimates (*solid lines*) *plotted* by ecoregion for data including all species. Individual points represent sampling events
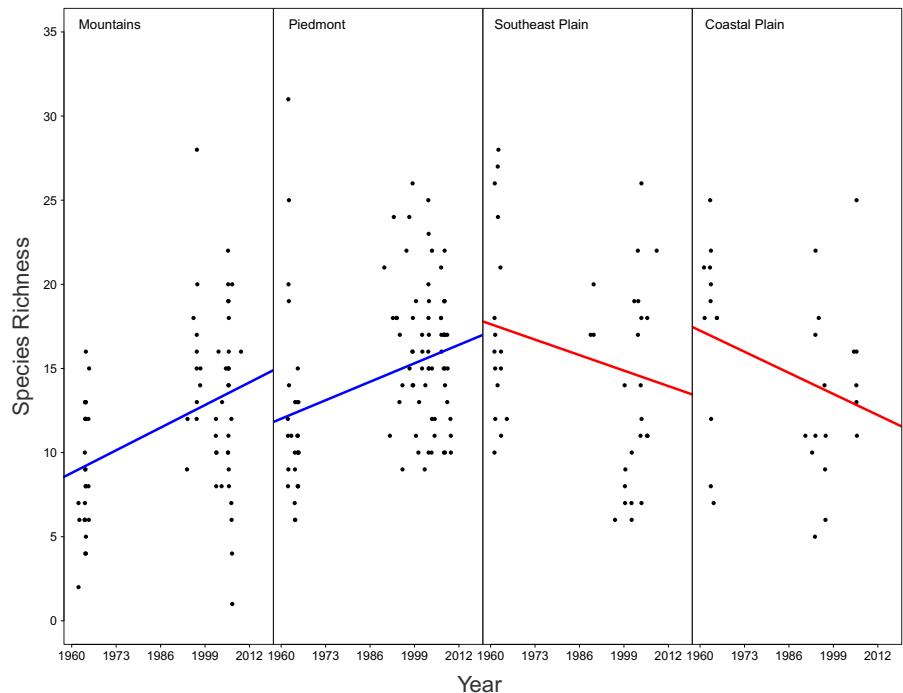
Table 2 Posterior means and 95 % credible intervals (in parentheses) for ecoregion specific slope estimates and standard deviations from models describing spatial and temporal patterns in stream fish richness

Parameter	Ecoregion covariate (all species)	Ecoregion covariate (natives species)
β_1	1.97	0.83
	(1.12, 2.81)	(0.03, 1.67)
β_2	1.61	1.21
	(0.78, 2.41)	(0.46, 1.98)
β_3	−1.37	−1.28
	(−2.53, −0.22)	(−2.35, −0.23)
β_4	−1.84	−1.97
	(−3.11, −0.41)	(−3.31, −0.66)
σ_α	3.65	3.29
	(2.90, 4.51)	(2.63, 4.05)
σ_β	0.85	0.95
	(0.02, 1.89)	(0.08, 1.86)
σ_y	3.36	2.99
	(2.84, 3.86)	(2.49, 3.50)
ρ	0.07	−0.07

Subscripts indicate the ecoregion, where β_1 = *Blue Ridge*; β_2 = Piedmont; β_3 = Southeastern Plain; β_4 = Middle Atlantic Coastal Plain; σ = standard deviations; ρ = correlation. The first model included both introduced and native species, while the second model was run only for native species

modest increases ($\sim$ 2 %) in all ecoregions, although this family included a few contemporary observations of Yellow Perch as opposed to being entirely darter observations. Changes in percent observation of introduced species by family showed that introduced cyprinids increased the most in all three ecoregions (Table 3; Fig. 8). Introduced catostomids and percids also showed marginal increases in all three ecoregions. Interestingly, introduced centrarchids showed considerable losses in percent occurrence; however, this is likely driven by their prominence in the historical data; i.e., they were the only introduced family in the historic piedmont data.

Discussion

We found strong evidence for species richness changes in North Carolina's wadeable streams over the past half-century and that the rate of change was positively correlated to the percentage forested land
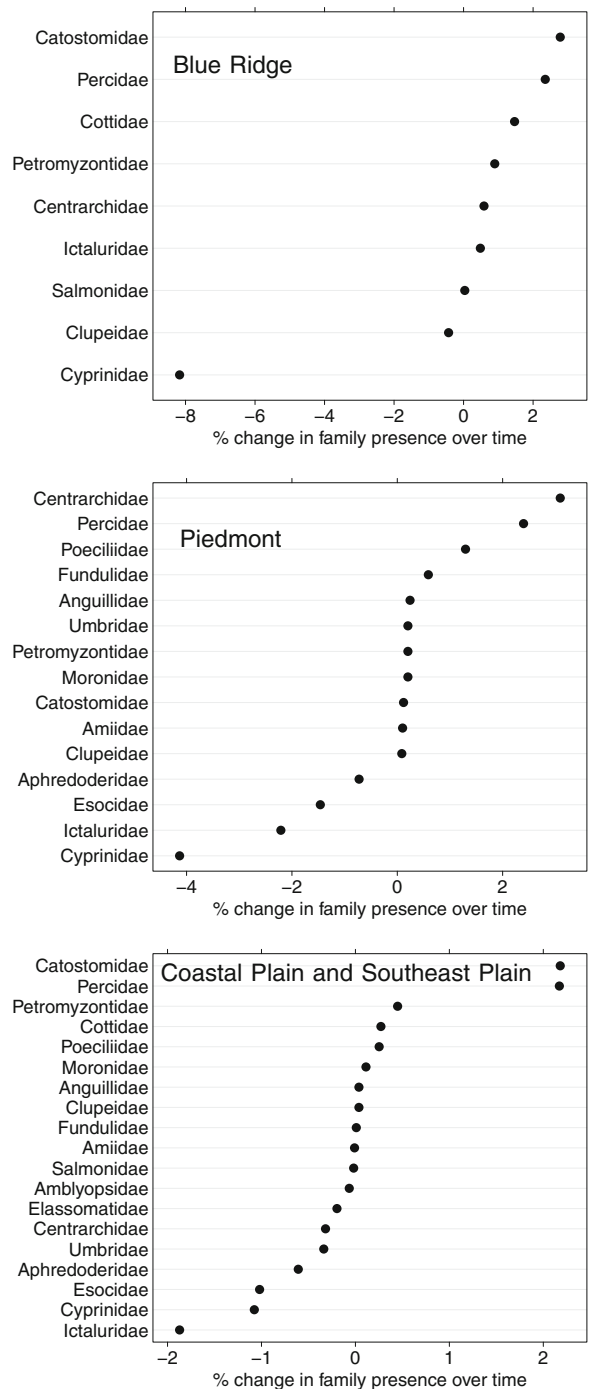
Fig. 7 Change in percent observation of native species by family from 1960s to current based on 83 revisited streams in North Carolina. Individual panels represent ecoregions: *top* = *Blue* Ridge; *middle* = Piedmont; *bottom* = combined Middle Atlantic Coastal Plain and Southeastern Plain

cover in the network catchment. In addition, site-specific trends in species richness were not positive,

Table 3 Changes in percent observation of introduced species (grouped by family) from past (1960s) to present sampling. Differences (in bold) are also seen in Fig. 8

| Family	Blue Ridge			Piedmont			SE and Coastal Plain		
	Past	Present	Change	Past	Present	Change	Past	Present	Change
Catostomidae	0.00	1.36	**1.36**	0.00	4.88	**4.88**	0.00	2.56	**2.56**
Centrarchidae	34.78	31.97	**−2.81**	100.00	67.07	**−32.93**	58.14	45.30	**−12.84**
Cyprinidae	17.39	25.85	**8.46**	0.00	14.63	**14.63**	9.30	21.37	**12.07**
Ictaluridae	4.35	0.00	**−4.35**	0.00	7.32	**7.32**	6.98	2.56	**−4.41**
Percidae	0.00	2.04	**2.04**	0.00	2.44	**2.44**	2.33	2.56	**0.24**
Salmonidae	43.48	38.78	**−4.70**	0.00	3.66	**3.66**	23.26	25.64	**2.39**

Note: This table includes naturally-reproducing salmonids (historically stocked by the NCWRC), which are not native to the Southeast and Coastal plains, but were briefly introduced there to experiment with creating a fishery

on average, until the percentage forest cover in the network catchment was about 55 %. Highly forested catchments tend to lead to cooler, less sedimented waters, which is generally considered higher quality habitat. Other studies have used historical data to address similar questions (e.g., Anderson et al. 1995; Patton et al. 1998; Johnston and Maceina 2009). However, to our knowledge this study is the only one to use Bayesian hierarchical modeling to explicitly evaluate trends while incorporating land use data, as well as to evaluate basin-scale information about introduced species. Whether we included introduced species in the base model (i.e., the model without landscape-level covariates) or not, the majority of the 83 sites we investigated showed increases in species richness over time. Furthermore, the relationship between site-specific trends in species richness and covariates was largely uninfluenced by introduced species.

Catchment land use is well documented to influence stream habitat, which in turn can influence the structure of species assemblages across the landscape (Allan 2004). We found significant effects of land use (percentage agriculture) and land cover (percentage forest) on site-specific species richness. However, the effect of agricultural land use was positive and the effect of developed land was not significant, which contrasts with other studies that have demonstrated decreases in native fish species richness with increasing anthropogenic land use in the catchment (e.g., Meador et al. 2005; Scott 2006). We hypothesize that the positive effect of percentage agriculture in the

catchments of the streams we studied was due to the fact that the more intensive agricultural land use occurs in the outer Coastal Plain. The Coastal Plain is also a region of naturally higher species richness as compared to inland, more depauperate streams, which occur in landscapes that are not as conducive to agriculture. The nonsignificant effect of population density may also be due to the lack of areas of higher population densities in our data.

Contrary to our expectations, we found weak effects of anthropogenic landscape covariates on site-specific trends in species richness. A few explanations could account for these weak effects. First, although our study streams were located in catchments that spanned a wide-range of percentage agricultural land and population density, both were deficient in higher values (maximum percentage agriculture and population density in the network catchment were 60 % and 268 people per km², respectively). An agricultural land use or population density threshold may need to be met in order to drive stronger changes, and our data did not approach that threshold. Weak visual evidence for a threshold may be argued for in our agriculture results; however, when adding a threshold parameter *post hoc* to the existing model, the threshold parameter was not significant. In addition, we used land use data from 2001 (approximately the middle of the contemporary sampling period), which might not reflect historical land use patterns that influenced fish communities (Harding et al. 1998). Despite this caveat, historical forest cover data suggests a loss of
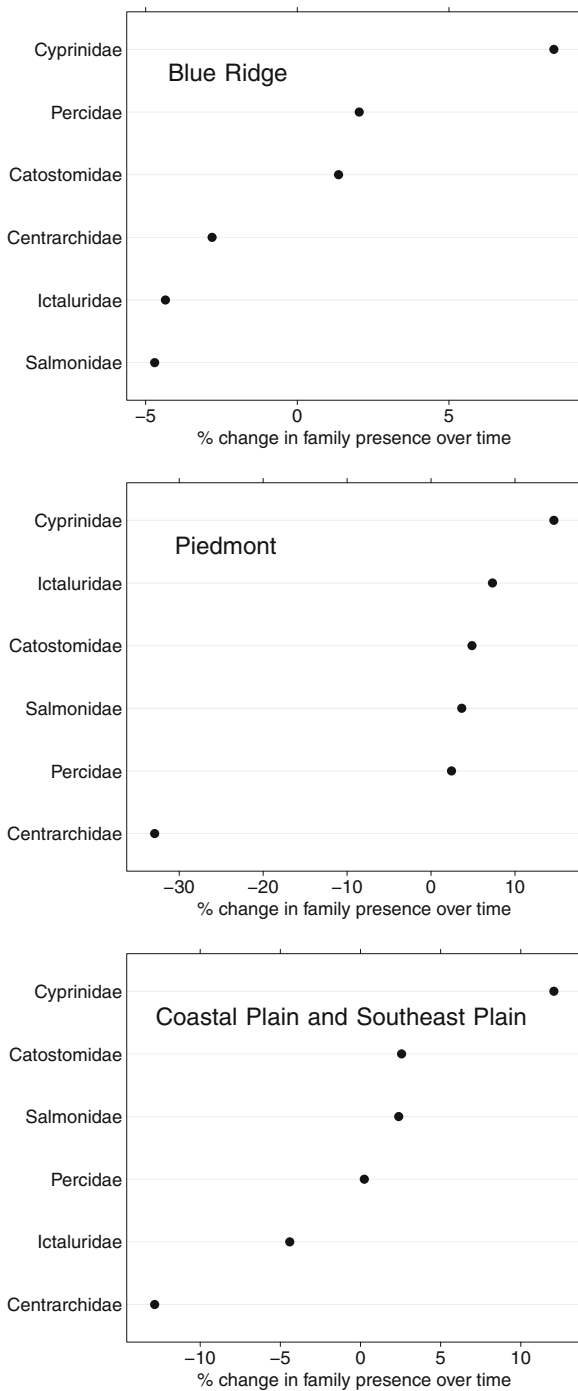
Fig. 8 Change in percent observation of introduced species by family from 1960s to current based on 83 revisited streams in North Carolina. Individual panels represent ecoregions: *top* = *Blue* Ridge; *middle* = Piedmont; *bottom* = combined Middle Atlantic Coastal Plain and Southeastern Plain

only around 10 % forest cover over our entire study period (NCFS 2010). A more likely explanation for the lack of strong anthropogenic land use effects could be that their effects are less obvious when isolated, but still contribute (along with other land uses we did not explore) to overall catchment degradation. Individually land uses likely have unique influence on stream habitat and fish assemblage, but at the scale of our study it may be more appropriate to classify them collectively as 'non-forested land.' The significant effect we observed across a range of forest coverage further supports pooling non-forested land use.

Although ecoregion was correlated to other variables we initially explored (e.g., elevation), ecoregion is best described as a group of similar ecosystems and in the type, quality, and quantity of environmental resources (Bryce et al. 1999). Ecoregion is also a primary influence on the geomorphology of flowing waters, which is a known influence on fish community (Sullivan et al. 2006). We found strong evidence of species richness increases in the Blue Ridge and Piedmont ecoregions, and species richness declines in the Southeastern and Middle Atlantic Coastal Plain ecoregions—trends that were largely independent of introduced species. Another benefit of viewing stream fish management through the lens of ecoregion is that the NCWRC—specifically (sportfish) biologists—identifies districts that fall largely within ecoregions. Non-game state biologists are more appropriately assigned to river basins, which are often correlated with ecoregions. Therefore, while there are land use effects on fish that supersede ecoregion, ecoregion remains a useful and established classifier in which to manage streams.

Introduced species have played a role in the structure of North Carolina stream communities, and we found that introduced species were more often sampled contemporarily in North Carolina streams than they were 50 years ago. Of the introduced species observed in the Blue Ridge and Piedmont, introduced cyprinids have had the greatest proportional increases. Introduced centrarchids were widely distributed across all ecoregions and are still abundant today. Due to the increase in introduced species from other families, percent observation of centrarchids has declined from the 1960s when they were

frequently the only introduced family at a site. These patterns of introduced species have been documented in other systems. Anderson et al. (1995) similarly found declines in the number of native species of cyprinids and ictalurids, and Patton et al. (1998) found both declines and increases in different groups of cyprinids. These patterns also conform to the idea that benthic species (either directly as an ictalurid, or indirectly through habitat used for reproduction as with many cyprinids) are predictably the first group of species impacted (Angermeier 1995).

Despite our results highlighting increased introduced species observations, we found that introduced species influenced the hierarchical models less than anticipated. This may be partly due to the relatively low number of introduced species (8.5 % of the full data were introduced species observations). Also, while often lumped as generalists, introduced species are still spatially constrained to some degree—such as with suitable habitat—and likely still have relationships to covariates that do not obscure the larger patterns in the data. One example of this was the consistency of the covariate effects when introduced species were removed. Covariate effect estimates were nearly identical with and without introduced species. Additionally, and as previously mentioned, we interpret the positive effect of agriculture on the intercept to be a function of the greater baseline species richness in lower elevations (Beecher et al. 1988), instead of an introduced species effect.

Positive slopes represented species richness increases both over time and as a function of landscape characteristics, and we operated under the assumption that increasing species richness was generally favorable compared to negative slopes. This assumption was largely due to two factors. First, while increases in species richness are less straightforward, negative slopes necessarily meant species loss, which we assumed was a negative outcome for a stream. Second, we excluded basin-level data on introduced species to further examine richness patterns only for native fish. Although we do not want to lessen the emphasis on introduced species, our results did suggest that the majority of sites have increased in native species richness since the 1960s and that introductions were not driving the patterns we observed. We would like to mention, however, that true patterns of assemblage change in the presence of introduced species can be difficult to ascertain. For example, stream

habitat degradation (channel widening, increased sediment load) often leads to a loss of native species and lower species richness comprised of more generalist, introduced species. However, the dynamic of degradation may not be a cleanly negative relationship, and in the early transitional stages both introduced species and natives may be present and combine to suggest an increase in overall species richness (Scott and Helfman 2001). To further confuse the issue, the definition of introduced species has multiple interpretations. Many fish invaders may simply be species native to downstream habitats, which means they can be overlooked as introduced, yet are frequently expanding into degraded habitat (Scott and Helfman 2001), and in the absence of fine-grained historical distributional data, can represent undetected alteration of native fish communities. Finally, although all of our streams were relatively similar in size (as defined by wadeability), introduced species might be expected to have different effects based on their size and habitat. For example, Blue Ridge streams may be more likely to experience an introduced cool water shiner, such as the Warpaint Shiner (*Luxilus coccogenis*), which may have negative effects on native species through resource competition, but do not necessarily extirpate them. Alternately, Flathead Catfish, *Pylodictis olivaris*, which have been widely successful in establishing populations in the Middle Atlantic Coastal Plain (Kaeser et al. 2011), have been documented to extirpate native stream species through predation (Thomas 1993; Dobbins et al. 2012).

Strengths and limitations

Ecological research is most often conducted at the site level, yet additional levels, such as sub-basin, basin, or physiographic region are often of interest. Hierarchical modeling provides an excellent framework in which to make inferences regarding multiple ecological levels (Wagner et al. 2006). This study provided an additional method of analysis to complement widely-used indices of similarity for evaluating temporal changes in stream fish communities. For example, a site-specific slope estimate (i.e., change in species richness) was largely a product of the data available to the site. Including a second model level permitted trend estimate for relatively data-poor sites to be informed by the entire ensemble of data (Kéry 2010). Our use of the historic data was generally

conservative, as we discarded sites that did not provide very high confidence (within one species) associated with species identification. Finally, although we were limited to streams in one state, North Carolina is geographically heterogeneous, containing 29 Level IV ecoregions ranging from mountain to coastal plain habitats, and supporting some of the greatest terrestrial and aquatic biodiversity in the US (Griffith et al. 2002; Burns et al. 2012). Therefore, our approach and findings are likely to be applicable elsewhere—particularly in the Southeast US.

There are always limitations when working with historic data. Most often, there can be issues with gear and effort mismatch. Although the historic sampling used (mainly) rotenone and the contemporary sampling used electrofishing, both surveys were designed by biologists to maximize the number of species collected. Rotenone has been effective in richness sampling (Weinstein and Davis 1980), and the reach lengths electrofished in our study were all double-pass sampled. Given our considerations of both of these sampling methods, we still limited our study to incidence (presence–absence) data and avoided the complexities in catch rate or abundance data when dealing with mismatched gear and effort. Based on the multiple site visits and area of stream sampled in the contemporary sampling, our results likely provide minimum estimates in site richness decline, as richness declines or species absence (despite increased sampling) provide strong evidence of decline (Patton et al. 1998). Additionally, our criteria for common sites meant the same specific location was sampled, as road crossings and coordinate data suggest.

We also recognize that detection probabilities may not have been equal across gears and samples, and as such our results are limited to producing apparent species richness. Based on the consistency of our sampling methods and the inferred high detection rates, we still caution against the use of our results toward inferring true richness. The effects of landscape covariates on species occurrence may be biased if detection probability is < 1 (Gu and Swihart 2004), resulting in underestimates of the effects of covariates for some species (Tyre et al. 2003). The fish community data, however, were from surveys that were performed with the specific goal of assessing the entire fish community and sampling followed standardized methods by trained field crews. Furthermore, studies have suggested that in many cases stream reach lengths of 235–555 m (reaches in our study totaled 366 m) are sufficient for presence-absence sampling (Paller 1995). Therefore, efforts were made to minimize the possibility of making false negative errors: failing to record a species as present when the species was in fact present.

Conclusions

In a time when an increasing number of flowing waters are reported as degraded and native and endemic fish are being lost (Jelks et al. 2008; Burkhead 2012),we found nearly two-thirds of sampled North Carolina streams contain greater native fish species richness than 50 years ago, before implementation of the Clean Water Act and more stringent water quality regulations (Howells 1990). However, Middle Atlantic Coastal Plain streams consistently showed the greatest losses in species, and introduced species are more widespread than in the 1960s. Streams can be particularly difficult from a management standpoint, as they are often influenced by seemingly minor and remote changes in the landscape. Despite these difficulties, streams in North Carolina and throughout the Southeast US may require continued protection to insure the future of its many endemic fishes, while simultaneously preventing habitat degradation and biotic homogenization documented in similar systems.

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