

Multiscale Fish Assemblage Distribution Models to Guide Riverscape Conservation Planning

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Abstract.—Scale influences the detection of relationships between landscape alterations and stream fishes and therefore has strong implications for conservation planning and implementation. This is especially true in riverscapes because terrestrial landscapes drain into riverscapes in a manner that can be measured at multiple scales. Two commonly employed scales in riverscape ecology and conservation include local catchment (i.e., the area of land draining directly into a segment of stream between two confluences) and network catchment (i.e., the total area of upstream land). We used a multispecies extension of species distribution modeling (i.e., gradient forest) to describe relationships between landscape alterations (measured at local catchment and network catchment scales) and stream fish occurrence patterns in portions of the Mississippi and Tennessee River basins in western Tennessee, USA. Landscape alterations included seven urban or agricultural classes, and densities of roads, road crossings, dams, human population, mines, and confined animal-feeding operations. At the network catchment scale, the most influential landscape alterations affecting fish distributions were cultivated crops and pasture/hay land uses, but at the local catchment scale, open-space development, human population density, and road density were most important for describing multispecies fish distributions. Despite these differences, gradient forest model performance measured as explained variation at the species level was consistent between local catchment and network catchment scales. Furthermore, when predictions for unsampled stream segments were mapped across the region, both scales produced consistent patterns in fish assemblages affected by low, medium, and high development or cultivated crops. Our results provide direction to conservation practitioners by identifying regions where limited resources might be allocated to increase efficiencies within two highly altered and taxonomically diverse riverscapes. The framework described here provides a case study for application of new statistical innovations to address

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conservation challenges and can be used in other landscapes and riverscapes to identify locations where management efforts might be best allocated.

Introduction

Determining the appropriate scale(s) for ecological assessment and application of conservation initiatives is often a challenge (Levin 1992; Boyd et al. 2008). Scale encompasses the grain and extent of observation, where grain represents the smallest spatial or temporal resolution and is generally the observational unit and extent represents the spatial dimension or time period over which all observations are made (Wiens 1989). The definitions of these components of scale strongly influence detection of linkages between environmental variables and fish occurrence, abundance, or community composition (Allan et al. 1997; Angermeier and Winston 1998; Kunin 1998; Lammert and Allan 1999). For example, Labbe and Fausch (2000) found that occurrence, population growth rate, and individual growth rate for a single species were each regulated by environmental variables measured at unique spatial scales. Other authors have identified similar scale-dependent regulators of fish populations and assemblages across a range of biomes (Jackson et al. 2001; Chick et al. 2004; Kennard et al. 2007). Consequently, scale has emerged as a focal research area for promoting the conservation of fishes (Fausch et al. 2002; Fagan et al. 2005; Gido et al. 2006). Despite previous advances in the application of scale theory in fish conservation (see overview by Fausch 2010), additional research is required to determine the most appropriate spatial scales for developing preservation or restoration plans for increasingly threatened freshwater fauna (Rivers-Moore et al. 2011; Stendera et al. 2012; Erős 2017).

In lotic ecosystems, applied principles of landscape ecology allow for addressing the issue of scale in fish conservation (Frissell

et al. 1986; Ward 1998; Wiens 2002). Fausch et al. (2002) reviewed the application of hierarchy theory in riverscapes as a means of connecting basic research on scaling with applied research focused on stream fish conservation. Because riverscapes drain terrestrial landscapes, riverscapes are linked to landscapes through processes mediated by hydrologic connectivity (Pringle 2003; Allan 2004; Burcher et al. 2007). Given these linkages, alterations to land use that result in land-cover transformation degrade ecological integrity and affect the abundance and distribution of fishes (Wang et al. 1997; Wenger et al. 2008). Terrestrial land-cover alterations, such as transformation from natural forest or prairie to urban or agricultural land uses, are among the most widely studied (Wang et al. 2001; Blann et al. 2009); however, these are not the only landscape factors affecting stream fishes. Multiple landscape alterations, including roadways and railways, roadway and railway crossings, confined animal feeding operations (CAFOs), mining runoff, human population density, and large and small dams, are all known to influence stream fishes (Fore et al. 2014; Perkin et al. 2016; Wellemeyer et al. 2018). The capacity of managers to address the ecological consequences associated with these landscape alterations is scale-dependent. Near-term and local-scale actions such as riparian planting, streambank stabilization, channel redesign, fish passage improvement, and small dam removal are most appropriate when fishes are responsive to fine-scale alterations not affecting entire basins (Kwak and Freeman 2010). Alternatively, long-term and large-scale habitat management actions such as natural flow regime mimicry or coordinated uses of cover crops to reduce soil erosion might be necessary to address landscape alterations associated with fish respons-

es at basin scales (Kwak and Freeman 2010; Strayer and Dudgeon 2010). A growing body of research has identified local and network catchments as relevant scales for assessing landscape–riverscape interactions, where local catchment describes the area draining immediately into a stream segment and network catchment describes the total upstream area draining to a point (Hill et al. 2017; Figure 1). Previous works have demonstrated that landscape alterations can correlate strongest with ecological change in streams at local scales (Wang et al. 2001, 2003), network catchment scales (Roth et al. 1996; Gido et al. 2006), or, in some cases, both scales (Hoehinghaus et al. 2007; Macedo et al. 2014; Leal et

al. 2016). Development of management plans aimed at conservation of stream fishes therefore require assessing linkages between landscape alterations and fish ecological integrity at multiple spatial scales, chiefly local catchment and network catchment scales (Closs et al. 2015; Jeffrey et al. 2015; Erós et al. 2018).

A further scale-related challenge in freshwater fish conservation involves the level of organizational complexity used in ecological assessment. Levin (1992) discussed the differential perspectives that come with studying organisms at the levels of individuals, populations, species, assemblages, communities, or ecosystems. Conservation programs have traditionally focused on groups of individuals

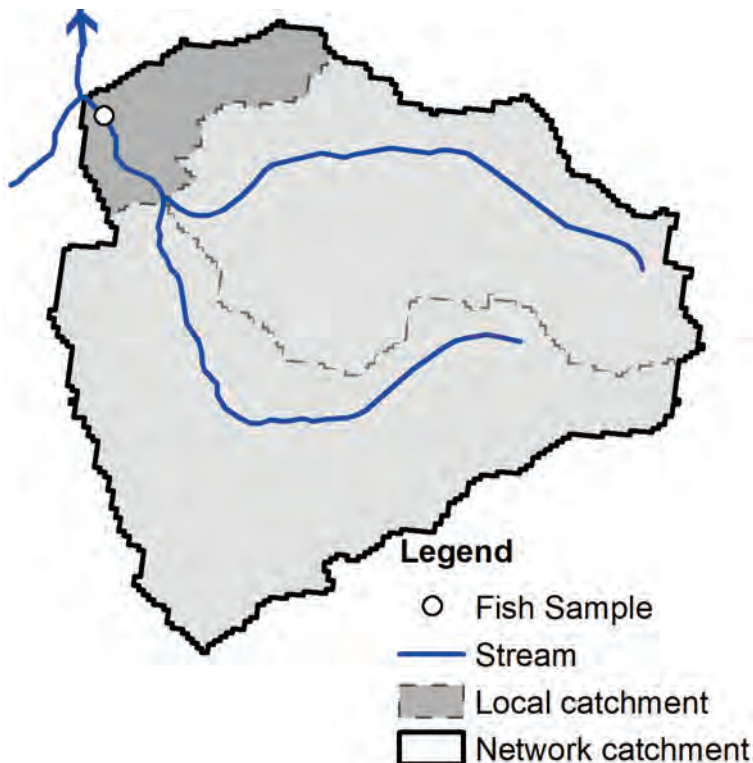


Figure 1. Conceptual diagram illustrating the spatial scales investigated in this study. Fish sampling sites (white circle) were located on stream segments defined as interconfluence sections of stream (blue lines; flow continues in direction of arrow). Each stream segment drains a local catchment (dark gray shading) as well as multiple upstream local catchments (dashed gray lines show outlines) that together are a network catchment (black outline).

within a single population or perhaps multiple populations of a single species (Soulé and Wilcox 1980). This focal level provides convenience in terms of targeted sampling and development of specified and complex models while operating at the level where most change in conservation status is measured (i.e., population decline or extirpation; Olden 2003). Conservation listings typically include species identity and sometimes specific population identities to create species-specific management plans, and this approach has been successful in preserving populations (Simberloff 1998). However, more recent advances in conservation biology advocate multispecies approaches that operate at the level of assemblages or communities rather than populations (Ferrier and Guisan 2006; Maguire et al. 2016). Assemblage-level models (ALMs) of species distributions provide benefits over single-species approaches because they allow for simultaneous consideration of multiple species, including rare species, and assess patterns of co-occurrence that are useful for detecting emergent properties (i.e., patterns not evident in single species approaches) in ecological degradation (Nieto-Lugilde et al. 2018). Furthermore, ALMs allow for identifying the environmental variables most pertinent to management by evaluating multispecies change in occurrence or abundance across ecological gradients (Ellis et al. 2012). In this context, applications of ALMs effectively scale up traditional population- or species-level approaches to assemblage or community levels (Pitcher et al. 2012). Yet ALMs have received relatively little attention in the application of biodiversity conservation (Nieto-Lugilde et al. 2018), and this is especially true of multiscale applications to benefit fish conservation in riverscapes (Leigh and Datry 2017). Given recent calls for scaling up fish conservation to multiple species across entire network catchments through establishment of protected areas such as native fish conser-

vation areas (Williams et al. 2011; Malone et al. 2018), ALMs have potential to contribute to emerging conservation initiatives at broadening spatial scales. Currently, additional research is necessary to determine the appropriate spatial and organizational complexity scales for relating riverscape alterations to stream fish species and assemblages as a means of informing conservation and management planning.

The goal of this study was to develop multiscale (local catchment and network catchment) predictions for stream fish ecological condition measured at two levels (species and assemblage) to inform riverscape conservation planning. Here, we define assemblage as a collection of fishes occurring together in space and time and differentiate this term from community in that only fishes and no other aquatic organisms (e.g., invertebrates, vegetation) are considered (Fauth et al. 1996). To accomplish our goal, we developed three objectives. Our first objective was to assemble data for 13 landscape alterations measured at local and network catchment scales for portions of the Mississippi and Tennessee basins in western Tennessee, USA. These basins are part of a regional fish diversity hotspot characterized by a globally significant level of biodiversity (Warren et al. 2000; Abell et al. 2008). Our second objective was to assess relationships between landscape alterations and the distributions of freshwater fishes compiled at species and assemblage levels. Our third objective was to develop spatially explicit descriptions of the multiscale relationships between landscape alterations and fish biodiversity as a tool for conservation planning across the region. We hypothesized that ecological responses to landscape alterations would not be uniform across the region because of spatial variation in landscape alterations. For example, urban areas should have a unique suite of alterations that affect fishes through pathways that differ

from alterations created in agricultural areas (Wang et al. 2001; Feist et al. 2018). We also hypothesized that the magnitude (i.e., measured as model R^2) of ecological responses associated with landscape alterations measured at the local catchment scale would differ from those measured at the network catchment scale. This is expected because some landscape alterations such as urbanization should have stronger localized effects compared to landscape alterations such as agriculture that generally occur over broader spatial extents (Thornbrugh et al. 2018). Tests of these hypotheses have direct implications for informing the locations and scales most appropriate for conservation actions aimed at managing stream fish ecological integrity.

Methods

Study Area

We assessed landscape alterations and fish distributions in the Southeastern Plains and Mississippi Valley Loess Plains ecoregions of Tennessee, USA (Omernik and Griffith 2014). The region is bordered by the Mississippi River to the west, the Tennessee River to the east, the Mississippi State border to the south, and the Kentucky State border to the north (Figure 2). The ecoregions are also separated by the division of the Mississippi and Tennessee basins, a bisection that represents a strong biogeographic barrier to fishes (Etnier and Starnes 1993). Consequently, two subregions were assessed independently: portions of the Mississippi and Tennessee basins. Although the northern and southern borders of the study area are political (rather than biogeographic), all major streams drain either to the west (Mississippi basin tributaries) or the west and east (Tennessee basin tributaries), and therefore most of the local catchments and network catchments assessed, were completely within the study area. Average annual air temperatures are 10–22°C, and average an-

nual rainfall is 136.39 cm/year across the region (Wellemeier et al. 2018). The dominant natural land cover was historically deciduous temperate forest, although considerable land-use transformation has occurred to support agriculture and urbanization. Agriculture land use dominates landscapes in the Mississippi Valley Loess Plains ecoregion draining into the Mississippi basin, including both cultivated crops and hay pastures, whereas forest land cover dominates the Southeastern Plains ecoregion draining into the Tennessee River basin (Homer et al. 2015).

Landscape Data

We collected landscape alteration data for 13 variables representing the dominant forms of alteration for the region and for which reliable data were available. Landscape alterations were compiled at local catchment and network catchment scales using a geographic information system, and the protocol is described in detail by Wellemeier et al. (2018). This protocol included defining stream segments as polylines from the National Hydrologic Dataset (NHD; USEPA and USGS 2012) across the entire region. The NHD is based on a digital elevation model and allows for ascribing the local catchment as the area of land draining immediately into a polyline and the network catchment as all upstream land area draining into the same polyline. We used local catchment and network catchment polygons from the NHD to compile landscape alteration data at each scale independently. Landscape alterations included proportion of the terrestrial landscape covered by cultivated crop (Crop), pasture and hay (Hay), or urban development (five classes: open, Dev1; low intensity, Dev2; medium intensity, Dev3; high intensity, Dev4; and impervious cover, Dev5) and density (#/km²) of length of paved roads and railroads (Road), roadway and railway crossings (Cross), human population (Pop), dams >3 m (Dam), mining permits (Mine), and CAFO

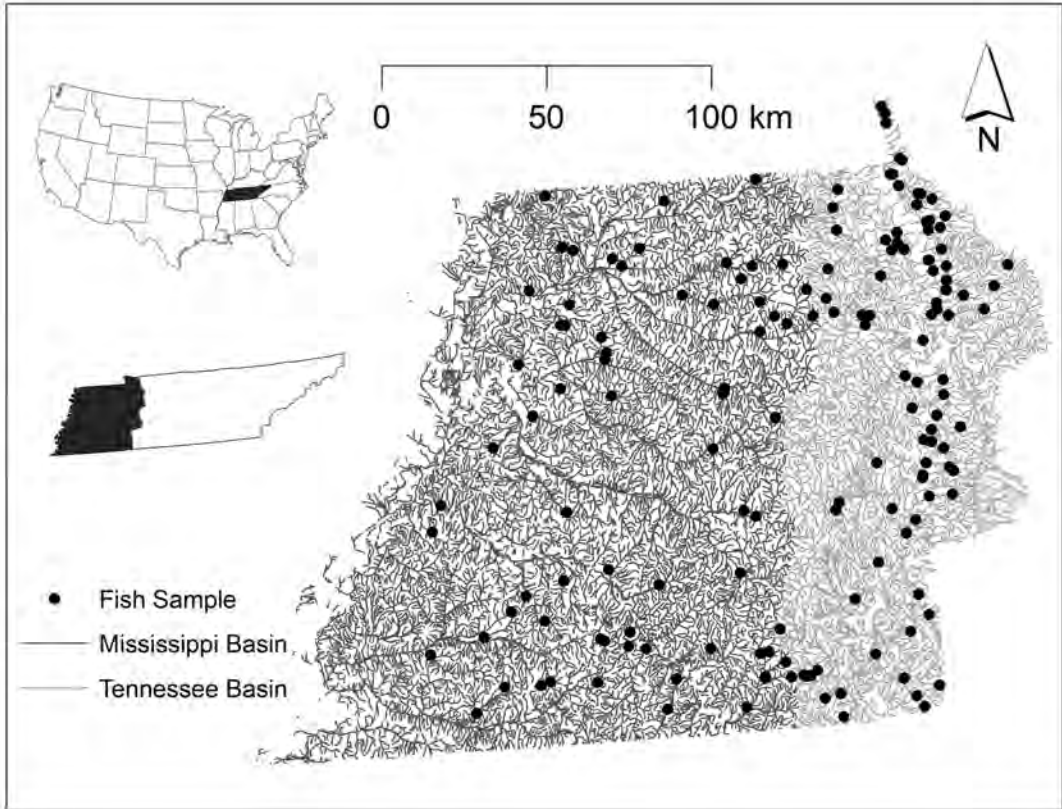


Figure 2. Study area map illustrating Tennessee in the southeastern United States, stream segments, and fish sampling sites in the Mississippi and Tennessee River basins

permits (CAFO) for local catchments and network catchments (Table 1). All land-cover data were obtained from the National Land Cover Dataset (Homer et al. 2015), roadway and railway data were obtained from the U.S. Census Bureau (2014), human population data were obtained from the U.S. Census Bureau (2010), dam locations were obtained from the National Inventory of Dams (USACE 2013), and CAFO and mining permit data were obtained from the Tennessee Department of Environmental Conservation (TDEC 2012).

Fish Data

We used fish occurrence data collected by the Tennessee Wildlife Resources Agency from across the study area during 2000–2015. Those data were collected by using a stan-

dardized sampling protocol that consisted of sampling 100–200 m of wadeable stream (i.e., stream order ≤ 3 ; Strahler 1957) in an upstream direction using single-pass electrofishing conducted using a single backpack electrofisher (100–200 V, direct current) and a single netter. This level of sampling effort is consistent with recommendations for assessments of ecological condition reported elsewhere (Reynolds et al. 2003). Fishes collected during sampling were held until the entire site was sampled, at which point species were identified and released. Detailed methods used to ensure the quality of these data are given in Wellemeyer et al. (2018) and included retention of only fishes identified to species, assignment of fish collections to NHD polylines using geographic positioning

Table 1. Landscape alteration magnitude medians (range) for stream segments with fish assemblage data in the Mississippi (MS) and Tennessee (TN) drainages at catchment and watershed spatial scales. Scales at which landscape alterations did not occur are shown as “-”. NLCD = National Land Cover Database.

Name	Description	MS local catchment	MS network catchment	TN local catchment	TN network catchment
Crop	Proportion of cultivated crop land cover (NLCD 82)	0.37 (0.00–0.93)	0.31 (0.00–0.92)	0.04 (0.00–0.66)	0.03 (0.00–0.49)
Hay	Proportion of hay and pasture land cover (NLCD 81)	0.05 (0.00–0.49)	0.08 (0.00–0.49)	0.02 (0.00–0.54)	0.05 (0.00–0.53)
Dev1	Proportion of open development land cover (NLCD 21)	0.05 (0.00–0.26)	0.05 (0.00–0.18)	0.03 (0.00–0.16)	0.02 (0.00–0.09)
Dev2	Proportion of low intensity development land cover (NLCD 22)	<0.01 (0.00–0.07)	<0.01 (0.00–0.12)	<0.01 (0.00–0.06)	<0.01 (0.00–0.05)
Dev3	Proportion of medium intensity development land cover (NLCD 23)	<0.01 (0.00–0.06)	<0.01 (0.00–0.04)	<0.01 (0.00–0.04)	<0.01 (0.00–0.02)
Dev4	Proportion of high intensity development land cover (NLCD 24)	<0.01 (0.00–0.02)	<0.01 (0.00–0.02)	<0.01 (0.00–0.01)	<0.01 (0.00–0.01)
Dev5	Proportion of impervious land cover	0.50 (0.00–0.83)	0.52 (0.00–0.90)	0.42 (0.00–0.35)	0.15 (0.00–0.34)
Road	Density of roadways and railways (m/km ²)	1,714 (0–8,465)	1,628 (0–5,399)	1,751 (0–9,200)	1,419 (0–5,831)
Cross	Density of roadway and railway crossings (m/km ²)	0.68 (0.00–33.17)	0.59 (0.00–2.69)	0.56 (0.00–6.21)	0.57 (0.00–2.14)
Dam	Density of dams (#/km ²)	<0.01 (0.00–0.24)	<0.01 (0.00–0.23)	-	<0.01 (0.00–0.06)
Pop	Density of human population (people/km ²)	90 (0–61,615)	12 (0–225)	57 (0–13,809)	10 (0–78)
Mine	Density of mining permits (#/km ²)	-	<0.01 (0.00–0.09)	<0.01 (0.00–0.47)	<0.01 (0.00–0.47)
CAFO	Density of confined animal feeding operation permits (#/km ²)	-	<0.01 (0.00–0.05)	-	<0.01 (0.00–0.07)

system coordinates collected during fish sampling, and combining fish occurrence data across multiple collections when the same site was sampled more than once (Gido et al. 2006). We also excluded species that occurred in fewer than five collections. Review of the database and exclusions as noted above resulted in 72 sites (50 species) from the Mississippi basin and 89 sites (62 species) from the Tennessee basin.

Statistical Analyses

We simultaneously modeled species and assemblage levels of organization using four gradient forest models built at two spatial scales for the two ecoregions. Gradient forest (GF) modeling is a multispecies extension of random forest (RF) modeling, a commonly applied tree-based machine learning algorithm. Benefits of RF models include increased classification accuracy when compared with traditional classification trees, the ability to model nonlinearity and threshold responses, and inclusion of complex interactions among predictor variables (Prasad et al. 2006). These models also have advantages over other machine learning models such as artificial neural networks because partial dependence plots give insight into conditioned responses to individual predictor variables (Cutler et al. 2007). An historical limitation to RF modeling was that only a single response variable (here, species) could be modeled, and scaling up to assemblages required stacking multiple independently developed models in a nonintegrated and computationally intensive fashion. This limitation was recently addressed with the advent of GF models (Ellis et al. 2012). In GF modeling, RF models are constructed for each species in a matrix of multiple species, and the relative importance of variables and locations of threshold responses along predictor variable gradients are provided at species and assemblage levels. This approach represents a powerful method

for determining how entire assemblages respond to environmental gradients while simultaneously incorporating individual species responses (Pitcher et al. 2011).

We fit GF models in R (R Core Team 2018) using the 'extendedForest' package, an extension of the 'randomForest' package (Liaw and Wiener 2002). We used a matrix of species occurrence data and fit classification-based models separately for each spatial scale and subregion combination (four models total) to test our hypothesis that landscape variables that correlate with fish assemblage structure differ across space and scales. For each model, we used the function 'gradientForest' with fish occurrence data as the response variable, used the 13 landscape alteration variables as predictor variables, constructed 500 trees, and included four randomly selected predictor variables as candidates for each split (Ellis et al. 2012). We used a series of diagnostic plots to assess relationships between landscape alterations and fish occurrences to measure the magnitude of ecological responses to landscape alterations. We plotted overall importance of landscape alteration variables using R^2 weighted importance, cumulative importance to illustrate responses to landscape alteration gradients averaged across all species, and model performance depicting out-of-bag error rate for each species for which the landscape alterations had some explanatory power (Ellis et al. 2012). Values for R^2 weighted importance represent average R^2 values across all species and therefore are generally smaller in magnitude compared with single-species R^2 values, but their relative magnitudes are nonetheless informative and equally interpretable. Finally, we transformed all environmental predictions from the GF model into a common biological scale to illustrate predicted fish assemblage composition based on landscape alteration data in a spatially explicit manner. We used the 'predict' function and landscape alteration data from

all sampled and unsampled stream segments to generate biological predictions and then ordinated results using principle components analysis with weighted species scores overlaid (Pitcher et al. 2011). This approach is comparable to direct ordination in that site scores, species scores, and landscape alteration data are simultaneously shown, but here, relationships are shown after accounting for nonlinearities and threshold responses by species. As with most ordination methodologies, a large number of axes are generated, and we retained only the first two for interpretation.

We mapped predictions for fish assemblage composition across the region. We used GF models for each of the two spatial scales in the two subregions to develop predictions for fish assemblage composition at all sampled and unsampled stream segments. We first filtered the data set of unsampled stream segments and removed any segments that had individual landscape alteration magnitudes greater than those in the subset of segments that were sampled for fishes, as well as stream segments with stream orders greater than three. This step was necessary to control for gradient lengths for natural (stream size) and anthropogenic gradients so that predictions were not made for streams outside the domain of our models. This resulted in the removal of highly urbanized stream segments in the Memphis, Tennessee and Jackson, Tennessee areas, as well as all large main-stem rivers. We clustered predictions from each model to improve interpretation using the 'clara' clustering function from the 'cluster' package (Maechler et al. 2018). This clustering technique is capable of handling large numbers of observations (Kaufman and Rousseeuw 1990), including 17,081 segments at the network catchment scale and 15,738 segments at the local catchment scale in the Mississippi basin and 6,961 segments at the network catchment scale and 6,973 segments at the local catchment scale in the Tennes-

see basin. The number of segments differed among scales within each basin because of exclusions of segments with large-magnitude landscape alterations, which differed across scales. We elected to use four clusters for each model because this number of clusters captured the major gradients in landscape alterations. Finally, we assigned predictions for assemblage composition to polylines from the NHD and mapped predictions as a means of producing spatially structured data useful for conservation planning.

Results

Landscape Alterations

Most landscape alterations occurred in both subregions, with few exceptions. No CAFO permits or mining permits occurred in the sampled catchments in the Mississippi basin, and no dams or CAFO permits occurred within the sampled catchments in the Tennessee basin. The dominant forms of land use in local catchments and network catchments were Crop, Hay, Dev1, and Dev5 (Table 1). The median values for land-use transformation to cultivated crops included more than 30% of the area in the Mississippi basin (0.31–0.37 across scales) but was less intense in the Tennessee basin (0.03–0.04 across scales). Conversely, median values for transformation to hay were largely consistent in the Tennessee (0.02–0.05 across scales) and Mississippi (0.05–0.08 across scales) basins. Development generally occurred to a greater extent in the Mississippi basin compared with the Tennessee basin, including Dev1, Dev5, and Pop.

Environmental Correlates for Fish Distributions

The most influential landscape alterations associated with fish distributions varied by basin and spatial scale. In the Mississippi basin, Crop, Hay, and Dev2 had the highest weighted importance at the network catch-

ment scale, but Dev1, Crop, and Pop became most important when data collection was scaled down to local catchments (Figure 3a). Among all 13 variables, weighted importance was higher at the network catchment scale for eight alterations and higher at the local catchment scale for five alterations. In the Tennessee basin, Crop, Hay, and Cross had the highest weighted importance at the network catchment scale, but Pop, Road, and Dev1 became most important when data collection was scaled down to local catchments (Figure 3b). Among all 13 variables, weighted importance was higher at the network catchment scale for eight alterations and higher at the local catchment scale for five alterations.

Cumulative importance plots highlighted linear (i.e., single species losses or gains) versus threshold (i.e., multiple species losses or gains) changes in assemblage composition and the scales at which these changes were most important for predicting fish assemblage structure. Assemblages changed in approximately linear patterns regardless of scale as the proportion of Crop increased at both network and local catchment scales in the Mississippi basin (Figure 4a), but in the Tennessee basin, Crop was more important at the network catchment scale than the local catchment scale and a threshold response in assemblage change was evident when 20–30% of catchments were cultivated (Figure

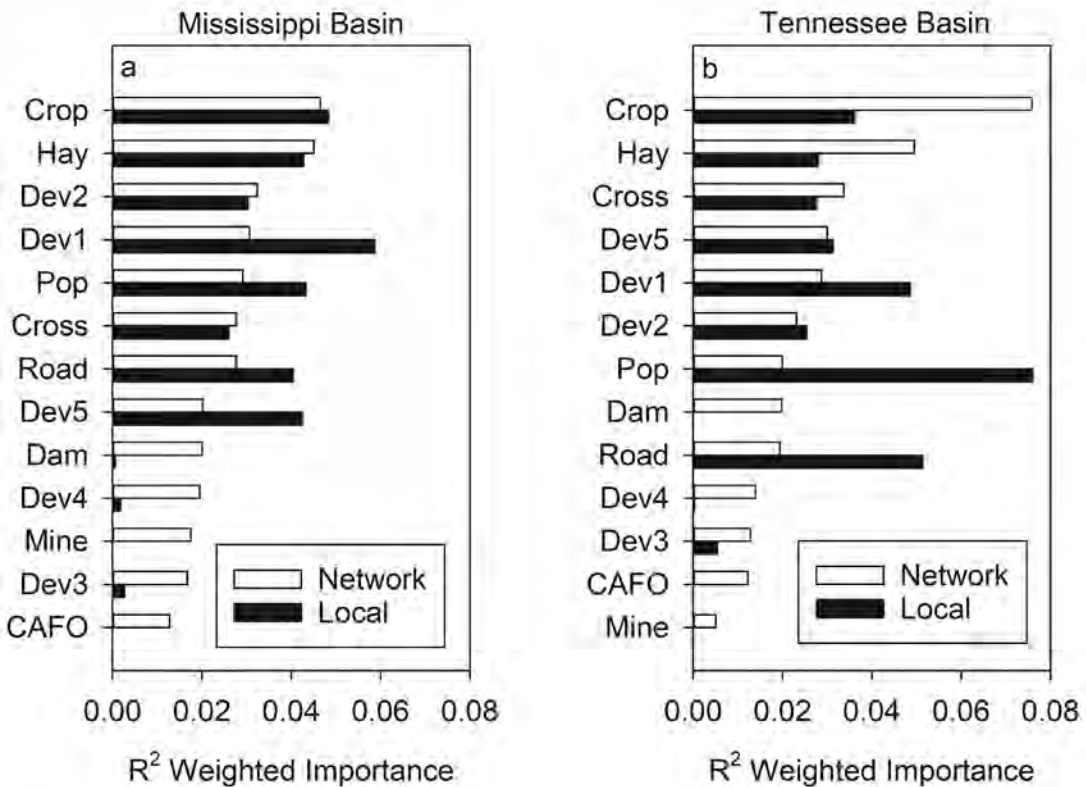


Figure 3. Influence of landscape alterations on stream fish assemblages as measured as R^2 weighted importance for gradient forest models fit to data from the (a) Mississippi and (b) Tennessee River basins at network catchment (white bars) and local catchment (black bars) scales. Variables are ranked by importance at the network catchment scale; see Table 1 for landscape alteration variable descriptions.

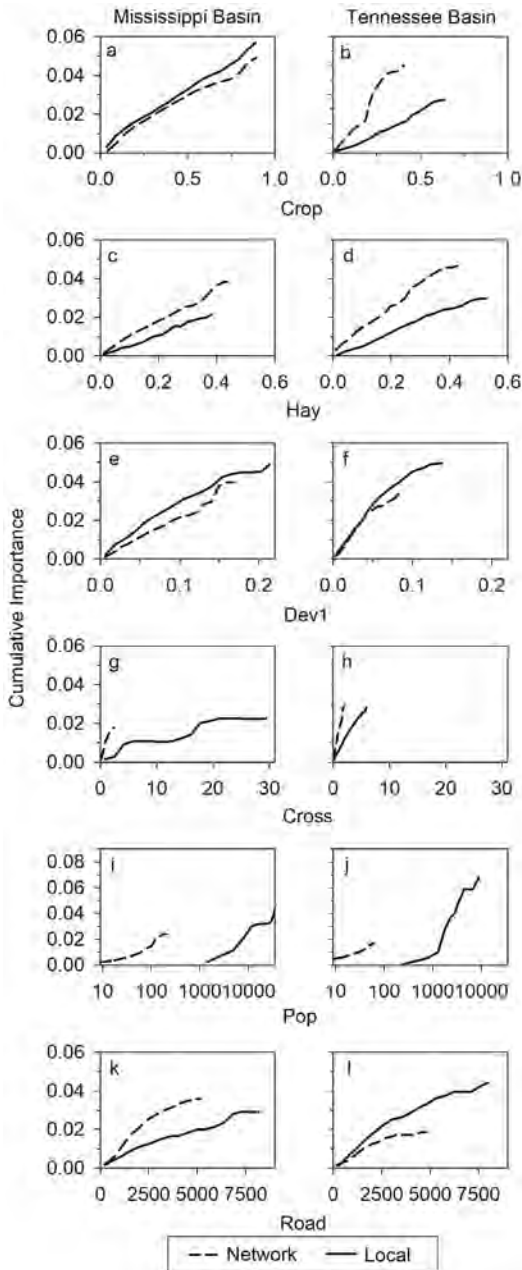


Figure 4. Change in fish assemblage composition across gradients in landscape alterations illustrated as cumulative importance plots from gradient forest models for the Mississippi and Tennessee River basins at network catchment (dashed lines) and local catchment (solid lines) scales. See Table 1 for landscape alteration variable descriptions; note panels (i) and (j) are shown on log scale.

4b). Assemblages in both the Mississippi and Tennessee basins changed in a linear pattern regardless of scale as proportions of Hay (Figure 4c, 4d) and Dev1 (Figure 4e, 4f) land uses increased, although Hay was more important at the network catchment scale and Dev1 was more important at the local catchment scale. Road crossing density was more important at the network catchment scale across both basins, but the range of magnitudes was smaller at the local catchment scale (Figure 4g, 4h). In the Mississippi basin, threshold changes in assemblage composition occurred when road-crossing densities ranged from 4 to 5 and 18–19 crossings/km² at both scales (Figure 4g). Assemblages changed in a curvilinear pattern before plateauing as human population density increased at both network and local catchment scales in the Mississippi and Tennessee basins, but a threshold was evident in the Mississippi basin when 30,000–39,000 people/km² were present in local catchments (Figure 4i, 4j). Road density was more important at the network catchment scale in the Mississippi basin (Figure 4k) but more important at the local catchment scale in the Tennessee basin (Figure 4l).

Species and Assemblage Patterns

Models had at least some explanatory power for 47 of 50 species in the Mississippi basin (Table 2) and 61 of 62 species in the Tennessee basin (Table 3). Box plots of random forest model performance were consistent between scales for the Mississippi and Tennessee basins (Figure 5). Among the top 10 species for which models explained the greatest amounts of variation in occurrence, model performance was either greater at the network catchment scale (3 in the Mississippi, 2 in the Tennessee) or was consistent between scales (7 in the Mississippi, 8 in the Tennessee). Among the remaining species in the Mississippi basin, network catchment-scale measurements performed best for 38% (14

Table 2. Common names, scientific names, identification code, random forest model performance measured as 1 - relative error rate (1 - RER), and transformed landscape alteration principal component (PC) scores along PC1 and PC2 for all fishes for which gradient forest models had some explanatory power in the Mississippi River basin at network catchment (NC) and local catchment (LC) spatial scales. Common names marked with an asterisk (*) are listed as imperiled or have limited distributions (<6 drainage units), according to Warren et al. (2000).

Common name	Scientific name	Code	1 - RER		Ordination scores			
			NC	LC	NC PC1	NC PC2	LC PC1	LC PC2
Yellow Bullhead	<i>Ameiurus natalis</i>	Amenat	0.20	0.38	0.0034	0.0001	0.0033	0.0038
Pirate Perch	<i>Aphredoderus sayanus</i>	Aphsay	0.00	0.02	0.0008	0.0055	0.0012	-0.0004
Bluntnose Shiner	<i>Cyprinella camura</i>	Cypcam	0.33	0.29	0.0055	0.0032	-0.0108	0.0053
Common Carp	<i>Cyprinus carpio</i>	Cypcar	0.46	0.36	0.0162	0.0396	0.0159	0.0172
Red Shiner	<i>Cyprinella lutrensis</i>	Cyplut	0.45	0.45	-0.0220	0.0021	-0.0232	-0.0175
Blacktail Shiner	<i>Cyprinella venusta</i>	Cypven	0.35	0.23	0.0217	-0.0087	0.0329	0.0002
Gizzard Shad	<i>Dorosoma cepedianum</i>	Dorcep	0.37	0.29	0.0076	-0.0114	0.0300	-0.0326
Eastern Creek Chubsucker	<i>Erimyzon oblongus</i>	Eriobl	0.36	0.36	-0.0190	-0.0026	-0.0164	0.0032
Grass Pickerel	<i>Esox americanus</i>	Esoame	0.25	0.25	0.0042	0.0145	0.0068	0.0192
Bluntnose Darter	<i>Etheostoma chlorosoma</i>	Ethchl	0.33	0.41	-0.0093	-0.0117	-0.0161	-0.0163
Slough Darter	<i>Etheostoma gracile</i>	Ethgra	0.45	0.45	-0.0118	-0.0013	-0.0090	-0.0056
*Brighteye Darter	<i>Etheostoma lyncium</i>	Ethlyn	0.37	0.30	0.0118	-0.0259	0.0042	-0.0199
Johnny Darter	<i>Etheostoma nigrum</i>	Ethnig	0.16	0.32	0.0057	0.0023	-0.0008	-0.0036
*Firebelly Darter	<i>Etheostoma pyrrhogaster</i>	Ethpyr	0.36	0.45	-0.0193	0.0000	-0.0347	-0.0086
Gulf Darter	<i>Etheostoma swaini</i>	Ethswa	0.30	0.30	-0.0212	-0.0085	0.0040	-0.0251
Blackstripe Topminnow	<i>Fundulus notatus</i>	Funnot	0.41	0.45	0.0289	-0.0170	0.0164	0.0190
Blackspotted Topminnow	<i>Fundulus olivaceus</i>	Funoli	0.23	0.23	0.0038	-0.0027	0.0008	0.0011
Cypress Minnow	<i>Hybognathus hayi</i>	Hybhay	0.41	0.41	-0.0149	0.0180	-0.0167	-0.0032
Northern Hog Sucker	<i>Hypentelium nigricans</i>	Hypnig	0.44	0.44	-0.0249	-0.0364	-0.0091	-0.0489
Channel Catfish	<i>Ictalurus punctatus</i>	Ictpun	0.43	0.37	0.0139	0.0058	0.0204	-0.0038
Green Sunfish	<i>Lepomis cyanellus</i>	Lepcya	0.43	0.37	-0.0002	-0.0064	0.0031	-0.0046
Warmouth	<i>Lepomis gulosus</i>	Lepgul	0.26	0.22	0.0104	-0.0134	0.0025	-0.0082
Orangespotted Sunfish	<i>Lepomis humilis</i>	Lephum	0.22	0.04	0.0021	-0.0038	0.0154	-0.0030
Bluegill	<i>Lepomis macrochirus</i>	Lepmac	0.46	0.36	0.0026	-0.0083	0.0046	-0.0043

Table 2. Continued

Common name	Scientific name	Code	1 - RER		Ordination scores					
			NC	LC	NC PC1	NC PC2	LC PC1	LC PC2		
Dollar Sunfish	<i>Lepomis marginatus</i>	Lepmar	0.36	0.25	0.0156	-0.0192	0.0097	0.0097	-0.0151	
Longear Sunfish	<i>Lepomis megalotis</i>	Lepmeg	0.37	0.31	0.0050	-0.0035	0.0117	0.0117	-0.0017	
Redear Sunfish	<i>Lepomis microlophus</i>	Lepmic	0.46	0.46	-0.0224	-0.0116	-0.0211	-0.0211	-0.0184	
Spotted Gar	<i>Lepisosteus oculatus</i>	Lepocu	0.37	0.37	-0.0143	-0.0354	-0.0051	-0.0051	-0.0444	
Ribbon Shiner	<i>Lythrurus fumeus</i>	Lytfum	0.34	0.30	0.0072	-0.0009	-0.0050	-0.0050	-0.0148	
Redfin Shiner	<i>Lythrurus umbratilis</i>	Lytumb	0.07	0.00	0.0045	-0.0050	0.0024	0.0024	0.0048	
Spotted Bass	<i>Micropertus punctulatus</i>	Micpun	0.30	0.30	0.0021	-0.0020	0.0150	0.0150	-0.0101	
Largemouth Bass	<i>Micropertus salmoides</i>	Micsal	0.23	0.27	0.0200	-0.0138	0.0221	0.0221	-0.0001	
Spotted Sucker	<i>Minytrema melanops</i>	Minmel	0.45	0.45	-0.0159	0.0009	-0.0336	-0.0336	0.0012	
Blacktail Redhorse	<i>Moxostoma poecilurum</i>	Moxpoe	0.25	0.33	-0.0144	-0.0012	0.0060	0.0060	-0.0239	
Golden Shiner	<i>Notemigonus crysoleucas</i>	Notchr	0.15	0.11	-0.0125	0.0316	-0.0277	-0.0277	0.0100	
*Orangefin Shiner	<i>Notropis ammophilus</i>	Notamm	0.46	0.36	-0.0394	-0.0336	-0.0273	-0.0273	-0.0269	
Emerald Shiner	<i>Notropis atherinoides</i>	Notath	0.37	0.43	0.0116	-0.0173	-0.0068	-0.0068	-0.0075	
Mimic Shiner	<i>Notropis volucellus</i>	Notvol	0.46	0.46	-0.0122	0.0125	-0.0041	-0.0041	0.0312	
Tadpole Madtom	<i>Noturus gyrinus</i>	Notgyr	0.36	0.52	0.0146	0.0053	-0.0050	-0.0050	0.0266	
*Least Madtom	<i>Noturus hildebrandi</i>	Nothil	0.25	0.35	-0.0246	0.0092	-0.0226	-0.0226	-0.0015	
Brindled Madtom	<i>Noturus miurus</i>	Notmiu	0.44	0.44	-0.0153	-0.0189	0.0182	0.0182	-0.0283	
Brown Madtom	<i>Noturus phaeus</i>	Notpha	0.17	0.03	-0.0256	-0.0200	-0.0083	-0.0083	-0.0324	
Pugnose Minnow	<i>Opsopoeodus emiliae</i>	Opsemi	0.46	0.46	-0.0185	-0.0174	-0.0312	-0.0312	-0.0238	
Dusky Darter	<i>Percina sciera</i>	Persci	0.42	0.42	-0.0159	-0.0085	0.0144	0.0144	-0.0247	
Suckermouth Minnow	<i>Phenacobius mirabilis</i>	Phemir	0.36	0.45	0.0547	-0.0310	0.0308	0.0308	0.0012	
Bullhead Minnow	<i>Pimephales vigilax</i>	Pimvig	0.30	0.36	-0.0142	0.0135	-0.0173	-0.0173	0.0034	
Creek Chub	<i>Semotilus atromaculatus</i>	Sematr	0.00	0.13	0.0127	0.0041	0.0071	0.0071	0.0140	

Table 3. Common names, scientific names, identification codes, random forest model performance measured as 1 - relative error rate (1 - RER), and transformed landscape alteration principal component (PC) scores along PC1 and PC2 for all fishes for which gradient forest models had some explanatory power in the Tennessee River basin at network catchment (NC) and local catchment (LC) spatial scales. Common names marked with an asterisk (*) are listed as imperiled or have limited distributions (≤ 6 drainage units) according to Warren et al. (2000).

Common name	Scientific name	Code	1 - RER		Ordination scores			
			NC	LC	NC PC1	NC PC2	LC PC1	LC PC2
Rock Bass	<i>Ambloplites rupestris</i>	Ambrup	0.36	0.18	-0.0168	-0.0176	0.0154	0.0163
Yellow Bullhead	<i>Ameiurus natalis</i>	Amenat	0.03	0.31	0.0103	0.0052	-0.0007	-0.0034
Pirate Perch	<i>Aphredoderus sayanus</i>	Aphsay	0.27	0.00	0.0005	0.0208	-0.0186	0.0046
Central Stoneroller	<i>Campostoma anomalum</i>	Camano	0.08	0.00	-0.0090	-0.0001	-0.0074	0.0065
Largescale Stoneroller	<i>Campostoma oligolepis</i>	Campul	0.19	0.21	-0.0035	-0.0093	0.0066	-0.0056
Southern Redbelly Dace	<i>Chrosomus erythrogaster</i>	Chrery	0.38	0.45	-0.0146	-0.0201	-0.0100	0.0100
Rosyside Dace	<i>Clinostomus funduloides</i>	Clifry	0.16	0.00	-0.0166	-0.0076	0.0030	0.0116
Banded Sculpin	<i>Cottus caroliniae</i>	Cotcar	0.23	0.04	-0.0177	-0.0131	0.0078	0.0110
Whitetail Shiner	<i>Cyprinella galactura</i>	Cyppal	0.46	0.46	0.0017	-0.0044	0.0381	0.0458
Spotfin Shiner	<i>Cyprinella spiloptera</i>	Cypspi	0.47	0.36	-0.0226	-0.0009	0.0112	-0.0059
Gizzard Shad	<i>Dorosoma cepedianum</i>	Dorcep	0.36	0.36	-0.0074	-0.0190	0.0425	0.0394
Creek Chubsucker	<i>Erimyzon oblongus</i>	Eriobl	0.36	0.40	-0.0006	0.0135	-0.0061	-0.0066
Grass Pickerel	<i>Esox americanus</i>	Esoame	0.32	0.40	0.0066	0.0166	0.0061	0.0019
Chain Pickerel	<i>Esox niger</i>	Esonig	0.47	0.47	0.0054	0.0125	-0.0202	0.0107
Greenside Darter	<i>Etheostoma blennioides</i>	Ethble	0.32	0.28	-0.0238	0.0013	0.0064	0.0317
Rainbow Darter	<i>Etheostoma caeruleum</i>	Ethcae	0.23	0.00	-0.0179	-0.0079	-0.0011	0.0124
Bluntnose Darter	<i>Etheostoma chlorosoma</i>	Ethchl	0.46	0.38	0.0396	0.0091	0.0236	-0.0055
*Fringed Darter	<i>Etheostoma crossotterum</i>	Ethcro	0.47	0.47	-0.0251	0.0051	-0.0186	0.0036
Fantail Darter	<i>Etheostoma flabellare</i>	Ethfla	0.01	0.12	-0.0065	-0.0027	-0.0043	0.0014
*Saffron Darter	<i>Etheostoma flavum</i>	Ethflav	0.26	0.29	-0.0198	-0.0120	0.0107	0.0054
Slough Darter	<i>Etheostoma gracile</i>	Ethgra	0.46	0.46	0.0462	0.0099	-0.0082	-0.0190
*Stripetail Darter	<i>Etheostoma kemicotti</i>	Ethken	0.47	0.47	-0.0199	-0.0132	0.0258	-0.0321
Johnny Darter	<i>Etheostoma nigrum</i>	Ethnig	0.46	0.38	0.0386	-0.0063	-0.0049	-0.0201
*Blackfin Darter	<i>Etheostoma nigripinne</i>	Ethnigri	0.46	0.46	-0.0284	0.0089	-0.0159	-0.0052
*Guardian Darter	<i>Etheostoma oophylax</i>	Ethoop	0.17	0.25	-0.0020	-0.0089	0.0079	-0.0142
*Redline Darter	<i>Etheostoma rufilineatum</i>	Ethruf	0.38	0.38	-0.0254	0.0023	0.0089	0.0017
Orangethroat Darter	<i>Etheostoma spectabile</i>	Ethspe	0.26	0.26	-0.0146	-0.0089	-0.0017	-0.0060
*Bandfin Darter	<i>Etheostoma zonistium</i>	Ethzoni	0.38	0.27	0.0277	0.0019	-0.0034	-0.0244
Northern Studfish	<i>Fundulus catenatus</i>	Funcat	0.28	0.15	-0.0156	-0.0191	0.0215	-0.0129

Table 3. Continued.

Common name	Scientific name	Code	1 - RER		Ordination scores			
			NC	LC	NC PC1	NC PC2	LC PC1	LC PC2
Blackstripe Topminnow	<i>Fundulus notatus</i>	Funnot	0.30	0.44	0.0378	0.0118	0.0108	-0.0196
Blackspotted Topminnow	<i>Fundulus olivaceus</i>	Funoli	0.15	0.01	0.0137	0.0004	0.0000	0.0003
Western Mosquitofish	<i>Gambusia affinis</i>	Gamaff	0.38	0.45	0.0184	0.0119	0.0094	0.0015
Northern Hog Sucker	<i>Hypentelium nigricans</i>	Hypnig	0.41	0.11	-0.0072	-0.0216	0.0153	0.0077
Green Sunfish	<i>Lepomis cyanellus</i>	Lepcya	0.38	0.31	-0.0017	-0.0019	0.0020	-0.0012
Warmouth	<i>Lepomis gulosus</i>	Lepgul	0.24	0.27	0.0082	-0.0030	0.0092	-0.0023
Orangespotted Sunfish	<i>Lepomis humilis</i>	Lephum	0.21	0.03	-0.0006	-0.0073	0.0169	-0.0023
Bluegill	<i>Lepomis macrochirus</i>	Lepmac	0.44	0.44	-0.0015	-0.0052	0.0028	-0.0020
Dollar Sunfish	<i>Lepomis marginatus</i>	Lepmar	0.32	0.28	0.0035	-0.0179	0.0460	0.0081
Longear Sunfish	<i>Lepomis megalotis</i>	Lepmeg	0.37	0.27	0.0013	-0.0098	0.0101	-0.0028
Redear Sunfish	<i>Lepomis microlophus</i>	Lepmic	0.33	0.33	0.0058	-0.0040	0.0247	0.0142
Striped Shiner	<i>Luxilus chrysocephalus</i>	Luxchr	0.30	0.14	-0.0033	-0.0160	0.0135	-0.0003
Scarlet Shiner	<i>Lythrurus fasciolaris</i>	Lytfas	0.31	0.35	-0.0128	-0.0048	-0.0096	-0.0009
Ribbon Shiner	<i>Lythrurus fumeus</i>	Lytfum	0.47	0.47	0.0735	0.0319	0.0078	-0.0029
Redfin Shiner	<i>Lythrurus umbratilis</i>	Lytumb	0.44	0.44	0.0489	0.0163	-0.0120	-0.0120
Smallmouth Bass	<i>Micropterus dolomieu</i>	Micdol	0.53	0.24	-0.0244	-0.0017	0.0073	0.0155
Spotted Bass	<i>Micropterus punctulatus</i>	Micpun	0.37	0.23	0.0117	-0.0392	0.0385	0.0125
Largemouth Bass	<i>Micropterus salmoides</i>	Micsal	0.14	0.17	-0.0024	-0.0037	0.0120	0.0012
Spotted Sucker	<i>Minytrema melanops</i>	Minmel	0.37	0.42	0.0116	-0.0017	0.0072	0.0080
Golden Redhorse	<i>Moxostoma erythrurum</i>	Moxery	0.28	0.41	-0.0169	-0.0200	0.0444	0.0351
Golden Shiner	<i>Notemigonus crysoleucas</i>	Notchr	0.44	0.32	0.0160	-0.0036	-0.0103	-0.0157
Emerald Shiner	<i>Notropis atherinoides</i>	Notath	0.38	0.45	0.0123	-0.0079	-0.0035	-0.0011
Bigeye Shiner	<i>Notropis boops</i>	Notboo	0.47	0.47	-0.0153	-0.0148	0.0167	-0.0049
Mimic Shiner	<i>Notropis volucellus</i>	Notvol	0.32	0.38	0.0211	-0.0025	0.0370	-0.0273
Slender Madtom	<i>Noturus exilis</i>	Notexi	0.38	0.44	-0.0034	-0.0299	-0.0102	0.0098
*Least Madtom	<i>Noturus hildebrandi</i>	Nothil	0.47	0.47	0.0412	0.0254	-0.0162	-0.0057
Tennessee Shiner	<i>Notropis leuciodus</i>	Notleu	0.43	0.43	-0.0114	-0.0351	0.0305	0.0016
Brown Madtom	<i>Noturus phaeus</i>	Notpha	0.46	0.46	0.0803	0.0491	-0.0134	-0.0081
Common Logperch	<i>Percina caprodes</i>	Percap	0.34	0.12	-0.0212	0.0127	0.0020	0.0049
Bluntnose Minnow	<i>Pimephales notatus</i>	Pimnot	0.40	0.40	0.0163	-0.0157	0.0199	0.0045
Blacknose Dace	<i>Rhinichthys atratulus</i>	Rhibot	0.35	0.31	-0.0258	0.0070	-0.0266	0.0158
Creek Chub	<i>Semotilus atromaculatus</i>	Sematr	0.00	0.21	-0.0009	0.0047	-0.0021	0.0052

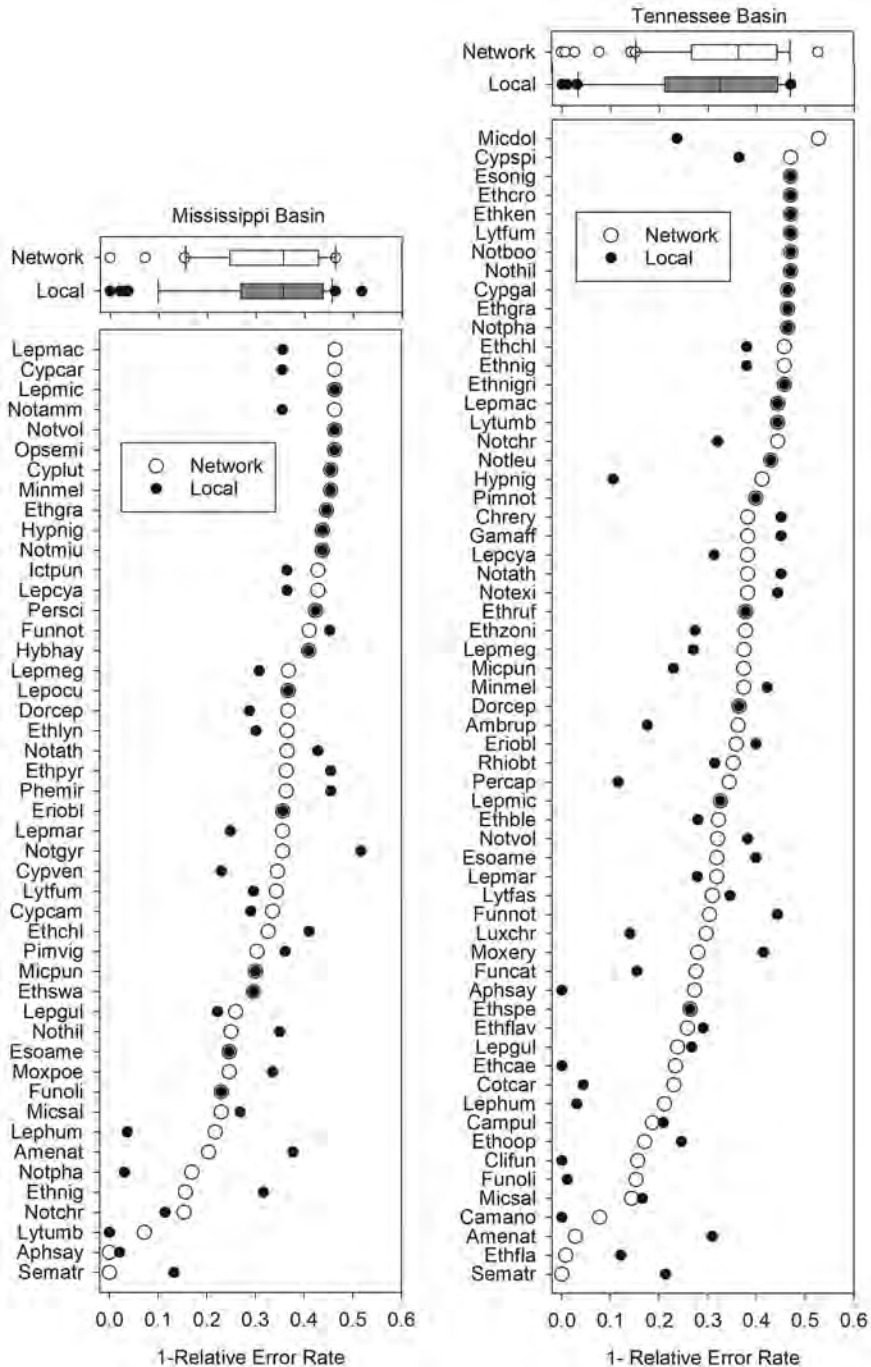


Figure 5. Performance of random forest models developed for species during gradient forest model fitting measured as 1-relative error rate (interpreted as with R^2) for data from the Mississippi and Tennessee River basins at network catchment (white boxes and circles) and local catchment (gray/black boxes and circles) scales. Box plots show the distributions for all species. Only species for which models had some explanatory power are shown; see Tables 2 and 3 for description of species codes.

of 37), local catchment-scale measurements performed best for 38% (14 of 37), and both scales produced equally accurate models for 24% (9 of 37). Among the remaining species in the Tennessee basin, network catchment-scale measurements performed best for 43% (22 of 51), local catchment-scale measurements performed best for 37% (19 of 51), and both scales produced equally accurate models for 20% (10 of 51).

Seventy percent of the variation in assemblage composition predicted by the network catchment GF model in the Mississippi basin was captured in PC1 (46%) and PC2 (24%). The first PC represented an agricultural gradient with catchments characterized by higher proportions of Hay land use arranged negatively and network catchments characterized by higher proportions of Crop land use arranged positively (Figure 6a). The second PC represented a development gradient with network catchments having greater densities or coverages by Road, Dev1, Dev2, Pop, Cross, and Dev 5 arranged positively and network catchments with lower magnitudes for all of those alterations arranged negatively. Along those gradients, predictions for fish assemblage composition clustered as four groups illustrated assemblage variation among catchments with low, medium, and high urban development as well as high Crop coverage (Figure 6b). Weighted species scores illustrated the major components of assemblage change across those gradients, including prevalence of Common Carp, Golden Shiner, and Grass Pickerel in Crop streams and prevalence of Suckermouth Minnow, Blackstripe Topminnow, and Largemouth Bass in heavily developed streams (Figure 6c). Least developed streams were characterized by high occurrences of Firebelly Darter, Gulf Darter, and Brown Madtom.

Sixty-nine percent of the variation in assemblage composition predicted by the local catchment GF model in the Mississippi basin

was captured in PC1 (45%) and PC2 (24%). The first PC represented an agricultural gradient, with local catchments characterized by a higher proportion of Hay land use arranged negatively and local catchments characterized by a higher proportion of Crop land use arranged positively (Figure 6d). The second PC represented an urban to rural gradient, with local catchments characterized by development, such as Dev1, Road, Dev5, and Dev2, arranged positively and local catchments with high population density arranged negatively. Along these gradients, predictions for fish assemblage composition clustered into four groups illustrated assemblage variation among local catchments, with low, medium, and high urban development coverage as well as high Crop coverage (Figure 6e). Weighted species scores illustrated the major components of assemblage change across these gradients, including prevalence of Common Carp, Mimic Shiner, and Tadpole Madtom in Crop streams, and Suckermouth Minnow, Blacktail Shiner, and Warmouth in rural streams (Figure 6f). Least developed streams were characterized by high occurrences of Orangefin Shiner, Northern Hog Sucker, and Spotted Gar.

Seventy-three percent of variation in assemblage composition predicted by the network catchment GF model in the Tennessee basin was captured in PC1 (49%) and PC2 (24%). The first PC represented a development gradient, with network catchments characterized by little urban development arranged negatively and network catchments characterized by a higher proportion of Hay, Crop, Dev1, and Dev5 land use arranged positively (Figure 7a). The second PC represented an agricultural gradient, with network catchments characterized by higher proportions of Hay arranged positively and network catchments characterized by higher proportions of Crop land use arranged negatively. Along these gradients, predictions for

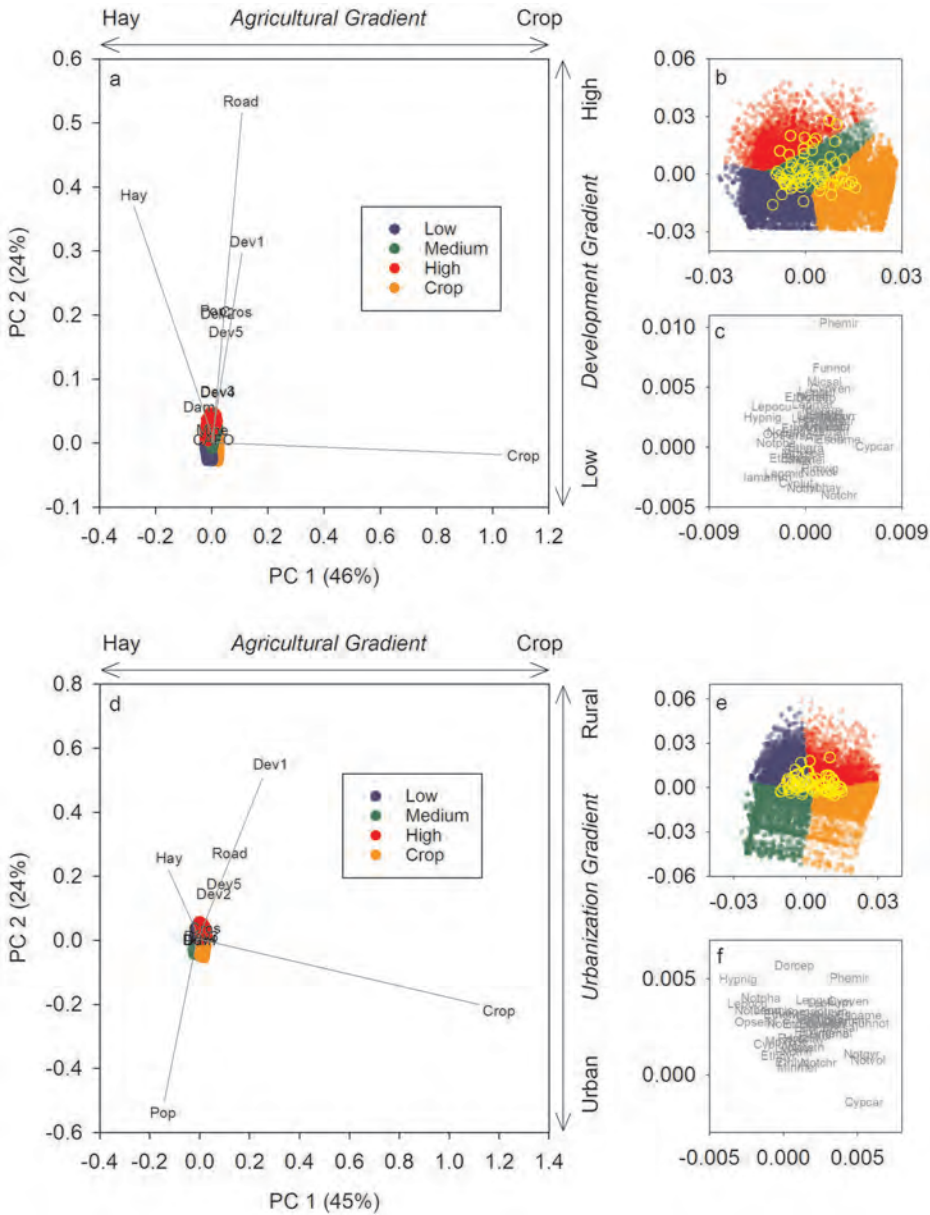


Figure 6. Principle component (PC) plot of biologically transformed landscape alteration variables illustrating predicted fish assemblage composition for stream segments in the Mississippi River basin at (a–c) network catchment and (d–f) local catchment scales. Panels (a) and (d) illustrate latent PC gradients (% variation explained by each) in predicted assemblage composition developed using gradient forest models, 13 landscape alteration variables (see Table 1 for definitions), and fish assemblage data. Assemblage compositions clustered into four groups illustrate stream segments affected by low (blue), medium (green), or high (red) development as well as cultivated crop land use (orange). Panels (b) and (e) illustrate a close up of the data cloud as well as the distribution of segments with fish assemblage samples (yellow circles) used in model development. Panels (c) and (f) illustrate weighted species scores; see Table 2 for species code descriptions.

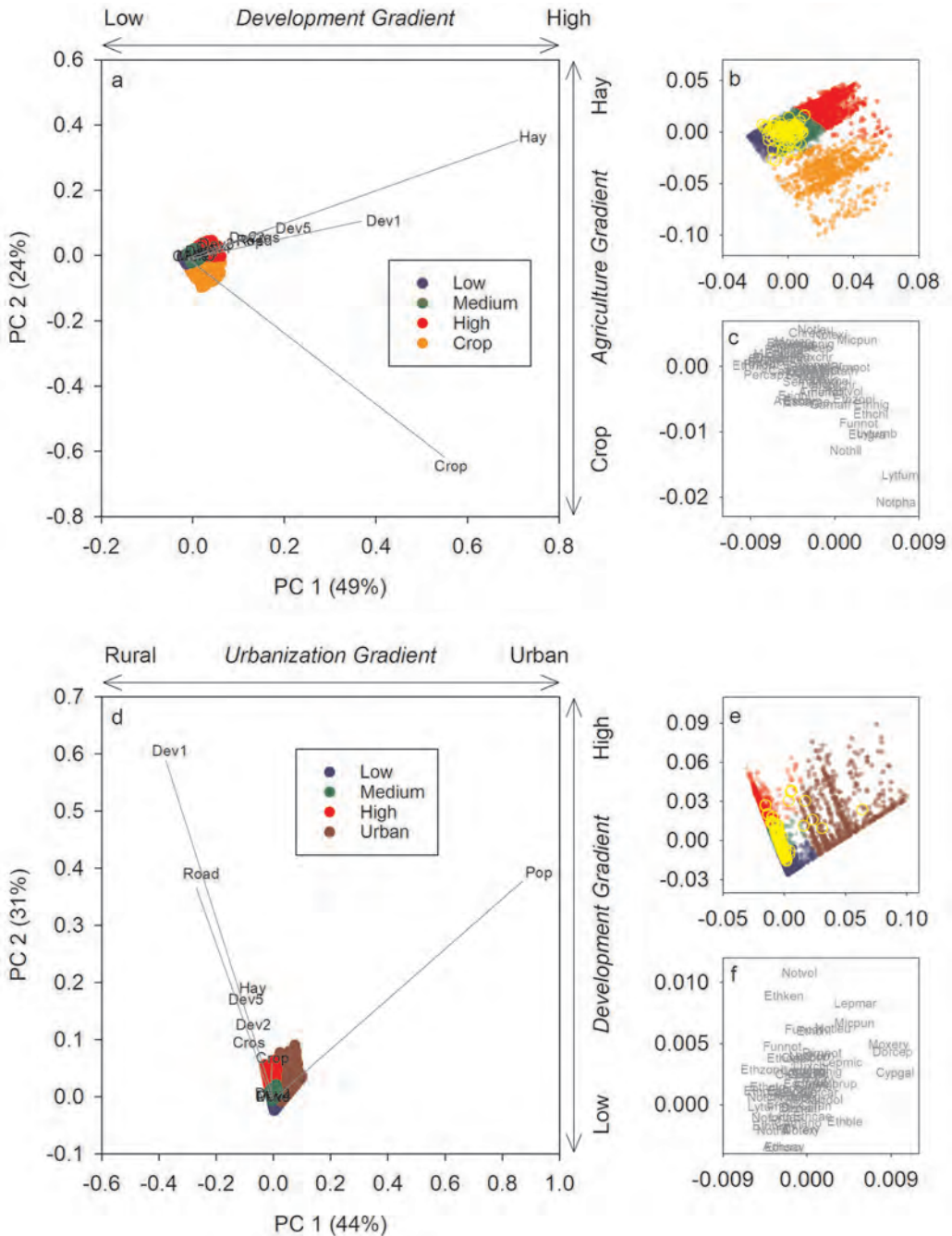


Figure 7. Principle component (PC) plot of biologically transformed landscape alteration variables illustrating predicted fish assemblage composition for stream segments in the Tennessee River basin at (a-c) network catchment and (d-f) local catchment scales. Panels are as in Figure 6 except that (d) illustrates assemblage compositions clustered into four groups to illustrate stream segments affected by low (blue), medium (green), or high (red) development as well as high human population density (dark red); see Table 3 for species code descriptions.

fish assemblage composition clustered into four groups illustrated assemblage variation among network catchments, with low, medium, and high urban development as well as high Crop coverage (Figure 7b). Weighted species scores illustrated the major components of assemblage change across these gradients, including prevalence of Brown Madtom, Ribbon Shiner, and Least Madtom in Crop streams, and Spotted Bass, Slender Madtom, and Bluntnose Minnow in highly developed streams (Figure 7c). Least developed streams were characterized by high occurrences of Blackfin Darter, Blacknose Dace, and Redline Darter.

Seventy-five percent of the variation in assemblage composition predicted by the local catchment GF model in the Tennessee basin was captured in PC1 (44%) and PC2 (31%). The first PC represented an urbanization gradient, with catchments characterized by rural developments such as Dev1, Road, Hay, and Dev5 arranged negatively and urban catchments with higher population density arranged positively (Figure 7 d). The second PC represented a development gradient, with catchments characterized by high proportions of Dev1, Hay, Dev2, and Dev5, as well as high densities of Road and Cross arranged positively and catchments with low values for each of these alterations arranged negatively. Along these gradients, predictions for fish assemblage composition clustered into four groups illustrated assemblage variation among catchments, with low, medium, and high urban development as well as high population density (Figure 7e). Weighted species scores illustrated the major components of assemblage change across these gradients, including prevalence of Mimic Shiner, Stripetail Darter, and Blackstripe Topminnow in rural streams and Gizzard Shad, Whitetail Shiner, and Golden Redhorse in urban streams (Figure 7f). Least developed streams were characterized by high occurrences of Blacknose

Dace, Fringed Darter, and Least Madtom.

Mapping Predictions

We mapped the spatial distribution of predicted assemblage compositions across the two basins at network and local catchment scales. At the network catchment scale in the Mississippi basin, a large swath of agriculturally induced alterations to stream fish assemblages was clear, but this swath was interrupted by intact riparian zones along tributaries near larger rivers (Figure 8). To the east and south of the agriculturally dominated area was a region characterized by a mix of low- and medium-development network catchments fragmented by roads. At the network catchment scale in the Tennessee basin, agriculturally affected fish assemblages attenuated in an easterly direction, although assemblages affected by urban development were centered around urban areas. At the local catchment scale in the Mississippi basin, the same swath of agriculturally influenced fish assemblages was still evident, although a pattern of development-induced alterations to fish assemblages in close proximity to this swath was apparent (Figure 9). In the Tennessee basin, local catchments with minimally altered fish assemblages were distributed to the east, whereas assemblages affected by urban development and human population density increased to the west and along corridors of major roadways.

Discussion

Our study provides strong evidence for spatial variation in relationships between landscape alterations and stream fish assemblages but mixed evidence for an effect of the selected scales on these relationships. Our first hypothesis was that ecological responses to landscape alterations would vary across space because landscape alterations are not spatially uniform. This hypothesis was supported by spatial segregation of fish assemblages af-

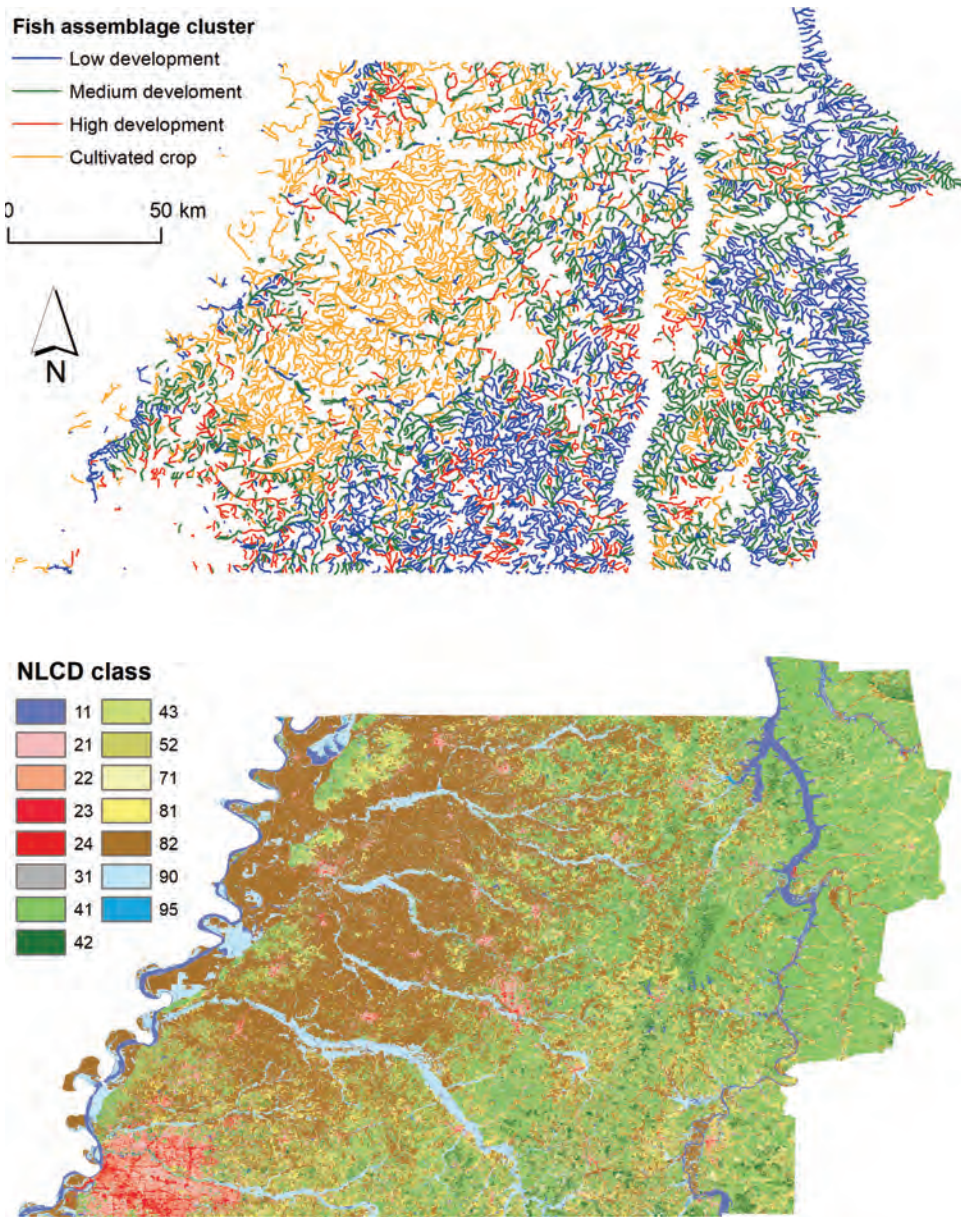


Figure 8. Map of predicted fish assemblage composition based on gradient forest models for stream segments in the Mississippi and Tennessee River basins at the network catchment scale (upper) and land uses from the National Land Cover Database (NLCD; lower). Colors in the upper panel represent predicted fish assemblages clustered into those primarily affected by low development (blue), medium development (green), high development (red), and cultivated crops (orange). Colors in the lower panel are from Homer et al. (2015) and represent land-use classes, including 11 (open water), 21 (developed, open space), 22 (developed, low intensity), 23 (developed, medium intensity), 24 (developed, high intensity), 31 (barren land), 41 (deciduous forest), 42 (evergreen forest), 43 (mixed forest), 52 (shrub/scrub), 71 (grassland), 81 (pasture/hay), 82 (cultivated crops), 90 (woody wetlands), and 95 (emergent herbaceous wetlands).

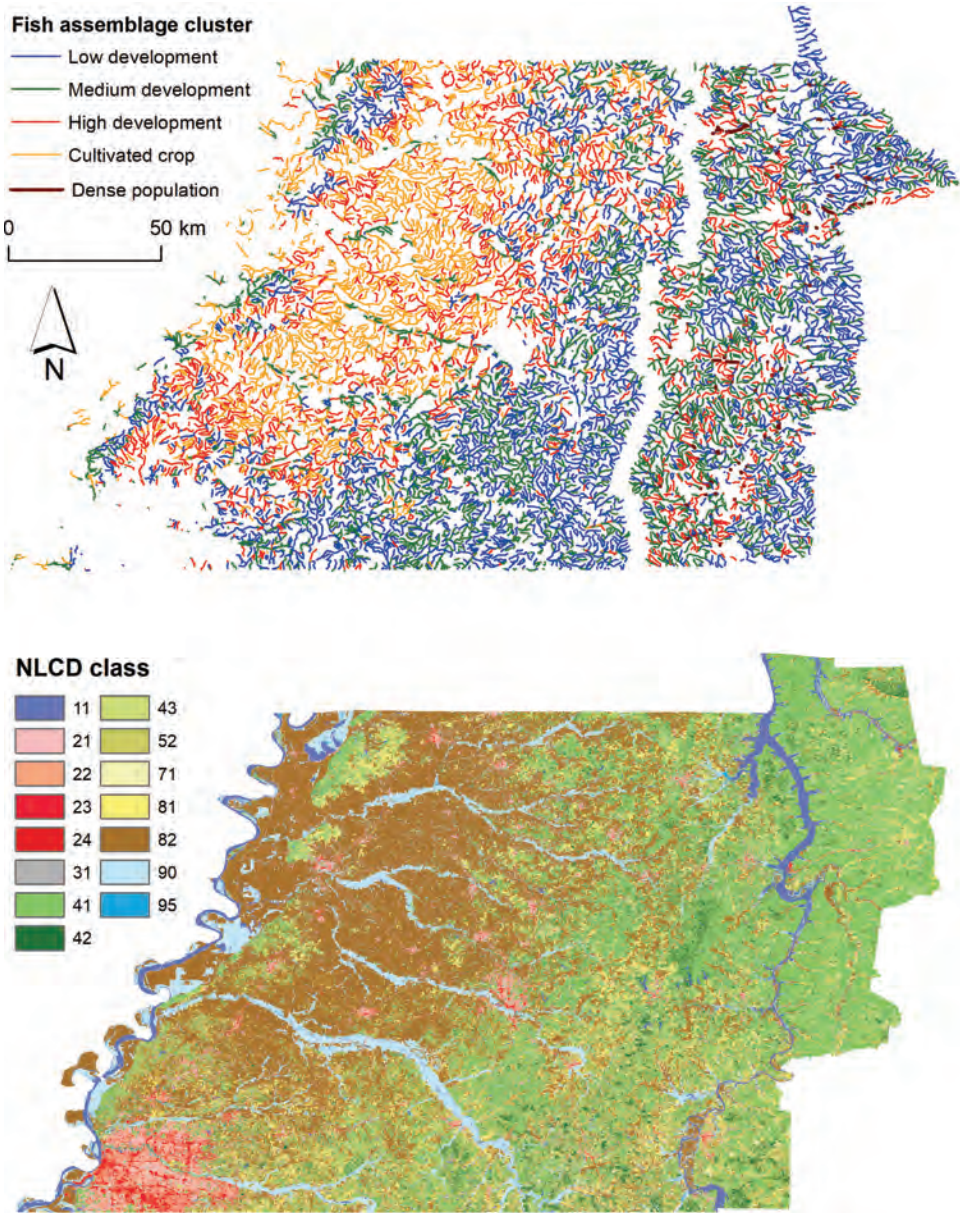


Figure 9. Map of predicted fish assemblage composition based on gradient forest models for stream segments in the Mississippi and Tennessee River basins at the local catchment scale (upper) and land uses from the National Land Cover Database (NLCD; lower). Colors represent predicted fish assemblages clustered into those primarily affected by low development (blue), medium development (green), high development (red), cultivated crops (orange), and high human population density (dark red). Colors in the lower panel are from Homer et al. (2015) and represent land use classes, including 11 (open water), 21 (developed, open space), 22 (developed, low intensity), 23 (developed, medium intensity), 24 (developed, high intensity), 31 (barren land), 41 (deciduous forest), 42 (evergreen forest), 43 (mixed forest), 52 (shrub/scrub), 71 (grassland), 81 (pasture/hay), 82 (cultivated crops), 90 (woody wetlands), and 95 (emergent herbaceous wetlands).

ected by low, medium, and high levels of urban development caused by road construction and impervious surfaces as well as agricultural land use. Previous works have demonstrated spatial variation in fish assemblage response to roads (Trombulak and Frissell 2000; Leitão et al. 2018) and agricultural land use (Leitão et al. 2018; Bierschenk et al. 2019), but the question of how scale might influence these relationships remains a focal research area (Strayer et al. 2003; Kautza and Sullivan 2015; Pease et al. 2015). Our second hypothesis was that the magnitude of ecological responses to landscape alterations would not be consistent when landscape alterations were measured at the network versus local catchment scale. This expectation was based on a growing body of research directed at understanding the relative influences of nearby versus far-upstream landscape alterations on stream fishes (Wang et al. 2001, 2003; Gido et al. 2006; Hoeinghaus et al. 2007; Sály et al. 2011; Marzin et al. 2013; Macedo et al. 2014; Leal et al. 2016; Leitão et al. 2018). Our results only partly supported our second hypothesis because fish assemblage patterns were largely consistent between network and local catchment scales when mapped across the landscape, yet the identities of the most important landscape alterations used in developing spatial predictions and the most responsive fish species varied with scale. Agricultural land uses such as crop and hay were the most important for describing fish assemblage distributions at the network catchment scale, whereas low-intensity development and human population density were most important at the local catchment scale. Combined, our results provide insight into landscape-riverscape linkages that could be included in management planning to advance conservation of freshwater biota (Strayer et al. 2003; Boyd et al. 2008; Kautza and Sullivan 2015).

Including two levels of organizational complexity (species and assemblages) provided inferences not attainable through species-

or assemblage-only approaches. The majority of scaling studies in freshwater ecosystems focus on space, time, or a combination of space and time without varying the level of organizational complexity in the response variable. That is, focus is generally on either a single species or assemblage composition. Despite their long history (Caughley 1994), single-species assessments have become less common with the rise of assessments of ecological condition through multimetric indices (Karr 1981; Ruaro and Gubiani 2013; Wellemeyer et al. 2018). However, management of ecological condition cannot ignore the needs of individual species when management plans are developed (Collares-Pereira and Cowx 2004). Consequently, ensemble approaches in which multiple levels of organizational complexity are considered stand the best chance for developing the robust information required for management planning (Olden 2003). The GF models employed here address this need directly by extending single-species RF models into the multispecies realm (Ellis et al. 2012). Our results suggest that multiple species were characteristic of the assemblages inhabiting stream segments affected by a variety of landscape alterations, and these species may represent either indicator or surrogate species. Indicator species allow for targeted monitoring and reduced sampling efforts at the assemblage level to gain the same level of information (Dufrêne and Legendre 1997), whereas surrogate species are defined as those responding in a similar fashion as those of conservation concern but are more easily monitored (Caro and O'Doherty 1999). We found several regionally endemic or listed species that were representative of least-altered stream segments and could be used as ecological indicators (see Tables 2 and 3) as well as nonlisted fishes occupying the same habitats that could be monitored in their place as surrogate species. This promotes efficiencies in resource allocation by

reducing the level of effort required to assess or monitor ecological condition and is a level of insight that would not have been possible if we had used a single-species approach. Another benefit of the GF approach is that species for which models have little explanatory power can be identified and inference appropriately constrained. This is a limitation of most direct-ordination assemblage ecology methods that provide species scores, but no insight into how well variation in species occurrence is actually described by the model. Among the species for which GF models explained the most variation in occurrence, local catchment- and network catchment-scale models captured identical levels of variation for most of these species across both basins. These findings suggest consistency in species responses to landscape alterations measured at both local and network catchment scales, a finding reported by some previous researchers (Hoeinghaus et al. 2007; Macedo et al. 2014; Leal et al. 2016). However, other studies suggest that species are responsive to landscape alterations measured at specific scales (Wang et al. 2001, 2003) or across a gradient of scales (Labbe and Fausch 2000). Thus, the question remains: which is the most appropriate scale for measuring landscape alterations? The answer to this question is most likely dependent upon a number of contexts related to scaling.

Scale is “the central problem in biology” (Levin 1992) and remains a challenge for effective management of biodiversity (Boyd et al. 2008). Ecological investigations with a focus on scale are best conducted by maintaining consistent predictor and response variables while varying some component of scale (Allen and Starr 2017). We conducted a study with a focus on scale (*sensu* Allen and Starr 2017) by maintaining consistent landscape alterations as predictor variables, fish species/assemblage occurrence as response variables, and a fixed spatial extent, but we varied the

grain size used to assemble landscape alterations. The two grain sizes we assessed, network catchment and local catchment, are commonly included in multiscale assessments comparing effects of nearby versus distant-upstream landscape alterations (Ward 1998; Wiens 2002; Allan 2004). In theory, nearby landscape alterations should have a greater effect on stream fishes compared with distant alterations if influences are diluted by flow or distance (e.g., Kinsolving and Bain 1993), but this expectation might shift when alterations are classified as point-source versus diffuse-source alterations (Lowrance and Sheridan 1985). Point-source alterations are known to exert strong local-scale influences on stream fishes at the location where the alteration enters the stream (Meyer et al. 2005), but diffuse-source alterations can be more challenging to detect. This is, in part, because diffuse-source alterations operate across broader spatiotemporal scales and do not enter streams at a single location. Agricultural land use is a well-studied form of diffuse-source landscape alteration and was generally of greatest importance at the broader network-catchment grain size in our study. In contrast, urban streams and impervious surface runoff are considered point-source disturbances because water is channeled into streams at specific locations, either through stormwater discharge points or culverts (Walsh et al. 2005). In our study, multiple measures of urban or impervious cover alterations ranked most important at the finer local-catchment grain size, including Pop, Dev1, and Road. In reality, fish distributions are governed by interactions among alterations at multiple spatial and temporal scales (e.g., Harding et al. 1998), and our results suggest that mitigating effects of network-scale agricultural activities and local catchment-scale urban development activities might benefit conservation of stream fishes across the region.

Additional Research and Management Needs

Our study informs conservation efforts by assessing potential fish assemblage composition (and indirectly, ecological condition) and the most influential landscape alterations across a large region of mostly unsampled streams. These results can guide decision making regarding scale-specific prioritization of fish conservation resources and funding allocations. For management goals involving the preservation of currently intact stream segments (i.e., conservation sensu Dauwalter et al. 2010), targeting the stream segments identified here as experiencing low development at either network or local catchment scales might be appropriate. For management goals involving rehabilitating natural conditions (i.e., rehabilitation sensu Dauwalter et al. 2010) through near-term, local-scale actions such as riparian planting, bank stabilization, or channel redesign (see Kwak and Freeman 2010 for other examples), targeting stream segments identified as experiencing medium or high urban development at the local catchment scale might be most appropriate. But not if the network catchment is heavily altered (Hughes et al. 2014). The greater challenge will ultimately involve addressing broadscale improvements in agriculturally dominated network catchments. Agriculturally dominated network catchments were common in portions of our study area and often require substantial conservation practice implementation rates (i.e., >50% of their catchment areas) to reduce stressors impairing fish assemblages (Fore et al. 2017; Scavia et al. 2017). However, in these agriculturally dominated systems, it is likely that combinations of network catchment- and local catchment-scale (e.g., riparian planting) interventions could improve conservation outcomes (Sowa et al. 2016). This is especially true given the large number of stressors that influence stream ecosystems but were not measured in this study

(Ormerod et al. 2010). Determining where to target those actions is a management need partly identified in our study. It is only partly identified because although clear patterns existed for relationships between landscape alterations and fish assemblages, we emphasize that the predicted assemblage clusters shown in Figures 8 and 9 are only hypothesized conditions that require validation. This validation is possible through additional research targeting sampling at currently unsampled locations and comparing the observed fish assemblage with predictions generated here. Other future directions for research might include mixing data measured at multiple spatial scales to identify the optimum scale(s) for assessing individual landscape alterations, as well as historical land uses that might have had unmeasured influences on the patterns we observed. For example, Harding et al. (1998) assessed 14 different spatial scales and the temporal influences of land use on several measures of fish and invertebrate diversity and, generally, found that historic catchment-scale land use best predicted present-day assemblages. If we better understand scales at which landscape alterations influence fish assemblages, conservationists could develop more effective conservation strategies. Future studies should seek to derive more explicitly how landscape alterations and management actions are influenced by spatial scale and to identify related economic tradeoffs (Keeler et al. 2012).

Challenges and Policy Implications

This study provides insights about how policies could be improved to more effectively address conservation challenges. In both basins, cultivated crop agriculture had the largest influence on ecological condition at the network catchment scale. In the United States, these lands are nearly all privately owned and implementation of conservation practices on these lands is nearly entirely done on a volun-

tary basis. Several studies have demonstrated that addressing alterations from cultivated crop agriculture requires high implementation rates of conservation practices, and current cost-share programs are insufficient to address the magnitude of the problem (e.g., Sowa et al. 2016; Fore et al. 2017; Scavia et al. 2017). That is, there is not enough public funding to pay for widespread incentive-based adoption of agricultural conservation practices. Therefore, increasing adoption of conservation practices in these landscapes requires developing and funding new research and technologies that seek to maximize both on-farm economic and environmental outcomes, such that voluntary adoption of these practices is greatly improved. At the local catchment scale, we identified impervious surfaces and road crossings as stressors to ecological condition. Though we did not evaluate specific stresses caused by these alterations, other researchers have found that traditional approaches to managing these types of infrastructure could be improved by developing policies and practices that employ green infrastructure techniques (Shafer et al. 2013; Vogel et al. 2015). For example, road crossings are often barriers to fish passage and can negatively affect fish assemblage structure (Perkin and Gido 2012; Leitão et al. 2018), but new culvert designs promote fish passage while reducing culvert maintenance (Gillespie et al. 2014). In fact, simultaneous ecological and economic benefits associated with culvert replacement are an effective solution to conservation challenges associated with roads (Sleight and Neeson 2018). Similarly, most existing stormwater management infrastructure occurs in highly populated areas and is designed to rapidly move stormwater to lotic systems, which can exacerbate downstream flooding issues in municipalities and often negatively affects fish assemblages (Walsh et al. 2005). Developing policies and funding sources that prioritize stormwater retention and infiltration can reduce many of these ecological

effects and benefit urbanized areas that require improved stormwater management (Roy et al. 2008). Finally, the diversity of stream fishes in western Tennessee is still intact and few extinctions have occurred (Etnier and Starnes 1993), meaning that there is still time to rise to the challenge of effective stream fish conservation management in this and other regions. Our work provides examples for how new statistical innovations can be applied to conservation challenges to establish where management efforts might be allocated in the future.

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