Articles

Long-Term Monitoring Data Provide Evidence of Declining Species Richness in a River Valued for Biodiversity Conservation

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Abstract

Free-flowing river segments provide refuges for many imperiled aquatic biota that have been extirpated elsewhere in their native ranges. These biodiversity refuges are also foci of conservation concerns because species persisting within isolated habitat fragments may be particularly vulnerable to local environmental change. We have analyzed long-term (14- and 20-y) survey data to assess evidence of fish species declines in two southeastern U.S. rivers where managers and stakeholders have identified potentially detrimental impacts of current and future land uses. The Conasauga River (Georgia and Tennessee) and the Etowah River (Georgia) form free-flowing headwaters of the extensively dammed Coosa River system. These rivers are valued in part because they harbor multiple species of conservation concern, including three federally endangered and two federally threatened fishes. We used data sets comprising annual surveys for fish species at multiple, fixed sites located at river shoals to analyze occupancy dynamics and temporal changes in species richness. Our analyses incorporated repeated site-specific surveys in some years to estimate and account for incomplete species detection, and test for species-specific (rarity, mainstem-restriction) and year-specific (elevated frequencies of low- or high-flow days) covariates on occupancy dynamics. In the Conasauga River, analysis of 26 species at 13 sites showed evidence of temporal declines in colonization rates for nearly all taxa, accompanied by declining species richness. Four taxa (including one federally endangered species) had reduced occupancy across the Conasauga study sites, with three of these taxa apparently absent for at least the last 5 y of the study. In contrast, a similar fauna of 28 taxa at 10 sites in the Etowah River showed no trends in species persistence, colonization, or occupancy. None of the tested covariates showed strong effects on persistence or colonization rates in either river. Previous studies and observations identified contaminants, nutrient loading, or changes in benthic habitat as possible causes for fish species declines in the Conasauga River. Our analysis provides baseline information that could be used to assess effectiveness of future management actions in the Conasauga or Etowah rivers, and illustrates the use of dynamic occupancy models to evaluate evidence of faunal decline from time-series data.

Keywords: freshwater fishes; occupancy dynamics; southeastern U.S.; species loss

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Introduction

Natural resource managers face a growing challenge to conserve biodiversity and the biological integrity of natural systems as climate change and human demands for resources intensify. Freshwater fauna exemplify this challenge. In many parts of the world, free-flowing river systems have been dammed, diverted, channelized, or altered by runoff from human activities to the extent that native riverine biota now persist only in isolated headwaters or river fragments between impoundments (Dudgeon 2000; Pringle et al. 2000; Strayer and Dudgeon 2010). In many cases, these isolated portions of river systems provide the least-disturbed remaining habitats and the best opportunities to conserve species that have been extirpated elsewhere in their native ranges. Within such biodiversity refuges, however, species may be particularly vulnerable to local environmental change. Thus, monitoring data and analyses that allow managers to detect and diagnose species declines can become essential to effective conservation.

The Conasauga River in northwestern Georgia and southeastern Tennessee, and the Etowah River in north-central Georgia, have long been valued as refuges for freshwater biota native to the southeastern United States (Freeman et al. 1996; Burkhead et al. 1997). The rivers form headwaters of the Coosa River within the Mobile River system, one of the most biologically diverse river systems in North America (Abell et al. 2000). Widespread damming and dredging have fragmented and transformed much of the Coosa and Mobile river systems, resulting in species extirpations and imperilment (Boschung and Mayden 2004; Freeman et al. 2005) and extinction of $>$40 endemic mollusks (Lydeard and Mayden 1995). As a result, many Mobile-endemic species are now isolated in the system's remaining free-flowing river segments. The Conasauga River forms one of these refuges, harboring $\geq$75 native fishes (Walters 1997), including multiple species that have been extirpated in other portions of the Coosa River system. The Conasauga fauna includes three fishes listed pursuant to the U.S. Endangered Species Act (ESA 1973, as amended)—the Amber Darter *Percina antesella* (Endangered; USFWS 1985), Blue Shiner *Cyprinella caerulea* (Threatened; USFWS 1992), and Conasauga Logperch *P. jenkinsi* (Endangered; USFWS 1985)—as well as 12 other fishes listed as being of conservation concern by the state of Georgia (GDNR undated) and 4 by Tennessee (TWRC 2000). The upper Etowah River, upstream from Allatoona Dam and reservoir, forms another refuge for imperiled fishes. These include two federally endangered species—the Amber Darter and the Etowah Darter *Etheostoma etowahae* (USFWS 1994)—as well as the federally threatened Cherokee Darter *E. scotti* (primarily in tributaries to the mainstem; USFWS 1994) and seven other fishes of conservation concern to the state of Georgia (GDNR undated). Together, these two river mainstems contain the entire extant range of the Conasauga Logperch and the majority of known occurrences of the Etowah Darter and Amber Darter.

Previous studies have prompted concern about the conservation status of native biota in the Conasauga and Etowah rivers (Burkhead et al. 1997; Freeman et al. 2007). Genetic analyses (George et al. 2010) and survey data (Hagler et al. 2011) have provided evidence of population decline in the endangered Conasauga Logperch. Native mollusks have disappeared from many historically occupied sites in the Conasauga River system (Evans 2001) and biologists have documented potentially harmful contaminants in the river mainstem and tributaries (Sharpe and Nichols 2007; Jacobs 2013; Lasier et al. 2016). Conservation concerns in the Etowah River system have focused on potential effects of urban growth on imperiled fishes (Burkhead et al. 1997; Wenger et al. 2010), based in part on analyses showing negative correlations between present-day occurrences of native stream fishes and impervious land-cover associated with urban development (Wenger et al. 2008). Together, these studies elevate concerns that ongoing, local environmental changes may impair the ability of these two rivers to conserve native aquatic biota.

Our objective is to use time-series of periodic surveys conducted at fixed locations to evaluate evidence that fish species occurrences have declined in either the Conasauga or Etowah river mainstems over the past 20 y. Managers often rely on periodic survey data to assess changes in the status of imperiled species or in the integrity of biologically diverse assemblages. Change, however, can be difficult to detect. Survey data for stream fishes typically comprise lists of species encountered at particular times and places, often with counts of individuals. However, count data typically lack explicit measures of capture efficiency, which may vary depending on habitat conditions during sampling and thus confound comparisons among counts made at different times (Yoccoz et al. 2001; Price and Peterson 2010). In this study, we have used changes in observed species occurrences, rather than count data, to evaluate evidence of temporal faunal change. However, even apparent changes in species occurrence can provide ambiguous information because of incomplete detection (i.e., species may in fact be present but not detected). Rare species may be particularly difficult to detect, especially in larger streams and rivers by biologists using nondestructive sampling methods.

Our analysis addresses common issues in using species observations to infer faunal change in two ways. First, we use occasions when multiple surveys have been conducted at $\geq$1 sites in a single year to estimate species detection probabilities and thereby account for incomplete detection when estimating changes in species occupancy (MacKenzie et al. 2003; Royle and Kéry 2007). And secondly, we analyze these survey data using a multispecies framework (Ruiz-Gutiérrez et al. 2010; Peterson and Shea 2015; Shea et al. 2015), allowing us to infer dynamics for a suite of

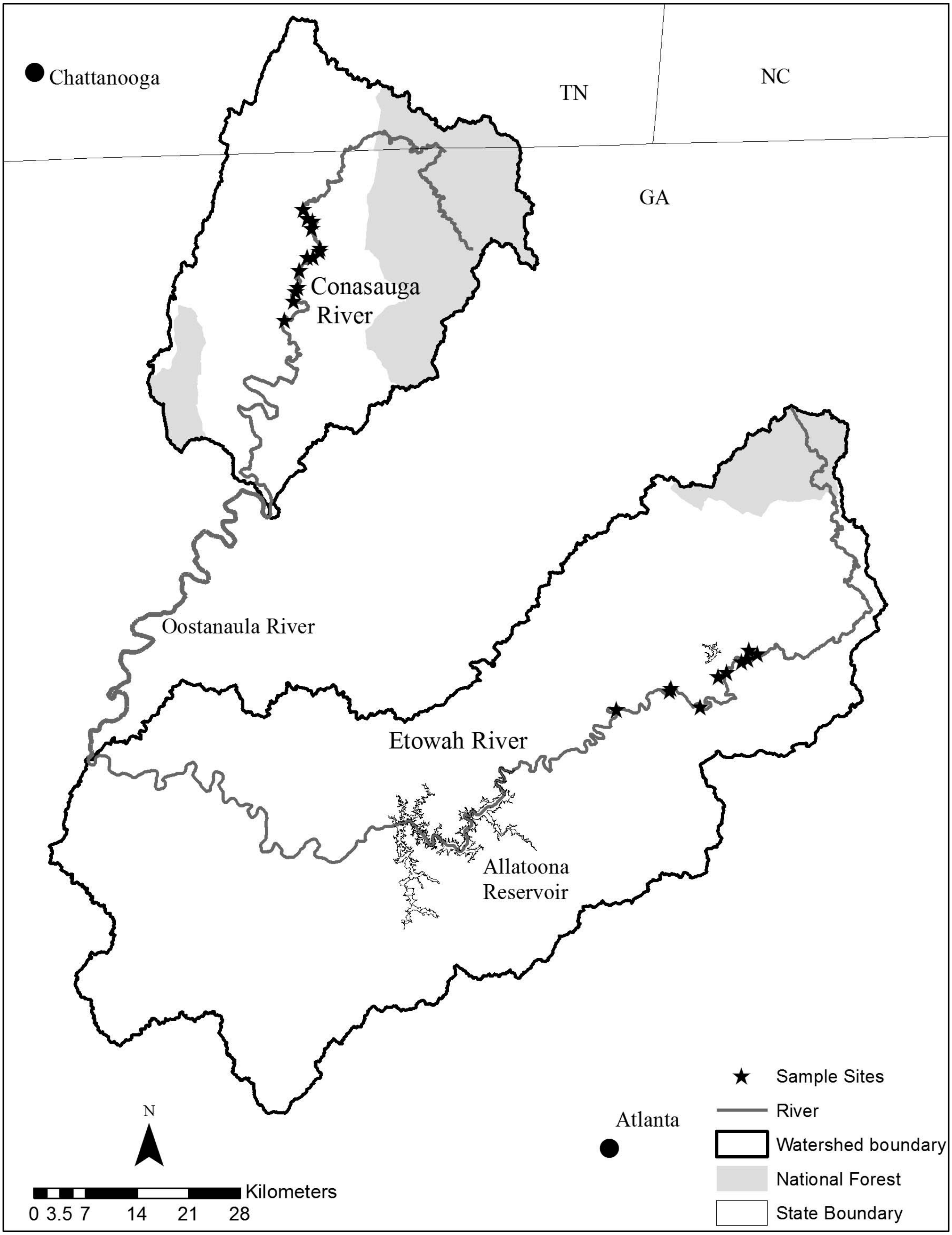

Figure 1. Study site locations (stars) on the Conasauga and Etowah river mainstems, north Georgia, USA. Watershed and state boundaries, and locations for Atlanta, Georgia and Chattanooga, Tennessee are shown for reference. Shaded areas represent national forest property within the Conasauga and Etowah watersheds.

species assumed to respond similarly to environmental change, including taxa with relatively few observed occurrences (Gelman and Hill 2007). Using this model framework, we test whether species-specific covariates reflecting restricted distribution (and thus availability of colonizers) or low abundance characterize species having lower rates of colonization or persistence (Gotelli and Taylor 1999). We also assess evidence that interannual variation in streamflow conditions, and in particular the occurrence of prolonged periods of unusually low or high streamflow, drive changes in species occurrences from year to year. Although change in the flow regime is one of many possible causes of species losses from a river system, the effects of unusual flow conditions on biological dynamics are of particular interest to those concerned with effects of water use or climate-driven changes in flow regimes (Xenopoulos et al. 2005; Wenger et al. 2011; Walters 2016). Our results should be useful to conservation stakeholders, including U.S. Fish and Wildlife Service and state agency biologists, concerned with status and trends of native fishes in the Conasauga and Etowah rivers. Moreover, our analysis provides an example of how monitoring data may be useful for identifying declining species, including rarer taxa, and for testing for effects of suspected drivers of decline, while accounting for incomplete detection.

Methods

Study areas and survey data

We have used observations of species occurrences at 13 shoals (shallow areas with swift currents and predominantly bedrock, cobble, and gravel bed-sediments) in a 28-km reach of the Conasauga River mainstem, extending from just downstream of the GA State Route 2 crossing at Beaverdale, Georgia to near the US Highway 76/GA State Route 52 crossing, Murray and Whitfield counties (Figure 1). Although the Conasauga River originates in national forest, land use in this portion of the basin totals approximately 15–24% agriculture, including row crops (comprising 2.5–2.8% of land use; 2011 National Land Cover Data, Homer et al. 2015), pasture, and ≥1 dairy operation (Baker 2012; Lasier et al. 2016). Our study reach begins approximately 20 km downstream from the national forest boundary. We initiated annual surveys at the study shoals as part of a study designed to detect changes in fish communities downstream of a pump-storage reservoir constructed adjacent to the Conasauga River in the late 1990s near the middle of the study reach. The specific survey sites represent shoal habitats occupied by the Amber Darter as well as the Conasauga Logperch, the primary species of conservation concern, in this middle reach of the Conasauga River. The study reach spans the approximate downstream-half of the extant range of the Amber Darter in the Conasauga, ending near the influence of Dalton, Georgia. Drainage area increases from 472 to 794 km^2 within the study reach, with three major tributaries joining the mainstem between the upstream- and downstream-most sites.

We have analyzed a similar data set of annual surveys at 10 mainstem shoals in a 42-km reach of the Etowah River, from just upstream of the mouth of Amicalola Creek (Dawson County, Georgia) to the road crossing at East Cherokee Drive (Cherokee County, Georgia; Figure 1). The headwaters of the Etowah River also originate in national forest; our study reach begins approximately 80 km downstream from the national forest boundary. In contrast to the Conasauga, agriculture comprises <10% of land use upstream of the Etowah study reach and is almost entirely pasture; row-crop agriculture is a minor land use (<0.1%; 2011 National Land Cover Data, Homer et al. 2015). Similar to the Conasauga, we initiated annual surveys at the Etowah River shoals to test for effects of operations of a pump-storage reservoir constructed on Yellow Creek, which joins the Etowah mainstem near the midpoint of the study reach. The specific survey sites represent the variety of shoal habitats occupied by the Amber Darter in this reach of the Etowah, which spans the majority of the Amber Darter range in the system. Five other major tributaries join the mainstem within the study reach, with drainage area increasing from 461 to 1,502 km^2 from the upstream- to downstream-most site.

Survey data in the Conasauga study reach comprised 202 samples collected at the 13 shoals in 17 y from 1995 through 2014. No sites were surveyed in 2004, 2009, or 2011. Otherwise, we surveyed 5–13 sites in any given year. We surveyed eight of the 13 sites in ≥10 y. We conducted annual surveys during September and October except in 2012 (seven samples in June). Forty-one of the 202 samples were repeated within-year surveys at particular study shoals, including 29 early summer (31 May–30 June) samples collected at most sites during the first 3 y of the study (1995–1997) in addition to October samples in those same years. The remaining within-year replicates were 10 summer (June–September) and 2 spring (March) surveys made in conjunction with other studies (e.g., Argentina et al. 2010b) using the same methods as described below.

Survey data for the Etowah comprised 113 annual surveys (including 10 within-year replicates) conducted in 12 y from 2001 through 2014 at the 10 mainstem shoal sites. We sampled nine of the 10 sites in ≥10 y. No sites were surveyed in 2010 or 2011 and we sampled only one site in 2013. We conducted annual sampling in late summer and autumn (August–November); the 10 within-year replicate samples were collected in June–November.

All surveys were made by a crew of ≥3 persons using a seine (2.4 m × 1.8 m; 3-mm mesh) in wadeable shoal habitat during low-flow conditions. Annual surveys comprised multiple seine-sets, in which 2 persons held the seine in flowing water with the lead-line on the substrate, while ≥1 others moved toward the seine

Table 1. Estimated species-specific occupancy by fishes at fixed sites in the Conasauga River (13 sites, monitored from 1995 through 2014) and Etowah River (10 sites, monitored from 2001 to 2014), Georgia. Estimates are the posterior mean (and 95% credible interval) number of sites occupied for the first and last 5 y in each data series, derived using multitaxa dynamic occupancy models for each river system, with random variation in rates of persistence and colonization among species, sites, and years. Species with nonoverlapping credible intervals for the two periods, indicating support for a change in occupancy dynamics, are shown in bold. Federal (E = Endangered, T = Threatened) and State (Georgia [GA], R = Rare; Tennessee [TN], MC = Management Concern) protected status, if applicable, is shown in parentheses. Dashes indicate that a species was not included in the river system-specific analysis.

	Estimated number of sites occupied			
	Conasauga River, 13 sites total		Etowah River, 10 sites total	
Species	**1995–1999**	**2010–2014**	**2001–2005**	**2010–2014**
Cyprinidae				
Campostoma oligolepis, Largescale Stoneroller	12.3 (11.8–12.6)	12.0 (10.8–12.8)	7.0 (6.2–8.2)	8.6 (6.8–10.0)
Cyprinella caerulea, Blue Shiner (T)	11.0 (10.1–11.8)	12.8 (12.0–13.0)	–	–
Cyprinella callistia, Alabama Shiner	12.9 (12.4–13.0)	12.9 (12.0–13.0)	10.0 (9.8–10.0)	10.0 (9.8–10.0)
***Cyprinella trichroistia,* Tricolor Shiner**	**10.0 (9.0–11.4)**	**0.6 (0–2.6)**	**6.2 (5.8–7.0)**	**8.0 (7.6–8.4)**
Cyprinella venusta, Blacktail Shiner	12.9 (12.4–13.0)	12.9 (12.0–13.0)	4.7 (3.4–6.8)	7.3 (4.8–10.0)
Luxilus chrysocephalus, Striped Shiner	10.5 (9.4–11.8)	12.1(10.8–13.0)	–	–
Luxilus zonistius, Bandfin Shiner	–	–	7.8 (5.8–9.6)	9.7 (8.0–10.0)
***Macrhybopsis etnieri,* Coosa Chub (GA-E)**	**11.9 (11.0–12.4)**	**0.3 (0–2.0)**	9.9 (9.8–10.0)	9.8 (9.0–10.0)
Nocomis leptocephalus, Bluehead Chub	–	–	8.7 (7.4–10.0)	9.3 (7.0–10.0)
Notropis longirostris, Longnose Shiner	–	–	3.2 (2.4–4.6)	2.8 (1.0–4.4)
Notropis lutipinnis, Yellowfin Shiner	–	–	9.8 (8.8–10.0)	9.9 (8.8–10.0)
Notropis stilbius, Silverstripe Shiner	12.9 (12.4–13.0)	12.4 (12.0–13.0)	9.1 (8.0–10.0)	7.9 (6.0–10.0)
Notropis xaenocephalus, Coosa Shiner	6.6 (3.0–12.2)	1.5 (0–8.6)	5.4 (1.8–9.4)	8.0 (3.6–10.0)
Phenacobius catostomus, Riffle Minnow	12.9 (12.4–13.0)	12.2 (11.0–13.0)	9.9 (9.6–10.0)	9.8 (8.8–10.0)
Semotilus atromaculatus, Creek Chub	_	_	4.7 (0.4–9.2)	7.0 (1.0–10.0)
Catostomidae				
Hypentelium etowanum, Alabama Hogsucker	12.7 (12.2–13.0)	12.7 (12.0–13.0)	10.0 (9.8–10.0)	10.0 (9.8–10.0)
Ictaluridae				
Noturus leptacanthus, Speckled Madtom	12.2 (10.8–13.0)	11.5 (7.2–13.0)	8.0 (7.2–9.2)	9.1 (7.0–10.0)
***Noturus* sp., Coosa madtom[a] (GA-E , TN-MC[b])**	**5.3 (3.4–8.6)**	**0.2 (0–1.4)**	10.0 (9.8–10.0)	9.9 (9.4–10.0)
Fundulidae				
Fundulus stellifer, Southern Studfish	11.8 (10.4–13.0)	11.0 (7.2–13.0)	1.1 (1.0–2.0)	1.3 (1.0–2.2)
Cottidae				
Cottus carolinae, Banded Sculpin	12.9 (12.4–13.0)	12.9 (12.0–13.0)	10.0 (9.8–10.0)	10.0 (9.8–10.0)
Centrarchidae				
Micropterus coosae, Redeye Bass	9.0 (4.0–12.8)	6.7 (0.6–13.0)	6.9 (4.0–10.0)	7.9 (4.6–10.0)
Percidae				
Etheostoma coosae, Coosa Darter	12.4 (11.4–13.0)	11.5 (9.4–12.6)	–	–
Etheostoma etowahae, Etowah Darter (E)	–	–	6.5 (4.6–8.0)	8.5 (6.8–9.8)
Etheostoma jordani, Greenbreast Darter	12.7 (12.2–13.0)	12.5 (11.4–13.0)	–	–
Etheostoma rupestre, Rock Darter (GA-R)	12.3 (11.8–12.6)	12.1 (11.0–13.0)	10.0 (9.8–10.0)	10.0 (9.8–10.0)
Etheostoma scotti, Cherokee Darter (T)	–	–	1.3 (1.0–3.0)	1.2 (1.0–2.6)
Etheostoma stigmaeum, Speckled Darter	12.6 (12.0–13.0)	12.9 (12.0–13.0)	9.9 (9.6–10.0)	10.0 (9.6–10.0)
Etheostoma trisella, Trispot Darter (GA-E, TN-MC)	11.9 (10.4–13.0)	12.6 (11.0–13.0)	–	–
***Percina antesella,* Amber Darter (E)**	**12.0 (11.2–12.6)**	**6.4 (3.8–9.2)**	10.0 (9.6–10.0)	9.7 (8.0–10.0)
Percina jenkinsi, Conasauga Logperch (E)	10.0 (6.4–12.8)	8.4 (3.2–13.0)	–	–
Percina kathae, Mobile Logperch	11.6 (9.4–13.0)	9.5 (4.8–13.0)	9.7 (8.6–10.0)	9.3 (6.8–10.0)
Percina lenticula, Freckled Darter (GA-E)	–	–	6.0 (4.8–7.4)	6.4 (5.2–8.6)
Percina nigrofasciata, Blackbanded Darter	12.9 (12.4–13.0)	12.8 (12.0–13.0)	9.8 (9.6–10.0)	9.9 (9.6–10.0)
Percina palmaris, Bronze Darter	10.7 (7.0–13.0)	9.3 (3.0–13.0)	10.0 (9.8–10.0)	10.0 (9.6–10.0)

[a] Undescribed species endemic to the Coosa River system (Warren et al. 2000; Boschung and Mayden 2004).

[b] Listed as *Noturus munitus* on the Georgia Department of Natural Resources Protected Species List and the Tennessee Wildlife Resource Commission Endangered or Threatened Species.

from approximately 2 m upstream, disturbing bed sediments to motivate fish into the net. We augmented seine-sets with seine-hauls in eddies and low-velocity areas. The sampling crew attempted to sample the full range of wadeable habitats at each site on each date. We scaled sampling effort (the number of seine-sets and hauls) to the size of the shoals, which varied from approximately 50 to >100 m in length. We typically identified, recorded, and released captured fish after each seine set; on some occasions, we retained individuals for laboratory identification (particularly small juveniles).

Analyses

We summarized survey data as species detections or nondetections by site and date, for each river. We treated surveys conducted in the same year at a site as replicates for that year. We coded as "NA" any sites and replicates that were not sampled in a given year. We included detections and nondetections for 26 fish species in the Conasauga sites and 28 fish species in the Etowah sites (Table 1). We excluded taxa such as sunfishes (Centrarchidae) and large-bodied suckers (Catostomidae) that were not characteristically found as adults in shallow, swiftly flowing shoals throughout the year. We also excluded taxa that were detected in <5% of all mainstem surveys. We analyzed the resulting matrix of species detections by site and year for each river system (File A1, *Archived Material*) using a model with no covariates (basic model), and four additional models with either species-specific or year-specific (streamflow) covariates on persistence and colonization probabilities.

Basic model. We used the binary representation of the survey data to estimate occupancy dynamics by fitting a multiyear, multitaxa model to the data for each river (Royle and Kéry 2007; Peterson and Shea 2015; Shea et al. 2015). Specifically, we modeled the observed detection (1) or nondetection (0) for each of the 26 (Conasauga model) or 28 (Etowah model) species at every site surveyed in a given year, as the result of two linked processes: dynamic occupancy and sampling. The dynamic occupancy part of the model described the change in species-specific occurrence at each site from year to year. For the first survey year, we set

$$z_{mi1} \sim \text{Bernoulli}\,(\psi_{m1}) \tag{1}$$

where z_{mi1} represents the true (unknown) presence or absence of species *m* at site *i* in the first year, and ψ_{m1} is the probability that species *m* is present at any site in year one. For each subsequent year, we modeled species-specific occupancy at each site as a function of persistence (the occurrence of a species at time *t* that was also present at time $t-1$) and colonization (the occurrence of a species at time *t* that was absent at time $t-1$):

$$\begin{aligned} z_{mik}|z_{mik-1} \sim \text{Bernoulli}\,\{&z_{mik-1} \times \Phi_{mik-1} \\ &+ (1 - z_{mik-1}) \times \gamma_{mik-1}\} \end{aligned} \tag{2}$$

where Φ_{mik} and γ_{mik} are species-, site-, and year-specific probabilities of persistence and colonization, respectively. We defined

$$\begin{aligned} \text{logit}(\Phi_{mik}) = {} & \textit{beta.phi} + \textit{epsilon.phi.taxon}_m \\ & + \textit{epsilon.phi.site}_i + \textit{epsilon.phi.year}_k \end{aligned} \tag{3}$$

and

$$\begin{aligned} \text{logit}(\gamma_{mik}) = {} & \textit{beta.gamma} + \textit{epsilon.gamma.taxon}_m \\ & + \textit{epsilon.gamma.site}_i \\ & + \textit{epsilon.gamma.year}_k \end{aligned} \tag{4}$$

where *beta.phi* and *beta.gamma* are intercept terms on the logit scale that define the mean probabilities of persistence and colonization, respectively, for all species, sites, and years. The *epsilon* terms represent random variation in persistence and colonization among species, sites, and years, each assumed to be normally distributed around zero with a random effect-specific variance.

The sampling component used the within-year replicates at particular sites to estimate species-specific detection probabilities, on the assumption that if a species was detected in any one of the within-year replicates at a site, it was present and available to be detected during the other surveys made at that site in the same year. Thus, we defined each observed detection (1) or nondetection (0) of species *m* in the *j*th replicate survey at site *i* in year *k* as

$$y_{mijk}|z_{mik} \sim \text{Bernoulli}\,(z_{mik} \times p_{mijk}) \tag{5}$$

where p_{mik} is the species- and survey-specific probability of detecting species *m,* given that species *m* was present ($z_{mik} = 1$). We allowed each species to have its own probability of detection. We also assumed that detection across all species varied from one survey to the next (e.g., depending on weather, site characteristics, personnel, effort and other unaccounted-for factors). Thus, we defined

$$\text{logit}(p_{mijk}) = \textit{beta.p}_m + \textit{epsilon.p}_{ijk} \tag{6}$$

where $\textit{beta.p}_m$ is an intercept term on the logit scale that defines the expected detection probability for species *m,* and $\textit{epsilon.p}_{ijk}$ is a survey-level random effect (normally distributed with a mean of 0) representing variation in detection.

Species covariates. Building on the basic model, we evaluated support for two species-specific covariates hypothesized to influence persistence or colonization probabilities. First, we hypothesized that species restricted to the river mainstem would have lower colonization probabilities than taxa also known to occur in tributary streams because mainstem-restricted species would only be able to colonize from other mainstem shoal habitats, whereas other species could also colonize from tributary populations. Thus, we estimated the effect of a binary variable coded as 1 for the mainstem-restricted species, included in definitions for persistence and colonization (eqs. 3 and 4). Secondly, we hypothesized that rare species would have lower persistence, colonization, or both. To represent rarity, we calculated the proportion of river-specific surveys (excluding those that lacked counts of individuals) in which each species, when detected, was represented by <5 individuals. We included this measure of rarity (scaled by subtracting the mean and dividing by the standard deviation of the untransformed data) as a covariate on persistence and colonization (eqs. 3 and 4) in a separate model. We did not include mainstem-restriction and rarity in the same model to avoid autocorrelation.

Streamflow covariates. To evaluate evidence that extended periods of either low or high discharge

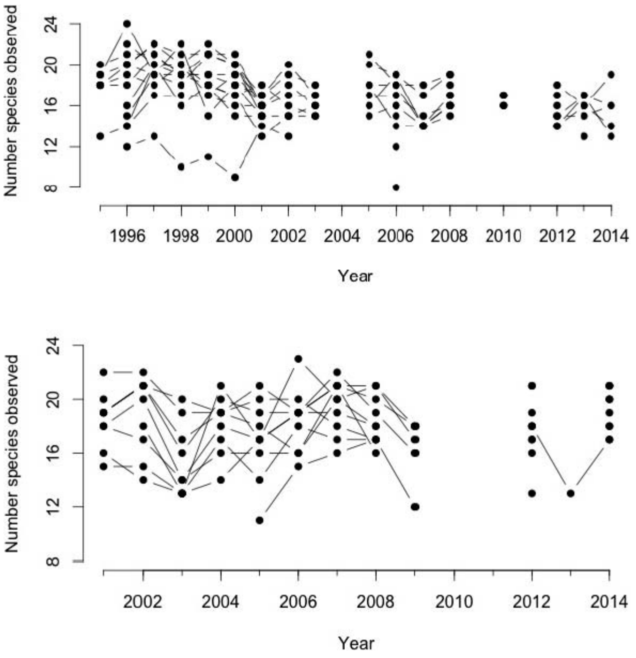

Figure 2. Counts of fish species observed by survey year in 13 shoals in the Conasauga River mainstem (upper graph; 1995-2014, 26 taxa included in analysis) and 10 shoals in the Etowah River mainstem (lower graph; 2001-2014, 28 taxa included in analysis). Data for some shoals having identical counts in a given year are plotted as a single point. Gaps indicate years lacking survey data.

influenced occupancy dynamics, we fit two additional models for each river in which we included a measure of annual low-flow or high-flow frequency as a covariate on persistence and colonization. We used daily discharge data for U.S. Geological Survey streamgage 02384500, Conasauga River near Eton, Georgia, and for U.S. Geological Survey streamgage 02392000, Etowah River at Canton, Georgia, from 1982 to 2014 to calculate monthly 10th and 90th percentile flows for each river, as measures of unusually low and high flow conditions. We then calculated the annual counts of low-flow and high-flow days during March through September (i.e., a period typically encompassing reproduction and greatest growth for the study taxa) for the years corresponding to surveys in each river. Low-flow and high-flow days were counted as those having an average daily discharge less than the monthly 10th percentile flow (low-flow) or greater than the monthly 90th percentile flow (high-flow). We transformed values for low-flow and high-flow days prior to analysis by subtracting the mean and dividing by the standard deviation of the untransformed data.

Using these measures, we evaluated support for the hypothesis that unusually frequent low- or high-flow conditions during spring and summer (i.e., March–September) influenced either persistence or colonization from the previous annual survey to the next (because most surveys were conducted in late summer or early autumn). We allowed species to differ in their responses to annual flow conditions by fitting random-slopes models in which effects of low- or high-flow duration on persistence and colonization were represented as mean effects plus species-specific random effects that were assumed to be normally distributed with a mean of 0. We fit separate models for low- and high-flow day effects on occupancy dynamics to avoid auto-correlation.

Model fitting. We fit models using a Bayesian framework implemented with the Markov chain Monte Carlo software JAGS (Plummer 2003), run using the R package “rjags” (Plummer 2014; R Core Team 2014). We used diffuse priors for parameter coefficients and ran 3 chains for $\geq$32,000 iterations, thinned by 4, after a burn-in of 8,000. We assessed convergence using the Brooks–Gelman–Rubin statistic (R-hat; Brooks and Gelman 1998). To assess model fit, we computed a Bayesian *P*-value for the basic models based on the discrepancy (Freeman–Tukey statistic) between the observed and (model-based) expected number of species detected in each survey, and the same statistic calculated for a replicate data set simulated using persistence, colonization, and detection estimates at each Markov chain Monte Carlo iteration (Kéry and Schaub 2012). The Bayesian *P*-value was the proportion of summed discrepancy values for the simulated data that exceeded the same for the observed data. A value of less than approximately 0.05 or greater than approximately 0.95 would indicate substantial model lack-of-fit (Kéry and Schaub 2012). As a perhaps more intuitive measure of performance of the basic models, we estimated the mean absolute proportional difference between observed and model-predicted number of species detections in individual surveys (omitting model estimates for missing surveys). Model code is provided in the Archived Material (File A2, *Archived Material*).

Results

Conasauga River species dynamics

Observed species richness varied from 8 to 24 species (out of 26 taxa included in analyses) across all surveys at the 13 Conasauga study sites (Figure 2). In 90% of the annual surveys, we observed $\geq$14 of the taxa included in analyses. Species counts were consistently lower at one site (Figure 2) where shoal habitat was limited and diminished over the years; we discontinued surveys after 2006 at this site. Across all sites, observed richness declined over time, from a mean of 18.5 in 1995–1997 to 15.5 in 2012–2014 (although these values were not strictly comparable because fewer sites were sampled in the latter years). Four taxa, Coosa Chub *Macrhybopsis etnieri*, Tricolor Shiner *Cyprinella trichroistia,* Coosa Madtom *Noturus* sp., and Amber Darter, became less common in surveys through time, with the first three of

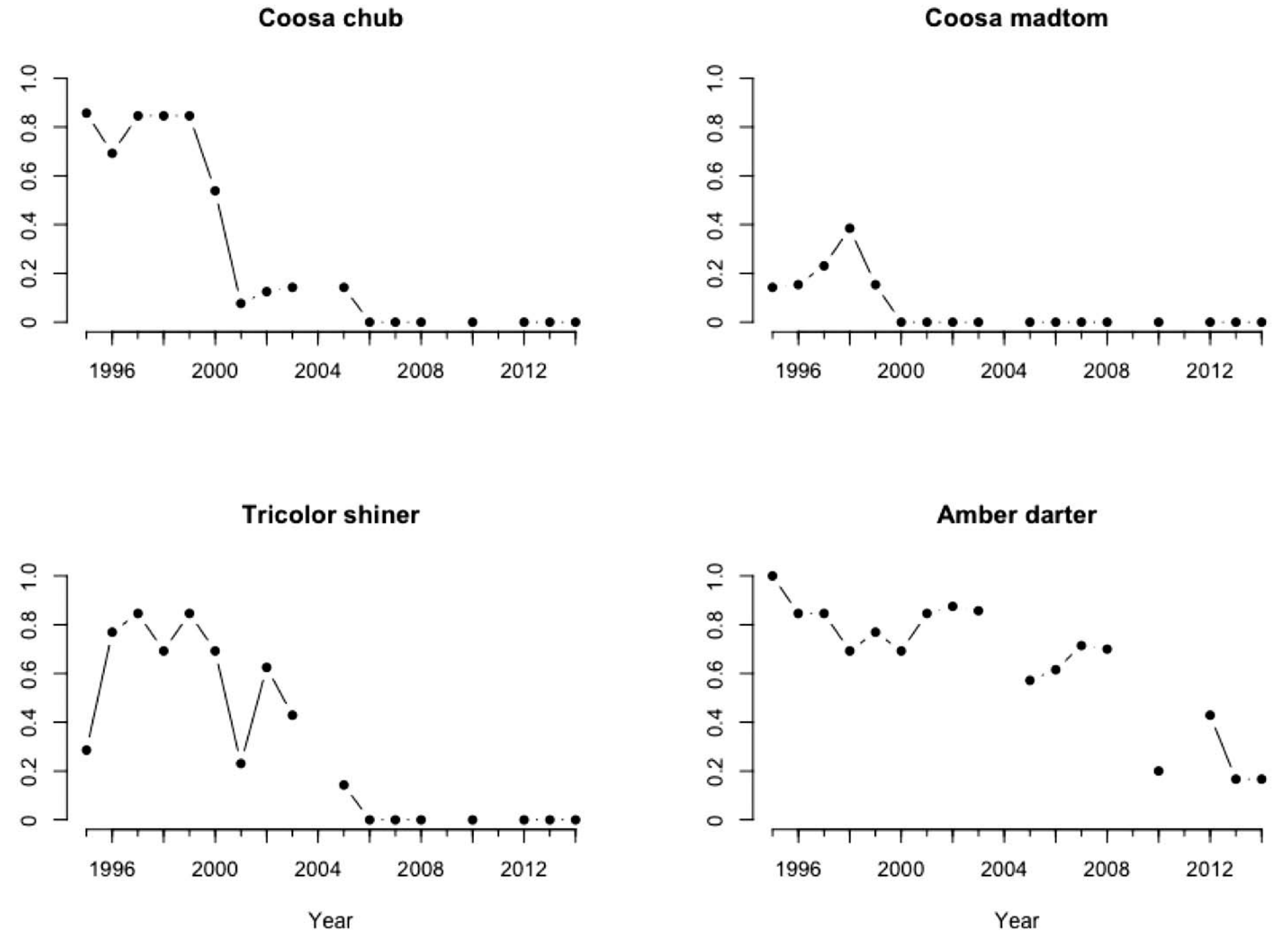

Figure 3. Temporal trends in observed occurrence for the Coosa Chub *Macrhybopsis etnieri,* Coosa Madtom *Noturus* sp. cf. *N. munitus,* Tricolor Shiner *Cyprinella trichroistia,* and Amber Darter *Percina antesella* at annually surveyed study sites in the Conasauga River mainstem. Plots show the proportion of sites sampled in any given year (maximum of 13 sites) where each species was observed; gaps indicate years lacking survey data.

these species essentially disappearing from the monitored sites (Figure 3).

The basic dynamic occupancy model, allowing for random variation in rates of persistence and colonization among taxa, sites, and years (and random variation in species-specific detection among surveys), appeared to fit the observed data well (Bayesian *P*-value = 0.45). Model-predicted numbers of species detections in a given survey were on average 5.1% different from the observed numbers, also indicating adequate representation of the survey data. Based on this model, and thus accounting for incomplete detection, the Coosa Chub, Tricolor Shiner, Coosa Madtom, and Amber Darter were each estimated to occur at substantially fewer of the 13 monitoring sites in the later years than during the initial survey years (Table 1). Three taxa—Coosa Chub, Tricolor Shiner, and Coosa Madtom—were estimated as plausibly absent from the study sites during the last 5 survey years; the Amber Darter declined from occupying nearly all to less than half of the monitored sites. Mean estimated occupancy also decreased for other taxa, including the Coosa Shiner *Notropis xaenocephalus* and Redeye Bass *Micropterus coosae* and, to a lesser extent, the Conasauga Logperch, Bronze Darter *Percina palmaris,* and Mobile Logperch *P. kathae* (Table 1), although low detection for these taxa (especially the first four; Table A1, *Archived Material*) resulted in high uncertainty around estimated occupancy. Conversely, 17 species were estimated to occupy $\geq$11 of the 13 sites in the last 5 y of the survey (Table 1). Overall, estimated species richness averaged over all sites declined from a mean (95% credible interval) of 22.9 (22.0–24.0) in 1995–1999, to 19.4 (18.0–20.9) in 2010–2014.

Declining species richness at the Conasauga sites was attributable to low species-specific persistence of some taxa combined with diminished colonization probabilities through time for all taxa. Estimated persistence approached 100% for most species, but was lower for the taxa with strong evidence of declining occupancy from early to late survey years (Figure 4; Table 1). Variation in persistence was higher among taxa than among sites or years (variance terms in Table 2). In

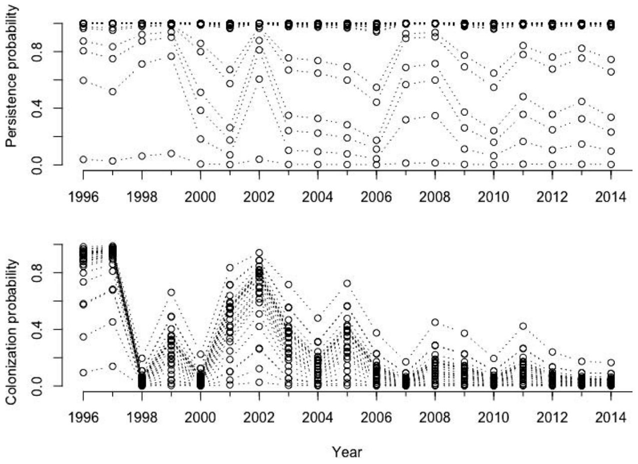

Figure 4. Posterior mean probabilities of taxa-specific persistence (upper graph) and colonization (lower graph) of fish, averaged over 13 study sites in the Conasauga River mainstem, plotted by year, 1996 to 2014. Values are persistence or colonization probabilities when present or absent, respectively, in the previous year, estimated using a multitaxa, dynamic occupancy model. Values are plotted for each of 26 taxa. In the upper graph, the six taxa with consistently lower overall persistence probabilities are (lowest to highest): Coosa Shiner *Notropis xaenocephalus,* Coosa Madtom *Noturus* sp. cf. *N. munitus,* Coosa Chub *Macrhybopsis etnieri,* Tricolor Shiner *Cyprinella trichroistia,* Redeye Bass *Micropterus coosae,* and Amber Darter *Percina antesella.*

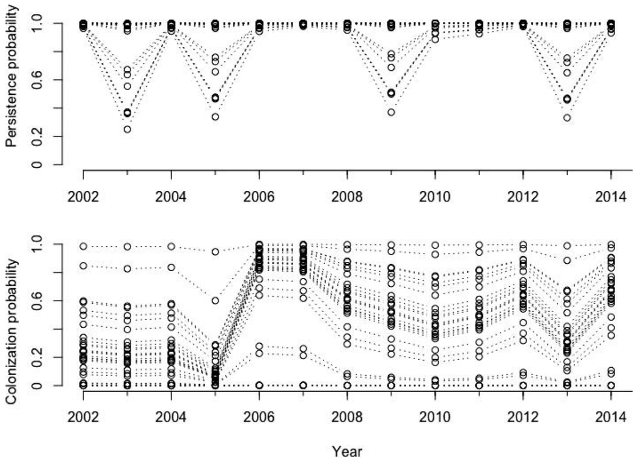

Figure 5. Posterior mean probabilities of taxa-specific persistence (upper graph) and colonization (lower graph) of fish, averaged over 10 study sites in the Etowah River mainstem, plotted by year, 2002 to 2014. Values are persistence or colonization probabilities when present or absent, respectively, in the previous year, estimated using a multitaxa, dynamic occupancy model. Values are plotted for each of 28 taxa.

contrast, colonization probability varied comparably among taxa and among years (Table 2). Colonization estimates were consistently low for Coosa Madtom ($<$15%, all years), but estimated probabilities for all taxa declined to $<$20% in the final 2 survey years (Figure 4).

Table 2. Estimated regression coefficients and random effect variances from multitaxa, dynamic occupancy models using a 20-y time-series (1995–2014) of detection for 26 species at 13 fixed sites in the Conasauga River, Georgia. Results are shown for 5 models, in which logistic regressions for persistence and colonization probabilities were fit as a function of an intercept with random variation among taxa, sites, and years and (1) no additional covariates ("No covariates"); one of two species-specific covariates, which were (2) occurrence only in the river mainstem ("Mainstem restriction") or (3) proportion of surveys in which 1–4 individuals were observed ("Rarity"); and, one of two continuous streamflow covariates with randomly varying species-specific slopes, the annual frequency of daily flows during March–September that were (4) less than the monthly 10th percentile flow ("Low-flow day count") or (5) greater than the monthly 90th percentile flow ("High-flow day count"). All models also included random variation among surveys in species-specific detection probabilities. All values are on the logit scale, and show the posterior means and 95% credible intervals (in parentheses). Dashes (–) indicate parameters not included in a particular model.

		Species covariates		Streamflow covariates	
Parameter	**No covariates**	**Mainstem restriction**	**Rarity**	**Low-flow day count**	**High-flow day count**
Persistence					
Intercept	3.9 (1.3–6.2)	3.9 (1.2–6.4)	4.2 (1.3–6.7)	3.8 (1.1–6.3)	4.0 (1.4–6.5)
Species covariate	–	−0.5 (−3.3–2.5)	−0.4 (−4.2–2.9)	–	–
Streamflow covariate	–	–	–	0.4 (−1.5–2.5)	0.4 (−1.4–2.4)
Variance among taxa, intercept	47.0 (10.9–95.5)	47.7 (10.8–95.9)	42.4 (4.1–95.4)	52.5 (13.2–97.0)	51.8 (12.7–97.0)
Variance among taxa, slope	–	–	–	5.2 (0.0–27.2)	2.2 (0.0–12.1)
Variance among sites	10.7 (1.9–40.0)	10.3 (0.2–38.9)	10.0 (0.2–40.3)	12.8 (2.2–51.2)	11.2 (0.0–48.2)
Variance among years	6.3 (0.8–22.8)	6.5 (0.8–23.7)	6.2 (0.6–23.8)	8.90 (1.1–36.2)	10.1 (1.2–44.2)
Colonization					
Intercept	−1.4 (−3.5–0.7)	−1.2 (−3.2–0.8)	−0.9 (−3.2–1.2)	−1.3 (−3.2–1.1)	−1.4 (−3.9–1.2)
Species covariate	–	−1.8 (−3.8–0.2)	−1.8 (−4.1–0.8)	–	–
Streamflow covariate	–	–	–	−1.2 (−3.3–1.1)	0.4 (−1.9–2.5)
Variance among taxa, intercept	8.7 (0.6–49.6)	4.5 (0.1–20.8)	7.2 (0.1–60.3)	13.0 (1.0–65.6)	19.4 (0.9–85.8)
Variance among taxa, slope	–	–	–	8.8 (0.0–64.2)	5.0 (0.0–38.9)
Variance among sites	0.5 (0.0–3.5)	0.4 (0.0–2.6)	0.6 (0.0–4.4)	0.6 (0.0–3.6)	1.7 (0.0–13.6)
Variance among years	10.7 (1.0–55.6)	7.8 (0.9–32.9)	11.2 (1.0–62.2)	9.9 (0.3–59.6)	23.5 (1.6–89.5)
Detection					
Variance among surveys	0.5 (0.3–0.8)	0.6 (0.3–0.9)	0.6 (0.3–0.9)	0.6 (0.3–0.8)	0.6 (0.3–1.0)

Table 3. Estimated regression coefficients and random effect variances from multitaxa, dynamic occupancy models using a 14-y time-series (2001–2014) of detection for 28 species at 10 fixed sites in the Etowah River, Georgia. Results are shown for 5 models, in which logistic regressions for persistence and colonization probabilities were fit as a function of an intercept with random variation among taxa, sites, and years and (1) no additional covariates ("No covariates"); one of two species-specific covariates, which were (2) occurrence only in the river mainstem ("Mainstem-restriction") or (3) proportion of surveys in which 1–4 individuals were observed ("Rarity"); and, one of two continuous streamflow covariates with randomly varying species-specific slopes, the annual frequency of daily flows during March–September that were (4) less than the monthly 10th percentile flow ("Low-flow day count") or (5) greater than the monthly 90th percentile flow ("High-flow day count"). All models also included random variation among surveys in species-specific detection probabilities. All values are on the logit scale, and show the posterior means and 95% credible intervals (in parentheses). Dashes (–) indicate parameters not included in a particular model.

		Species covariates		Streamflow covariates	
Parameter	**No covariates**	**Mainstem restriction**	**Rarity**	**Low-flow day count**	**High-flow day count**
Persistence					
Intercept	3.9 (0.6–6.6)	4.3 (1.2–6.8)	4.2 (1.1–6.6)	4.6 (1.4–7.1)	4.4 (1.0–6.7)
Species covariate	–	1.4 (−1.5–4.2)	0.0 (−2.9–3.2)	–	–
Streamflow covariate	–	–	–	1.5 (−0.4–3.4)	−0.7 (−2.1–1.0)
Variance among taxa, intercept	24.2 (2.6–81.6)	21.4 (2.6–77.9)	23.4 (2.2–83.2)	18.4 (2.0–69.0)	23.8 (3.0–82.2)
Variance among taxa, slope	–	–	–	2.4 (0.0–11.3)	3.5 (0.0–14.8)
Variance among sites	13.7 (0.0–85.3)	8.8 (0.1–64.6)	12.5 (0.1–84.4)	12.5 (0.1–76.9)	12.9 (0.1–84.7)
Variance among years	19.4 (0.3–88.1)	16.9 (0.3–84.8)	16.0 (0.2–81.4)	6.7 (0.0–61.4)	1.7 (0.0–10.5)
Colonization					
Intercept	−0.7 (−3.1–1.9)	−0.7 (−3.2–2.0)	−0.3 (−2.9–2.4)	−0.8 (−3.6–2.0)	−1.0 (−3.5–1.8)
Species covariate	–	−0.5 (−3.6–2.7)	−0.9 (−3.9–1.9)	–	–
Streamflow covariate	–	–	–	0.0 (−2.7–2.4)	−1.7 (−4.0–0.8)
Variance among taxa, intercept	38.2 (6.0–94.1)	37.7 (5.8–93.5)	34.5 (4.7–93.5)	57.2 (12.9–97.7)	38.0 (6.3–93.2)
Variance among taxa, slope	–	–	–	25.9 (0.6–87.1)	16.1 (0.1–79.9)
Variance among sites	8.0 (0.2–44.4)	7.6 (0.3–39.4)	7.2 (0.3–36.4)	16.1 (1.3–65.1)	7.2 (0.4–39.7)
Variance among years	8.6 (0.1–47.0)	8.7 (0.2–46.8)	7.9 (0.1–44.1)	12.3 (0.2–57.1)	3.8 (0.0–23.8)
Detection					
Variance among surveys	0.4 (0.2–0.8)	0.4 (0.2–0.8)	0.4 (0.2–0.8)	0.4 (0.2–0.8)	0.5 (0.2–0.9)

Species covariates. Neither restriction to the river mainstem nor rarity were estimated to influence species persistence at the Conasauga sites. Regression coefficients for both covariates had 95% credible intervals that included zero (no effect; Table 2). However, estimated effects on colonization were strongly shifted negative for both covariates (although 95% credible intervals again included zero; Table 2). Only 5 of the 26 taxa were considered mainstem-restricted (Coosa Chub, Coosa Madtom, Amber Darter, Conasauga Logperch, and Rock Darter *Etheostoma rupestre*); whereas, rarity varied from <2% to 100% (i.e., percent of surveys with 1–4 individuals counted; Table A2, *Archived Material*).

Streamflow covariates. The Conasauga River experienced wide variation in flow conditions over the study period; in particular, the count of low-flow days varied from 0 (7 out of 19 y starting with 1996) to 155 (in 2007), with 6 of the 8 lowest-flow years on record at the Conasauga River gage occurring since 2000 (Figure A1, *Archived Material*). The count of high-flow days varied from 2 to 66 over the study period. Average effects (Table 2) and species-specific slopes (Table A3, *Archived Material*) for effects of both low-flow and high-flow frequency on persistence and colonization had 95% credible intervals that included zero (no effect) for all species. Estimated low-flow effects on persistence tended strongly negative only for the two madtom catfishes (Coosa Madtom, Speckled Madtom *Noturus leptacanthus*), and on colonization for the Coosa Chub, Tricolor Shiner, and Coosa Shiner (Table A3, *Archived Material*). In contrast, high-flow effects were shifted positive for persistence of Coosa Madtom (Table A4, *Archived Material*). However, broad uncertainty around these estimates obscured conclusive evidence that low- or high-flow frequency influenced metapopulation dynamics.

Etowah River species dynamics

Observed species richness across all years and sites ranged from 11 to 23 (out of the 28 species included in analyses), with no apparent temporal trend at the Etowah sites (Figure 2). The basic dynamic occupancy model appeared to fit the observed data well (Bayesian P-value $= 0.51$), and model-predicted numbers of species detections were on average 3.5% different from the observed numbers, again indicating adequate representation of the survey data. Based on this model, none of the 28 taxa included in the Etowah analyses had lower estimated occupancy in the last 5 y of the time series compared with the initial 5 y (Table 1). Even though only 4 y separate these 2 intervals, compared with 10 y for the longer Conasauga data set, it is of particular note that the 4 species with strongly declining occupancy at the Conasauga sites were consistently observed at a majority of the Etowah sites throughout the time period. Specifically, the Coosa Chub, Coosa Madtom, and Amber Darter were each estimated to occur at all 10 Etowah sites at the beginning and end of the time series, and estimated occupancy by the Tricolor Shiner actually increased at the Etowah sites over the study period (Table 1). Similar to the Conasauga analysis, low estimated detection probability (Table A1, *Archived Material*) contributed to wide credible intervals around occupancy estimates for some taxa (e.g., Creek Chub, *Semotilus atromaculatus*). Estimated species richness averaged over all sites was similar between early (2001–2005) and late (2010–2014) survey years, with means and 95% credible intervals of 21.4 (20.4–22.5) and 23.0 (21.5–24.5), respectively.

In contrast to the Conasauga analysis, neither persistence nor colonization estimates displayed apparent temporal trends in the Etowah (Figure 5). Persistence probability estimates for seven species dropped below 80% in 4 separate y, but in most other years estimates for all taxa exceeded 90% (Figure 5). Colonization probability estimates displayed greater variation among taxa than among years (Table 3; Figure 5), and were consistently $<1\%$ for four taxa—Cherokee Darter, Longnose Shiner *Notropis longirostris,* Freckled Darter *P. lenticula*, and Southern Studfish *Fundulus stellifer*—that were only ever observed at a subset of the study sites. All other taxa had estimated colonization probabilities $>20\%$ in ≥ 2 y.

Species covariates. We found no support for hypothesized effects of mainstem-restriction or rarity on species-specific persistence or colonization in the Etowah sites (Table 3). Regression coefficients for both covariates had 95% credible intervals that included zero (no effect; Table 3). Similar to the Conasauga, only four taxa were considered mainstem-restricted (Coosa Chub, Coosa Madtom, Amber Darter [primarily but not entirely known from the mainstem], and Freckled Darter), whereas rarity varied from $<1\%$ to $>90\%$ (Table A2, *Archived Material*).

Streamflow covariates. Counts of low-flow days at the Etowah River gage ranged from 0 (6 out of 13 y beginning in 2002) to 134 (in 2008), with 4 of the 6 lowest-flow years in the 35-y record occurring since 2002 (Figure A2, *Archived Material*). Counts of high-flow days also varied widely, from 1 to 102 over the study interval. Species-specific slopes for effects of low-flow frequency were generally positive (but with 95% credible intervals that included zero) for persistence, and near zero for colonization, for most taxa (Table 3 shows average effects; Table A5 shows species-specific slopes, *Archived Material*). Two species—Blacktail Shiner *Cyprinella venusta* and Speckled Madtom—had significant or nearly significant positive slopes for effects of low-flow frequency on both persistence and colonization (Table A5, *Archived Material*). Counts of high-flow days were generally negatively correlated with persistence and colonization, although 95% credible intervals for average effects (Table 3) and most species-specific slopes (Table A6, *Archived Material*) included zero (no effect). Three species (Blacktail Shiner, Largescale Stoneroller *Campostoma oligolepis*, Speckled Madtom) had significantly negative slopes for effects of high-flow frequency on persistence, colonization, or both (Table A6, *Archived Material*).

Discussion

Our objective has been to use monitoring data spanning 14–20 y to evaluate evidence that native fishes may be declining in two rivers valued for conserving freshwater biodiversity. Additionally, we have explored the application of dynamic occupancy models to a common type of monitoring data (i.e., periodic observations of species occurrences at multiple sites) to test hypotheses about causes underlying observed trends in faunal richness. Our analysis of long-term monitoring data from fixed-sites in the Conasauga River reveals strong evidence of population declines in ≥ 4 taxa, in contrast to estimates from a similar data set for the Etowah River, where no taxa show evidence of declining occupancy. Below, we discuss possible causes of species losses from the Conasauga River mainstem and potential management implications, followed by consideration of benefits of applying hierarchical, dynamic occupancy models to these types of survey data to test for temporal trends in species occurrences.

Possible causes and management implications of species declines

Occurrences of ≥ 4 fishes, including one federally endangered species (Amber Darter) and another that has been petitioned for listing (Coosa Madtom, as *Noturus munitus*), appear to have declined steeply in the study reach of the Conasauga River. We lack obvious explanations for why these four taxa in particular show large declines in the Conasauga system. These taxa represent diverse phylogenies (two cyprinids, one ictalurid, and one percid), feeding behaviors (i.e., water-column and benthic foragers), and spawning modes (i.e., crevice-spawning, broadcast-spawning, nest-guarding, and gravel spawning). Whereas species traits have proven useful in identifying fishes that are most responsive to environmental change in other contexts (Craven et al. 2010; Carlisle et al. 2011; Mims and Olden 2012; Perkin et al. 2015), there are no obvious unifying traits among these declining taxa. At the same time, three of the declining taxa have one or more congeners (i.e., species with likely similar traits) that do not show evidence of decline at the Conasauga River sites.

Ultimately, low persistence combined with decreasing probability of colonization underlies species declines in the Conasauga River. The four strongly declining species, as well as two others with evidence of decline (Coosa

Shiner, Redeye Bass), show lower overall persistence rates than the other examined taxa. We had hypothesized that declining species would be characterized by lower abundances (Gotelli and Taylor 1999) or fewer sources of colonizers, and this is partly supported. Three of the four strongly declining taxa are only known from the mainstem river in the Conasauga system and the rarity index for the six taxa with lower persistence rates ranges from nearly half to >80% of species-specific counts comprising fewer than five individuals. However, our model results suggest that rarity and mainstem-restriction may lower colonization (with negatively skewed posterior estimates of effects) but not persistence. Our failure to find strong relationships between rarity and mainstem-restriction and metapopulation rates results in part because other species that are similarly rare, and at least one mainstem-restricted species (Rock Darter), do not yet show signs of declining occupancy. Additionally, colonization probabilities appear to have declined for all taxa examined in the Conasauga—rare and common—in recent years. This finding of reduced colonization across the entire suite of small-bodied, shoal species implies that the entire assemblage may be at risk of future declines in species occurrences.

Comparing species dynamics between the Conasauga and the Etowah study reaches may help diagnose causes of underlying species declines in the Conasauga River mainstem. The four strongly declining taxa in the Conasauga show no declines in occupancy at the monitored Etowah sites, nor do any other examined species. Persistence and colonization probabilities vary temporally at the Etowah sites but do not display temporal trends. We conclude that the factors dampening colonization rates in the Conasauga River mainstem are not regional. We had hypothesized that the recent occurrence of several unusually severe droughts could be driving species losses in the Conasauga. However, both river systems have experienced similarly low relative flows, and our model results do not provide compelling evidence for detrimental effects of either unusually low- or high-flow frequency on persistence or colonization rates in either river system. Several taxa in the Conasauga have species-specific slopes for effects of low-flow frequency on persistence or colonization that are negatively skewed, but with credible intervals that include zero (no effect). However, the Etowah models only show evidence of positive effects of low-flow frequency on persistence or colonization, and the majority of species display no effects of flow extremes on metapopulation dynamics.

The Conasauga and Etowah study reaches differ in the extent and intensity of row-crop agriculture, which flanks much of the upper Conasauga mainstem in Georgia but is, at present, a minor land use in the upper Etowah watershed. Several studies have reported elevated levels of agriculturally derived nutrients and contaminants in the Conasauga River study reach (Sharpe and Nichols 2007; Jacobs 2013; Lasier et al. 2016). Jacobs (2013) additionally documents occurrence of bioavailable estrogen in water and sediments of tributaries that join the Conasauga mainstem either upstream or in our study reach, occurrence of intersex condition in approximately 13% of the fish collected in these tributaries, and lowered growth in two fish species exposed to sediment from tributaries with the highest estrogen levels. Widespread application of poultry litter on agricultural fields is a likely source of steroid hormones in the Conasauga (Lasier et al. 2016). Water and sediments in the river also have detectable levels of the pesticide glyphosate or its breakdown products, derived from pesticide applications to agricultural fields along the Conasauga mainstem and tributaries (Lasier et al. 2016).

Runoff from row-crop and animal husbandry operations may also contribute to elevated nutrient levels in the Conasauga River study reach. Mainstem water samples from the study reach show occurrence of particularly high levels of total nitrogen (e.g., >5 mg/l) and total phosphorus (e.g., >300 ug/L; Freeman et al. 2007; Sharpe and Nichols 2007; Lasier et al. 2016). Stable nitrogen isotope ratios of herbivorous consumers in the Conasauga mainstem downstream from the national forest also show evidence of nitrogen enrichment from agricultural sources (Sharpe and Nichols 2007; Baker 2012). Other studies have found changes in fish community structure associated with increased nutrients (Evans-White et al. 2013; Taylor et al. 2014), although mechanisms are unclear. However, elevated nutrient loading may be responsible for changes in water clarity and benthic habitats that we have observed in the Conasauga River. In particular, recent synoptic surveys along the mainstem have documented increases in water turbidity from <2 nephelometric turbidity units in national forest, to >10 nephelometric turbidity units within our study reach (Argentina et al. 2010b), even during periods of limited runoff. This contrasts sharply with conditions during the late 1980s, when at least two of the monitored shoals in our study reach had sufficiently low turbidity (e.g., <5 nephelometric turbidity units) to permit snorkeling observations of Amber Darter habitat use (Freeman and Freeman 1994). Currently, visual surveys of fishes by snorkelers are only effective in the more upstream reaches of the river (Hagler et al. 2011). Shifts in benthic habitat in the Conasauga study reach include loss of previously lush growths of the benthic macrophyte *Podostemum ceratophyllum* (Freeman and Freeman 1994). *Podostemum* provides habitat for shoal-dwelling fishes and their macroinvertebrate prey (Hutchens et al. 2004; Argentina et al. 2010b), and currently is sparse at most sites in the study reach in contrast to thick growths at sites farther upstream (Argentina et al. 2010a; Baker 2012) and also in the majority of the Etowah River study sites. Finally, since about 2000, we have observed extensive mats of benthic algae in the study shoals during low-flow conditions of dry summers (Freeman et al. 2007). Field notes from 2000 include observations of dead juvenile minnows associated with algal mats in low-velocity areas. We had not made note of extensive algal mats during similar low-flow conditions when conducting habitat-use studies in the 1980s. Extensive algal blooms can alter habitat by covering gravel substrates where fishes deposit eggs and forage for macroinvertebrates, and can smother *Podostemum*. Algal blooms can also alter water chemistry (shifting e.g., ammonium [NH_4^+] to the more toxic unionized form, ammonia [NH_3]; Valenti et al. 2011; Strayer and Malcom 2012) by depleting dissolved carbon dioxide and elevating pH during daylight, and by depleting dissolved oxygen levels at night.

Whether contaminants (including pesticide derivatives and steroid hormones) or elevated nutrients are directly or indirectly responsible for declining fish species occurrences in the Conasauga study reach is not known. Other unidentified factors may be responsible, such as warming temperatures or disease. Whatever the cause(s) of species declines, the monitoring data and analyses presented here may provide a basis for assessing the effectiveness of future management actions taken to restore declining fish species. In particular, if management actions were taken to reduce the flux of agriculturally derived materials into the Conasauga, then continued monitoring to detect increases in colonization rates for small-bodied, shoal-dwelling fishes could provide evidence that those actions were in fact improving faunal viability.

Applying hierarchical, dynamic occupancy models to long-term data

Although our findings of faunal decline in the Conasauga River and the contrasting lack of apparent decline in the Etowah River could have been deduced from the field observations, we suggest that there are substantial benefits to fitting the data sets to dynamic occupancy models. For one, the modeling approach allows one to incorporate incomplete detection when estimating changes in taxa occurrence over the monitoring period, thus explicitly accounting for the possibility that species are sometimes missed during surveys when concluding that a species has declined. Species-specific abundances may strongly influence detection (Bayley and Peterson 2001; Royle and Nichols 2003), so it is possible that we have overestimated detection probabilities in the Conasauga (which are based mostly on early surveys) for recent years if fish abundances have declined along with colonization rates. If true, then our occupancy estimates could be biased low for the later years. We strongly suspect that this would not alter our inference that particular taxa have declined, but it does exemplify the difficulty of knowing whether a species is truly lost from a site or system when individual capture probabilities are low or unknown (Etnier 1994; Grogan and Boreman 1998). Nonetheless, accounting for incomplete detection using the best-available data will, at minimum, reduce the bias associated with false-negative observations.

Evaluating assemblage-wide metapopulation rates, made possible by the hierarchical model structure, has been helpful for identifying trends that might not be apparent from snapshots of species occupancy at differing points in time or from species-specific models. This assemblage approach uses the potential information contained in observations of multiple taxa declining (or increasing) in estimated occupancy in a given time interval to evaluate temporal variation in overall faunal persistence or colonization probabilities. By including time-interval specific covariates (in our case, frequencies of low- and high-flow days), one can also evaluate support for hypothesized causes of temporal variation in dynamics. Results can identify shifts in underlying dynamics, such as declining colonization rates in the Conasauga, as well as trends for data-poor species (for example, the Coosa Shiner, which our model predicts has declined in the Conasauga even though we have never observed the species in >3 sites in a given year). In comparison, if we had more simply estimated the number of species occupying the Conasauga study shoals at differing time points, we could have concluded that three or four taxa have declined in occupancy, but not that colonization rates have declined across the entire assemblage.

Identifying changes in metapopulation dynamics, and effects of environmental covariates on those dynamics, is useful for developing hypotheses about future trajectories, either for species richness or species-specific occupancy. For example, one could use estimated persistence (P) and colonization (C) probabilities for taxa of interest in an incidence function (i.e., occupancy at equilibrium $= C/(C + (1 - P))$; Hanski 1994) to forecast the expected proportion of sites that those taxa would occupy at equilibrium. Thus, given probabilities equal to 0.95 for persistence and 0.1 for colonization, we would expect an occupancy probability of 0.66, ignoring environmental stochasticity. These persistence and colonization probabilities are similar to estimates for approximately 20 taxa in the Conasauga, most of which were estimated to occupy ≥ 11 of our 13 monitored sites, at the end of our time-series. In the absence of any other events, we thus expect occupancy by these taxa to decline to approximately 9 of the 13 sites, on average. Stochastic extirpations will further lower expected occupancy, and more severely for taxa with low colonization potential. For example, substantially lower-than-average colonization rates for several taxa in the Etowah identify these species as less likely than other taxa to recover if lost from the subset of sites where each now occurs. Similarly, species such as the Blacktail Shiner that show measureable effects of low- and high-flow frequency on persistence and colonization probabilities can be predicted to respond to shifts in streamflow regime—in this case, expanding in occupancy in the Etowah in response to extended low-flows.

Conclusions

Ultimately, studies of fish survival and recruitment and associated changes in factors such as water chemistry, habitat conditions, and prey availability may be necessary to identify causal mechanisms of shoal fish decline in the Conasauga River. Nonetheless, the occupancy analyses presented here provide a starting point for assessing status and trends for a suite of species in two rivers valued for biodiversity conservation. Although causes are unknown, we conclude that faunal declines that have occurred in the Conasauga are not regional given that similar losses in occupancy are not evident in a nearby river with similar species composition. One could reasonably infer from our analysis that the assemblage of fishes at our Conasauga study sites will continue to decline unless future colonization rates increase.

Monitoring data have been essential for identifying declining taxa in the Conasauga River study sites. Lacking systematic monitoring, scientists often must cobble together information from unrelated sampling efforts to infer changes in population status. For example, only 3 of 27 studies reported in a symposium on historical changes in riverine fish assemblages were able to utilize systematically collected long-term data (Rinne et al. 2005). Continued monitoring in the Conasauga and Etowah rivers (particularly if expanded to include additional sites and within-year replicates) would allow assessment of future trends and population responses to management actions.

Archived Material

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File A1. Species detections by survey for 13 Conasauga River sites (1995–2014) and 10 Etowah River sites (2001–2014). Data fields are: species (Taxon); site name (Site.no); survey year and replicate number written as xxxx.y, where xxxx is year and y is replicate number (1–3). A value of "1" is shown where a species was detected in a survey; "0" indicates the species was not detected in the survey. Blanks indicate no survey data are available for a given site, year, and replicate combination.

Found at http://dx.doi.org/10.5061/dryad.645r/1 (55.99 KB XLS).

File A2. Just Another Gibbs Sampler (JAGS) code as implemented in Program R using the package r-jags to fit multitaxa dynamic occupancy models to detection/nondetection data for the Conasauga and Etowah river study sites. The terms "ntaxa," "nsite," and "nyear" refer to the number of taxa, sites, and years, respectively, included in the data set; nrep is the maximum number of replicate, within-year surveys across all sites and years. Code is shown for the basic (no covariates) model, with lines added and marked with "#" to show how random-slopes models were fit for streamflow covariates.

Found at http://dx.doi.org/10.5061/dryad.645r/2 (96 KB DOCX).

Table A1. Detection probabilities for 26 fish taxa at 13 sites in the Conasauga River mainstem sampled multiple years, 1995–2014, and for 28 fish taxa at 10 sites in the Etowah River mainstem sampled multiple years, 2001–2014. Values are posterior means (and 95% credible intervals) estimated using a multitaxa, dynamic occupancy model applied to detection data for each river.

Found at http://dx.doi.org/10.5061/dryad.645r/3 (123 KB DOCX).

Table A2. Species-specific rarity values used as covariates in dynamic occupancy models for 26 fish taxa in the Conasauga River (1995–2014) and 28 taxa in the Etowah River, Georgia (2001–2014). Values are the proportion of all surveys having counts of individuals in which a species was represented by 1–4 individuals.

Found at http://dx.doi.org/10.5061/dryad.645r/4 (92 KB DOCX).

Table A3. Species-specific slope estimates in logit-regression models of persistence and colonization probabilities as functions of a variable representing low-flow frequency in dynamic occupancy models for 26 fish taxa at 13 sites in the Conasauga River (1995–2014). The low-flow variable was an annual count of days in March through September with daily average discharge less than the 10th percentile of the mean monthly flow based on the period-of-record for U.S. Geological Survey streamgage 02384500, Conasauga River near Eton, Georgia. Prior to analysis, the flow variable was transformed by subtracting the mean and dividing by the standard deviation of the untransformed data. Species-specific slopes are on the logit scale and were calculated as the sum of the fixed-effect and the species-specific random effect for the slope relating low-flow days to persistence or colonization. The 2.5% and 97.5% values bracket the 95% credible interval for the slope estimate.

Found at http://dx.doi.org/10.5061/dryad.645r/5 (130 KB DOCX).

Table A4. Species-specific slope estimates in logit-regression models of persistence and colonization probabilities as functions of a variable representing high-flow frequency in dynamic occupancy models for 26 fish taxa at 13 sites in the Conasauga River (1995–2014). The high-flow variable was an annual count of days in March through September with daily average discharge greater than the 90th percentile of the mean monthly flow based on the period-of-record for U.S. Geological Survey streamgage 02384500, Conasauga River near Eton, Georgia. Prior to analysis, the flow variable was transformed by subtracting the mean and dividing by the standard deviation of the untransformed data. Species-specific slopes are on the logit scale and were calculated as the sum of the fixed-effect and the species-specific random effect for the slope relating high-flow days to persistence or colonization. The 2.5% and 97.5% values bracket the 95% credible interval for the slope estimate.

Found at http://dx.doi.org/10.5061/dryad.645r/6 (139 KB DOCX).

Table A5. Species-specific slope estimates in logit-regression models of persistence and colonization probabilities as functions of a variable representing low-flow frequency in dynamic occupancy models for 28 taxa at 10 sites in the Etowah River, Georgia (2001–2014). The low-flow variable was an annual count of days in March through September with daily average discharge less than the 10th percentile of the mean monthly flow based on the period-of-record for U.S. Geological Survey streamgage 02392000, Etowah River at Canton, Georgia. Prior to analysis, the flow variable was transformed by subtracting the mean and dividing by the standard deviation of the untransformed data. Species-specific slopes are on the logit scale and were calculated as the sum of the fixed-effect and the species-specific random effect for the slope relating low-flow days to persistence or colonization. The 2.5% and 97.5% values bracket the 95% credible interval for the slope estimate.

Found at http://dx.doi.org/10.5061/dryad.645r/7 (135 KB DOCX).

Table A6. Species-specific slope estimates in logit-regression models of persistence and colonization probabilities as functions of a variable representing high-flow frequency in dynamic occupancy models for 28 taxa at 10 sites in the Etowah River, Georgia (2001–2014). The high-flow variable was an annual count of days in March through September with daily average discharge greater than the 90th percentile of the mean monthly flow based on the period-of-record for U.S. Geological Survey streamgage 02392000, Etowah River at Canton, Georgia. Prior to analysis, the flow variable was transformed by subtracting the mean and dividing by the standard deviation of the untransformed data. Species-specific slopes are on the logit scale and were calculated as the sum of the fixed-effect and the species-specific random effect for the slope relating high-flow days to persistence or colonization. The 2.5% and 97.5% values bracket the 95% credible interval for the slope estimate.

Found at http://dx.doi.org/10.5061/dryad.645r/7 (140 KB DOCX).

Figure A1. March–September hydrograph, 1982–2014, U.S. Geological Survey streamgage 02384500 Conasauga River near Eton, Georgia, highlighting low-flow years during the study period (red).

Found at http://dx.doi.org/10.5061/dryad.645r/8 (86 KB JPG).

Figure A2. March–September hydrograph, 1982–2014, U.S. Geological Survey streamgage 02392000 Etowah River at Canton, Georgia, highlighting low-flow years during the study period (red).

Found at http://dx.doi.org/10.5061/dryad.645r/9 (84 KB JPG).

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