

ARTICLE

Shifting taxonomic and functional community composition of rivers under land use change

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Abstract

Land use intensification has led to conspicuous changes in plant and animal communities across the world. Shifts in trait-based functional composition have recently been hypothesized to manifest at lower levels of environmental change when compared to species-based taxonomic composition; however, little is known about the commonalities in these responses across taxonomic groups and geographic regions. We investigated this hypothesis by testing for taxonomic and geographic similarities in the composition of riverine fish and insect communities across gradients of land use in major hydrological regions of the conterminous United States. We analyzed an extensive data set representing 556 species and 33 functional trait modalities from 8023 fish communities and 1434 taxa and 50 trait modalities from 5197 aquatic insect communities. Our results demonstrate abrupt threshold changes in both taxonomic and functional community composition due to land use conversion. Functional composition consistently demonstrated lower land use threshold responses compared to taxonomic composition for both fish (urban $p = 0.069$; agriculture $p = 0.029$) and insect (urban $p = 0.095$; agriculture $p = 0.043$) communities according to gradient forest models. We found significantly lower thresholds for urban versus agricultural land use for fishes (taxonomic and functional $p < 0.001$) and insects (taxonomic $p = 0.001$; functional $p = 0.033$). We further revealed that threshold responses in functional composition were more geographically consistent than for taxonomic composition to both urban and agricultural land use change. Traits contributing the most to overall functional composition change differed along urban and agricultural land gradients and conformed to predicted ecological mechanisms underpinning community change. This study points to reliable early-warning thresholds that accurately forecast compositional shifts in riverine communities to land use conversion, and highlight the importance of considering trait-based indicators of community change to inform large-scale land use management strategies and policies.

KEYWORDS

deforestation, fish, freshwater conservation, functional traits, gradient forest model, macroinvertebrate

INTRODUCTION

Humans have rapidly transformed the global landscape, converting natural forests, grasslands, and wetlands into agricultural and urban/suburban developments (van Vliet, 2019; Winkler et al., 2021). Increasing intensity and spatial extent of human land use are major contributors to the global biodiversity crisis, causing dramatic taxonomic (species-based) and functional (trait-based) restructuring of biological communities (Cheung et al., 2013; de Castro et al., 2017; Flynn et al., 2009). By providing a mechanistic basis to community-environment relationships, functional approaches can help anticipate, and attempt to avoid, thresholds in land use conversion beyond which catastrophic ecological impacts occur (Barnosky et al., 2012; Dakos et al., 2019; Folke et al., 2004).

Emerging research shows that stark shifts in functional community composition can manifest at lower thresholds of environmental change than shifts in taxonomic composition (Clements & Ozgul, 2016; Rogers et al., 2018). This can occur because, although the taxonomic composition of a community may change (Rumschlag et al., 2023), whether or not concurrent changes in functional community composition also occur depends on trait constraints (phylogenetic and ecological) and redundancy among species, as well as the directional selection imposed by environmental pressures on particular trait(s). For example, Clements and Ozgul (2016) found that shifts in body size distributions signaled impending population decline well before changes in traditional demographic metrics. This evidence suggests that an exclusively taxonomic structure and composition perspective may restrict our ability to predict the biodiversity effects of land use change. However, few functional traits have even been identified as precursors to population or community change, suggesting the need for more careful evaluation. Furthermore, functional approaches transcending species identity allow for broader generalization of community-environment inference across diverse geographies and phylogenies (McGill et al., 2006; Menezes et al., 2010; Mouillot et al., 2013). Trait-based threshold detection involving multiple taxonomic groups therefore has the potential to enhance our understanding of the key biological mechanisms leading to abrupt community shifts in response to land use conversion, informing more transferable science that helps predict and prevent breaching these thresholds in the future (Mouillot et al., 2013; Olden et al., 2010).

Functional trait responses of freshwater communities to land use change suggest that potential commonalities among regions and taxonomic groups may exist (de Castro et al., 2017; Merckx et al., 2018; Olden et al., 2004). Communities in urban and agricultural landscapes

generally consist of species with small body size, rapid life histories (e.g., short-lived, early maturity), and high dispersal ability (Allan et al., 2015; Birkhofer et al., 2015; Merckx et al., 2018). Species with narrow dietary breadth and low fecundity are similarly sensitive to land use disturbance (Clavel et al., 2011; Doledec et al., 2011; Gámez-Virués et al., 2015). Despite these similarities, the degree of urban versus agricultural land use change that invokes significant shifts in functional community change occurs may differ. For example, urbanization can intensify stormwater hydrology that homogenizes instream habitat (Walsh et al., 2005), often resulting in greater impacts on stream biodiversity when compared to agricultural activities (Booth et al., 2016; Petsch et al., 2021; Watson et al., 2014). To date, major knowledge gaps exist with respect to whether taxonomic and functional community composition exhibit threshold responses to land use change and, if so, whether such thresholds are concordant or differ among land use types, geographic regions, or major taxonomic groups.

This study provides the first national-scale investigation of potential threshold responses of taxonomic and functional community composition to land use conversion for two major freshwater taxonomic groups. We compiled species taxa and trait data on thousands of riverine fish and insect communities across multiple decades in the conterminous United States. For major hydrological regions, we use gradient forest (GF) models to test for the existence of thresholds in urbanization and agricultural land use conversion beyond which communities demonstrate abrupt changes in taxonomic and functional composition. We then characterize and compare threshold values across geographic regions and investigate the relative contributions of traits to overall functional composition response to urban and agricultural land use change.

Informed by previous studies we make the following informed hypotheses for threshold community responses to land use conversion. First (H1), shifts in functional composition will occur at lower thresholds of human land use disturbance than changes in taxonomic composition (Dakos et al., 2019). Second (H2), threshold responses of taxonomic and functional composition will manifest at lower levels of watershed urbanization compared to agricultural land use due to the more acute changes caused by urbanization (i.e., the urban stream syndrome) (Booth et al., 2016; Watson et al., 2014). Third (H3), based on theoretical expectations of similar trait responses to environmental challenges irrespective of taxonomy (Mims et al., 2010; Zuellig & Schmidt, 2012), threshold responses to land use conversion will be more geographically consistent in functional than taxonomic community composition. Fourth (H4), because co-evolved traits confer fitness advantages in specific environmental

settings (Southwood, 1977), trait contributions to functional composition change will differ between gradients of urban and agricultural land use. By addressing these questions, our study provides a novel test of the possible existence and geographic and taxonomic consistency of threshold responses of freshwater communities to land use change at broad scales.

METHODS

Community data

We compiled freshwater fish and insect community data from 21,250 to 15,337 sites across the conterminous United States to provide an extensive national-scale representation of fish and aquatic insect community structure in a broad range of stream and river habitats. Fish data sources included the national and regional United States Environmental Protection Agency (USEPA) Environmental Monitoring and Assessment Program (EMAP), the United States Geological Survey (USGS) National Water Quality Assessment Program (NAWQA), numerous state agency biomonitoring programs, and large-scale sampling efforts by other organizations and universities (Midway et al., 2016; Moore & Olden, 2017; U.S. Environmental Protection Agency [U.S. EPA], 2016, 2020). The aquatic invertebrate database consisted of all available records collected from the USEPA's 2004–2005, 2008–2009, 2013–2014, and 2018–2019 National Rivers and Streams Assessment (U.S. EPA, 2006, 2016, 2020) and USGS NAWQA during 1993–2015.

Surveys were designed to accurately characterize species occurrence and abundance of the target biological assemblage at each site. Fish sampling methods primarily included standardized backpack or boat electrofishing (with seine netting in limited instances). All efforts involved sampling a defined stream reach length sufficient for characterizing local community structure, then identifying and enumerating all captured individuals. For example, small streams in EMAP involved backpack electrofishing within sample reaches 40 times the channel wetted width in length (Lazorchak et al., 2000), and large rivers in EMAP were sampled by raft electrofishing along 100 times the mean wetted width to achieve a similar sampling sufficiency (Hughes et al., 2002). Fish are reported at the species level, and scientific names were harmonized according to FishBase using the *rfishbase* package in R (Froese & Pauly, 2019). Aquatic invertebrate sampling methods included a standardized multiple- or target-habitat approach of defined length using a 500- μ m mesh D-frame net. Sampled reach lengths were typically

40 times the channel width, 150–300 m in length for wadeable streams or 500–1000 m in length for nonwadeable streams (Hughes & Peck, 2008; Moulton II et al., 2002). To provide consistent taxonomic treatment across all samples, we assigned all insects to the lowest but unambiguous taxonomic level, predominantly species (43%) and genus (49%). To further ensure comparability across sampling surveys, relative abundance of each taxon in a unique sample was computed to reduce the effects of different, but always comprehensive, sampling approaches.

We retained sites that were located on natural stream reaches (removing drainage canals, artificial connectors, and ditches) according to the National Hydrography Dataset (NHD) Plus Version 2 Dataset (NHDPlus V2 data model version 2.1 released on 2019, <https://nhdplus.com/NHDPlus/index.php>). For surveys conducted on multiple occasions on the same stream reach, we retained the sample collected closest to 2010, representing the timing of the land use survey (see details below). We further subsampled the remaining data set to only include sites separated by at least three linear kilometers. This subsampling approach avoided unbalanced spatial coverage of data that may contribute to spatial autocorrelation in community composition.

The final data set included 556 fish species occurring in 8023 sites and 1434 aquatic insect taxa from 5197 sites collected during the period 1990–2019 (Figure 1; Appendix S1: Table S1). The survey sites contained a median of 10 (range: 1–51) fish species and 34 (range: 1–83) aquatic insect taxa per site (Appendix S1: Table S1).

Trait data and functional composition

Fish species and aquatic insect taxa were characterized by a set of functional traits—behavioral, morphological, phenological, or physiological characteristics—which have been widely reported as being related to the sensitivity of organisms to environmental change (Tyler et al., 2012). Traits predominantly described attributes of dispersal and feeding modes (behavioral), morphology, physiology, and reproductive (phenology) ecology that contribute to a species' resistance and resilience to disturbance. Functional traits were deemed more readily altered through evolutionary processes independently of other traits and exhibited minimal correlation with others (Wilkes et al., 2020). Ordinal (e.g., substrate preference) and nominal (e.g., voltinism) traits were assigned a single modality based on a majority-of-evidence rule according to adult preferences, and median values were assigned for continuous traits when ranges were presented (Table 1). Continuous traits (e.g., maximum total body length) were then characterized into discrete trait modalities, which after combining with

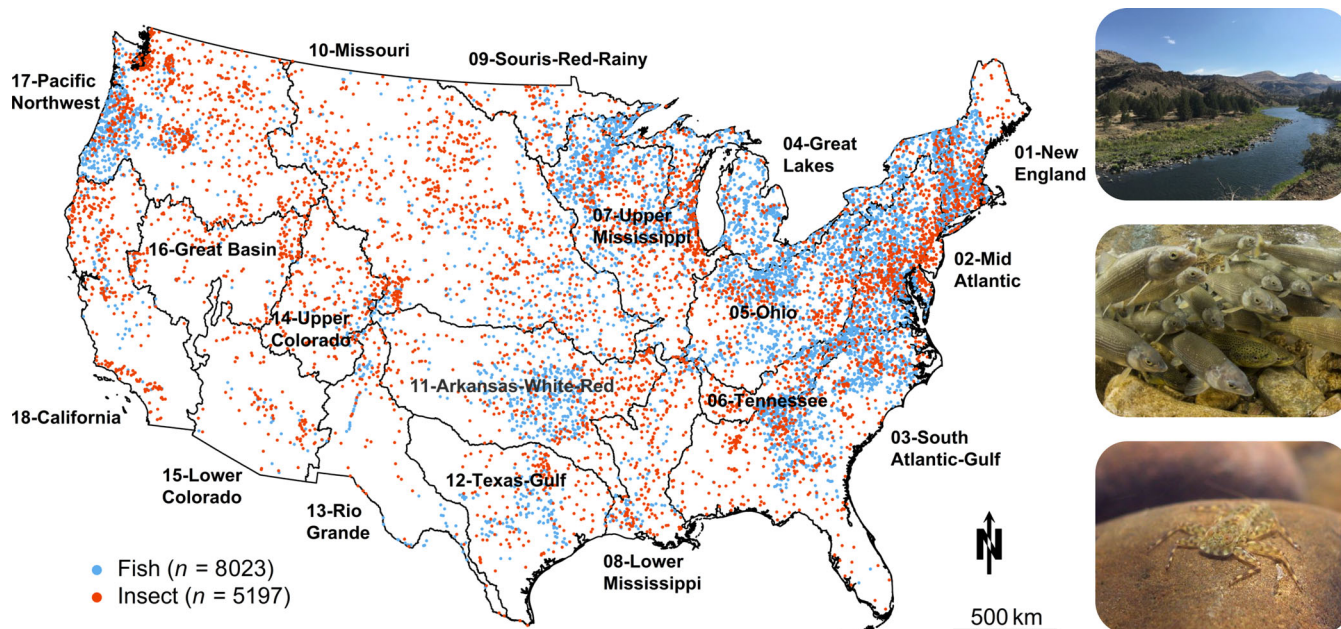


FIGURE 1 Locations of the 8023 fish community surveys (period: 1990–2013) and 5197 aquatic insect community surveys (period: 1993–2019) across the conterminous USA. Major hydrological regions are delineated according to HUC2 hydrological units. Images on right include the John Day River, Oregon (top, Julian Olden), mountain whitefish and brown trout (middle, Dave Herasimtschuk/Freshwaters Illustrated), and *Epeorus* mayfly larvae (bottom, Jeremy Monroe/Freshwaters Illustrated).

other categorical traits enabled the creation of a taxon-by-trait modality presence–absence matrix.

We sourced seven fish traits from an updated trait database presented in Giam and Olden (2016) and Sebastien et al. (2021) included fecundity, maturity, maximum total body length, reproductive guild, substrate preference, trophic guild, and water temperature preference; a total of 33 trait modalities were characterized (Table 1). Reproductive guilds were assigned according to Balon (1975) and substrate preference, temperature preference, and trophic guilds based on published life-history accounts for species. All fish functional traits were assigned at the species level. We selected 15 aquatic insect traits represented by adult flying strength, adult life span, body armoring, development rate and synchronization, desiccation resistance, habit, maximum crawling rate, occurrence in drift, respiration, rheophily, size at maturity, swimming ability, thermal, trophic guild, and voltinism; a total of 50 trait modalities were characterized (Table 1). Aquatic insect trait assignments were derived primarily from the freshwater insects CONUS database (Twardochleb et al., 2021) and supplemented with data from Poff et al. (2006). Most aquatic insect taxa traits were assigned at the genus (88%) level, and the remainder were assigned at the tribe, subfamily, or family level (9%). The remaining aquatic insect taxa (3%) had completely missing trait information. Overall, 4.7% and 16.8% of trait values

were missing for fish species and aquatic insect taxa, respectively (Appendix S1: Table S2).

We imputed missing trait values using a nonparametric random forest (RF) model. The RF algorithm outperforms alternative approaches (e.g., data deletion) even without phylogenetic information, being less likely to introduce statistical bias and interpretation error (Penone et al., 2014). Fish family and aquatic insect order, as a surrogate of phylogenetic relationships between taxa, were kept as imputation variables. The imputation was performed using the R package missForest (Stekhoven & Bühlmann, 2012) with a total of 1000 trees generated for each RF model in R version 4.0.3 (R Core Team, 2020). The imputed values were accurate with missForest out-of-bag proportion of correctly classified entries of 0.78 for fishes and 0.92 for aquatic insects.

We calculated relative trait modality abundance in a functional community composition matrix by multiplying the site-by-taxon abundance matrix by the taxon-by-trait modality presence–absence matrix and then dividing by the sum of taxa abundance values (Miller et al., 2019). This method accounted for the effects of different numbers of trait modalities among trait categories in the calculations. The end result was a site-by-trait modality matrix containing values that represented the proportion of taxa in each site exhibiting each trait modality, with the sum of relative abundance of all trait modalities in each trait category equaling 1.

TABLE 1 Trait categories and modalities of fish species and aquatic insect taxa used in this study.

Trait category	Type	Trait modality description and (or) units
Fish		
Fecundity	Continuous	Total fecundity (no. eggs or offspring) per spawning season per female (low: ≤ 300 ; low/medium: 300–1012; medium/high: 1012–6399; high: ≥ 6399)
Maturity	Continuous	Ratio of mean age of female (secondary male) at maturation to mean length of female (secondary male) at maturation (small: ≤ 0.27 ; small/medium: 0.27–0.37; medium/large: 0.37–0.50; large: ≥ 0.50)
Maximum total body length	Continuous	Maximum total body length (small: ≤ 80 mm; small/medium: 80–120 mm; medium/large: 120–305 mm; large: ≥ 305 mm)
Reproductive guild	Nominal	Bearer (e.g., internal, gill chamber), guarders (nest spawners or substratum choosers), nonguarders (brood hiders or open substratum spawners), and offshore (catadromous species)
Substrate preference	Nominal	Rubble (bedrock, cobble, gravel), sand, silt/mud, vegetation, and various
Trophic guild	Nominal	Herbivore–detritivore (ca. $\geq 25\%$ plant matter), invertivore, invertivore/piscivore, omnivore (ca. $\leq 5\%$ plant matter), and piscivore (including parasites)
Water temperature preference	Ordinal	Cold (10–17°C), cold/cool, cool (17–26°C), cool/warm, and warm ($\geq 26^\circ\text{C}$)
Aquatic insect		
Adult flying strength	Nominal	Weak (taking frequent breaks while flying, or flight is low to the ground) and strong (able to fly into a light breeze or fly for several miles without breaks)
Adult life span	Ordinal	Very short (≤ 1 week), short (< 1 month), and long (≥ 1 month)
Armoring	Nominal	Good (e.g., some cased caddisflies), none (soft-bodied forms), and poor (heavily sclerotized)
Development rate and synchronization	Nominal	Slow seasonal (slow growth, often over winter, tend to mature in spring), fast seasonal (rapid growth during one season or after egg diapause), and nonseasonal (individuals of all stages present at all times)
Desiccation resistance	Nominal	Absent (i.e., cannot survive desiccation), and present
Habit	Nominal	Burrower, clinger, skater, swimmer, sprawler, and climber
Maximum crawling rate	Ordinal	Very low (≤ 10 cm/h), low (< 100 cm/h), and high (≥ 100 cm/h)
Occurrence in drift	Nominal	Abundant (dominant in drift samples), common (typically observed), and rare (catastrophic only)
Respiration	Nominal	Tegument, gills, and plastron spiracle
Rheophily	Nominal	Depositional (occupies running-water pools or margins with fine sediments, e.g., sand and silt), depositional-erosional (occupies both erosional and depositional habitats), and erosional (occupies running-water riffles with coarse sediments cobbles, pebble, gravel)
Size at maturity	Ordinal	Maximum body size: small (≤ 9 mm), large (≥ 16 mm), and medium (9–16 mm)
Swimming ability	Nominal	None, weak, and strong
Thermal	Ordinal	Cold stenothermal ($\leq 5^\circ\text{C}$), cold-cool eurythermal (0–15°C), cool-warm eurythermal (5–30°C), warm eurythermal (15–30°C), and hot eurythermal ($\geq 30^\circ\text{C}$)
Trophic guild	Nominal	Collector-filterer, collector-gatherer, herbivore (scraper, piercer, and shredder), predator (piercer and engulfer), and shredder (detritivore)
Voltinism	Nominal	No. generations per year. Semivoltine (< 1 generation per year), univoltine (1 generation per year), and bi_multivoltine (> 1 generation per year)

Note: Continuous trait characteristics were converted into categorical data based on the 25th, 50th, and 75th percentile values.

Land use and environmental data

For each site, we calculated the percent area of the contributing subwatershed in urban (summed impervious area) and agricultural land (summed across crop and

perennial grasses for grazing categories). The contributing subwatershed for each site was delineated according to HUC12 hydrological units as defined by the USGS (2016) from the Watershed Boundary Dataset (Appendix S1: Figure S1). The land use classes were

derived from the Global Man-made Impervious Surface data set (de Colstoun et al., 2017) and North American Land-Change Monitoring System (Latifovic et al., 2016) with both data sets at a spatial resolution of 30 m referenced to 2010. Urban surface area of subwatersheds ranged from 0% to 60.0% (mean \pm SD: $1.9\% \pm 5.2\%$) for the fish community sites and ranged from 0% to 71.8% ($2.5\% \pm 6.7\%$) for the aquatic insect community sites (Appendix S1: Table S3). Agricultural surface area of subwatersheds ranged from 0% to 95.0% ($27.0\% \pm 28.0\%$) and 0% to 95.6% ($24.3\% \pm 27.5\%$) for the fish and aquatic insect community sites, respectively. Land use has remained largely unchanged during the time period represented by the biological community data, with an estimated expansion in percent urban at a median of 1.5 (± 2.3) km² but a loss in percent agriculture at a median of 2.2 (± 5.3) km² across all subwatersheds of all hydrological units during the recent past half century (Chen & Olden, 2020).

A suite of natural and anthropogenic environmental variables was collated for each site to broadly describe habitat availability, productivity, and hydrologic alteration—factors commonly predictive of aquatic community composition and covary with land use (Fullerton et al., 2010; Jackson et al., 2001; Rice et al., 2001). Variables included total upstream catchment area (in square kilometers), elevation (in meters), long-term (1971–2000) average annual air temperature (in degrees Celsius), modeled long-term (1971–2000) average annual “naturalized” discharge without anthropogenic water use in the form of abstractions or impoundments (in cubic meters per second), and degree of flow regulation (in percentage) (Appendix S1: Table S3), which were sourced from NHDPlus (McKay et al., 2010, 2019) and the 3D Elevation Program data set (USGS, 2017). The total upstream catchment area was delineated from the downstream end of the NHD flowline for each site. Elevation was extracted at each sampling site according to a 1 arc-second (~30 m) resolution of digital elevation models of the 3D Elevation Program data set. The long-term average annual air temperature was computed over the catchment area for each site according to the Parameter-elevation Regressions on Independent Slopes Model data (Daly et al., 2002). The modeled long-term average annual “naturalized” discharge was estimated according to the Enhanced Runoff Method (McKay et al., 2019). Degree of flow regulation was calculated as a percentage of estimated annual stream discharge volume that could be stored by all upstream reservoirs (Cooper & Infante, 2017). The community sites varied in the total upstream catchment area (fish: $2018.1 \pm 16,503.8$ km²; insect: $34,413.2 \pm 264,683.0$ km²), elevation (fish: 408.4 ± 488.3 m; insect: 575.9 ± 671.3 m), long-term average annual air temperature (fish: $10.4 \pm 4.1^\circ\text{C}$; insect: $10.6 \pm 4.5^\circ\text{C}$),

modeled long-term average annual “naturalized” discharge (fish: 362.8 ± 5107.6 m³/s; insect: $6161.4 \pm 51,557.6$ m³/s), and degree of flow regulation (fish: $9.0\% \pm 60.0\%$; insect: $17.7\% \pm 91.7\%$), thus representing a broad range of riverine types and sizes across a wide range of regions (Appendix S1: Figure S1 and Table S3).

Quantifying land use thresholds of taxonomic and functional community change

We developed GF models to test for threshold responses of aquatic taxonomic and functional community composition change to percent urban and percent agricultural land use for different hydrological regions according to HUC2 hydrological units. GF is a highly flexible, non-parametric, and nonlinear method that can be used to describe the magnitude and pattern of change in community composition in relation to environmental gradients (e.g., land use changes), while simultaneously accounting for other potential explanatory variables (e.g., catchment area and climatic variables, also described in more detail below) in a multivariate manner (Ellis et al., 2012; Pitcher et al., 2012). GF is an ensemble of RF models (Breiman, 2001) that averages results from a forest of regression trees, where each tree uses a recursive partitioning algorithm to split data into a nested series of mutually exclusive groups with the goal of maximizing the homogeneity of the response variable (i.e., relative abundance of species taxa and trait modality in our case). GF extends these strengths to all responses of taxonomic taxa and functional trait modalities and then quantifies community compositional change along gradients that includes a test of threshold responses by collating all the individual split values and improvements from the RF models (Pitcher et al., 2012). The goodness-of-fit R^2 is the proportion of the variance explained for each taxon and trait modality by the RF model through out-of-bag cross-validation, which measures predictive ability by the predictors on each particular taxon and trait modality (Ellis et al., 2012). We then aggregated split values (standardized by the density of observations) for all taxa and trait modality models with $R^2 > 0$ to quantify the magnitude of compositional change with increasing percent urban or agricultural land use. The shape of the cumulative distribution curves with the standardized ratio of split density >1 indicates the highest manifestation of abrupt changes in community composition (Pitcher et al., 2012). If the split density did not exceed 1, we treated this as the absence of a threshold. From the distribution curve we identified all peaks and the 95% confidence

interval (CI) of all standardized ratios of split density identified >1 . Threshold values of percent urban and percent agricultural land use for each hydrological region was identified as the first encountered (minimum) peak value that exceeded the 95% CI value (Chen & Olden, 2020) (Appendix S1: Figures S2–S9). The threshold values indicate where the first substantial change in aquatic taxonomic and functional community composition occurs in relation to increasing urban and agricultural land use.

For each fish and aquatic insect community, we used GF to model taxonomic (relative taxa abundance) and functional (relative trait modality abundance) composition as a function of urban land use, agricultural land use, total upstream catchment area, long-term average annual air temperature, elevation, modeled long-term average annual “naturalized” discharge, and degree of flow regulation (described above; Appendix S1: Figures S10–S13). Relative abundance data for taxa and trait modality were ln-transformed to meet statistical requirements, whereas GFs are invariant to monotonic transformations of explanatory variables (Wagenhoff et al., 2017). We developed GF models by using the R packages *extendedForest* (Liaw & Wiener, 2002) and *gradientForest* (Ellis et al., 2012), with a total of 1000 trees generated for each RF model (Chen et al., 2023). We used the default constrained permutations with a correlation threshold of 0.5 to reduce the influence of multicollinearity (Ellis et al., 2012). We tested for a significant change between threshold responses of taxonomic and functional composition along each urban and agricultural land use gradient (H1) and in threshold responses of taxonomic and functional composition between urban and agricultural land use (H2), by means of one-tailed paired *t*-test at a 0.05 significant level across hydrological regions. We used a nonparametric Fligner–Killeen (FK) test to determine the differences in the homogeneity of variance across hydrological regions between threshold response of taxonomic and functional composition to land use changes (H3).

Contribution of trait modalities to threshold responses in functional community change

We quantified the contributions of individual trait modalities to the overall functional composition change along the urbanization and agricultural gradients. Each split value from the aforementioned GF model is associated with an importance reflecting the degree of change in relative abundance of each trait modality with increasing

percent urban or agricultural land use. We calculated the maximum accumulated split importance values for trait modality models with $R^2 > 0$ for each hydrological region (Appendix S1: Figures S14–S17). All split importance values were standardized by the density distribution of the observations to control for nonuniform sampling along the gradients and then normalized by their respective R^2 to facilitate comparisons among hydrological regions (Pitcher et al., 2012). Larger importance value indicates a trait modality contributes more to the overall functional composition response to increasing percent urbanization or agricultural land use. For each fish and aquatic insect trait modality, we plotted the median and fifth to 95th percentile distribution of standardized and normalized split importance across all hydrological regions with $R^2 > 0$. We identified the most influential trait modalities with ranked top median percentile of standardized and normalized split importance of at least half the number of HUC2 hydrological units with $R^2 > 0$. We also used a nonparametric paired *t*-test to compare the difference in the importance of each modality between urban and agricultural land use at a 0.05 significant level (H4).

Using the GF-identified functional composition threshold values from each hydrological region, we estimated the response direction of relative abundance of each trait modality with increasing land use gradient. For each hydrological region, we used a nonparametric *t*-test to compare the mean relative abundance of each trait modality between groups with percent land use lower and greater than the threshold values of urban and agricultural land use. Where a *t*-value <0 indicated a negative and a *t*-value >0 indicate a positive response of relative abundance of trait modality in response to increasing percent urbanization and agricultural land use. For each trait modality, we calculated the percentage of negative and positive responses of all hydrological regions with GF $R^2 > 0$ and *t*-test *p*-value at a 0.05 significant level.

All data manipulation and statistical and spatial analyses were undertaken using the packages *missForest*, *extendedForest*, *gradientForest*, *dplyr*, *ggplot2*, *sf*, *stats*, *raster*, and *rgdal*.

RESULTS

Fish and aquatic insect communities showed strong taxonomic and functional turnover and demonstrated threshold responses to land use conversion across rivers of the conterminous United States. The relative contributions of urban and agricultural land use extent to community composition change were generally high in the GF

models, albeit with marked variability across hydrological units (Appendix S1: Figures S10–S13).

In support of H1, we found that threshold values for both urban and agricultural land use were predominantly higher for taxonomic composition compared to functional composition. Abrupt shifts in community composition occurred at relatively low percentages of land use conversion; urban thresholds for taxonomic and functional fish communities were estimated at a median level of 3.0% (range: 0.3%–12.4%) and 2.6% (range: 0.3%–5.4%), respectively (Figure 2, Appendix S1: Table S4, Figures S2 and S4). Urban thresholds for sudden taxonomic compositional change exceeded those for functional compositional change in 72% (13 out of 18) of hydrological regions for fish (one-tailed paired t -test: $t_{17} = 1.56$, $p = 0.069$). Similarly, taxonomic threshold (median 4.6%, range: 0.7%–18.6%) responses of aquatic insect communities to urban land use exceeded functional threshold responses (median 3.8%, range: 1.0%–10.7%) in 78% (14 out of 18) of hydrological regions for aquatic insects ($t_{17} = 1.36$, $p = 0.095$) (Figure 2, Appendix S1: Table S4, Figures S6 and S8).

Threshold responses to agricultural land use showed similar patterns. Taxonomic and functional composition of fish communities demonstrated abrupt shifts at an estimated median level of 20.5% (range: 2.5%–46.6%) and 11.4% (range: 0.8%–42.3%) agricultural watershed cover, respectively (Figure 2, Appendix S1: Table S4, Figures S3 and S5). Agricultural land use threshold values for significant taxonomic compositional change exceeded those for functional

compositional change in 89% (16 out of 18) of hydrological regions for fish ($t_{17} = 2.02$, $p = 0.029$). Taxonomic threshold (median 12.3%, range: 0.5%–65.5%) responses of aquatic insect communities to agricultural watershed cover exceeded functional threshold responses (median 8.3%, range: 1.0%–77.1%) in 72% (13 out of 18) of hydrological regions for aquatic insects ($t_{17} = 1.83$, $p = 0.043$) (Figure 2, Appendix S1: Table S4, Figures S7 and S9).

In support of H2, threshold changes in taxonomic and functional composition for both fish and aquatic insect communities were predominantly lower in response to urban versus agricultural land use. With respect to functional community change, the median threshold response to agricultural land use was four times greater than urban land use for fishes (11.4% vs. 2.6%) and two times greater for aquatic insects (8.3% vs. 3.8%) (Figure 2, Appendix S1: Table S4). Similarly, the median threshold response of taxonomic composition to agricultural land use exceeded that observed for urban land use by seven times for fishes (20.5% vs. 3.0%) and three times for aquatic insects (12.3% vs. 4.6%). Except for one hydrological unit, thresholds for fish communities occurred at higher values of agricultural versus urban land use. Likewise, for 83% of the hydrological regions (15 out of 18), aquatic insect communities demonstrated higher threshold values for agricultural versus urban land use for both taxonomic and functional composition (Figure 3, Appendix S1: Table S4). Across hydrological

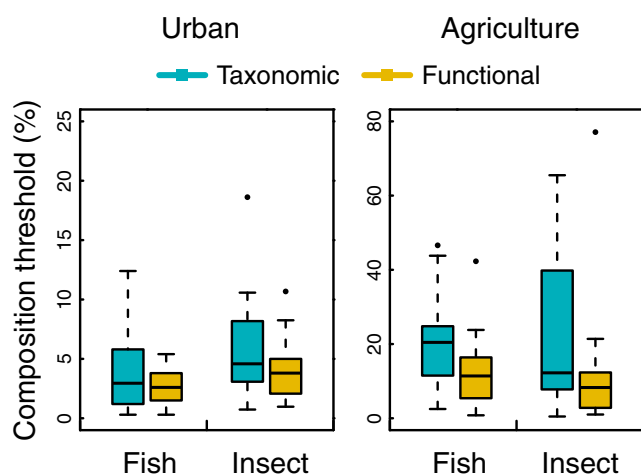


FIGURE 2 Threshold values (in percentage) for taxonomic and functional compositional change of aquatic fish and insect community in response to urban and agricultural land use for major hydrological regions. Boxplots include 25th and 75th percentiles (lower and upper lines), median (middle line), whiskers indicating the fifth and 95th percentiles, and solid circles representing regions with outlier threshold values.

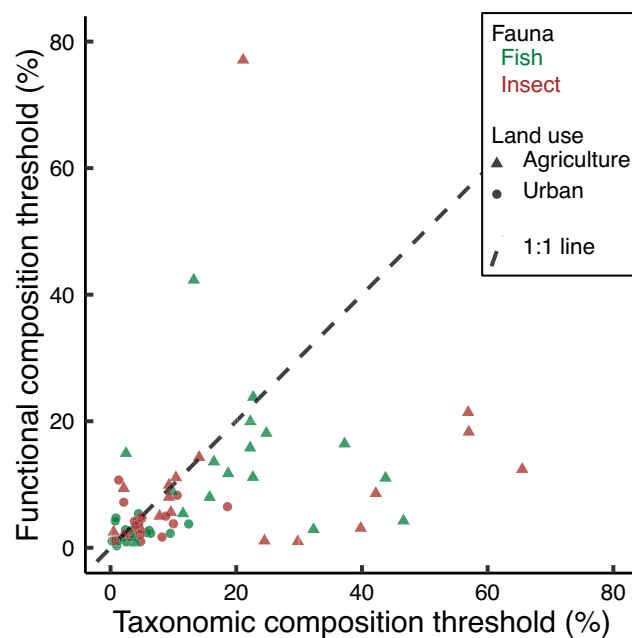


FIGURE 3 Threshold values (in percentage) for taxonomic versus functional compositional change of aquatic fish and insect community (colors) in response to urban and agricultural land use (symbols) for major hydrological regions.

regions agricultural land use threshold values were significantly higher than urban land use threshold values for both fish (taxonomic $t_{17} = 5.35$, $p < 0.001$; functional $t_{17} = 4.87$, $p < 0.001$) and aquatic insect (taxonomic $t_{17} = 3.60$, $p = 0.001$; functional $t_{17} = 1.96$, $p = 0.033$) community compositional change.

In support of H3, we observed greater basin-level geographic consistency in the threshold responses of functional composition compared to taxonomic composition with respect to both urban and agricultural land use gradients. This pattern held for both fishes and aquatic insects. With respect to urban land use, between basin variability in the threshold responses of taxonomic composition exceeded functional composition by two times for fishes (SD 3.2% vs. 1.4%; with FK median $\chi^2_1 = 4.82$, $p = 0.028$) and 1.6 times for aquatic insects (SD 4.3% vs. 2.7%; FK median $\chi^2_1 = 0.31$, $p = 0.577$) (Figure 2, Appendix S1: Table S4). Basin variability in the threshold responses of taxonomic versus functional composition to

agricultural land use differed for fishes (SD 12.9% vs. 9.8%; FK median $\chi^2_1 = 1.38$, $p = 0.240$) and aquatic insects (SD 21.1% vs. 17.3%; FK median $\chi^2_1 = 3.81$, $p = 0.051$). Overall, basin-level threshold responses for fish and aquatic insects were moderately to highly congruent with respect to taxonomic (Pearson correlation coefficients; urban: $r = 0.70$; agricultural: $r = 0.42$) and functional (urban: $r = 0.26$; agricultural: $r = 0.71$) community composition (Figure 4).

In partial support of H4, fish species traits contributing the most to overall functional composition showed varying levels of consistency along urban and agricultural land use gradients. Nearly half (16 out of 33) of the fish trait modalities showed significant difference in their responses to urban and agricultural land use (Figure 5). The most influential trait modalities responsible for changes in functional composition to increasing watershed urbanization included silt/mud (positive) and various (positive) substrate preferences, warm (positive) and

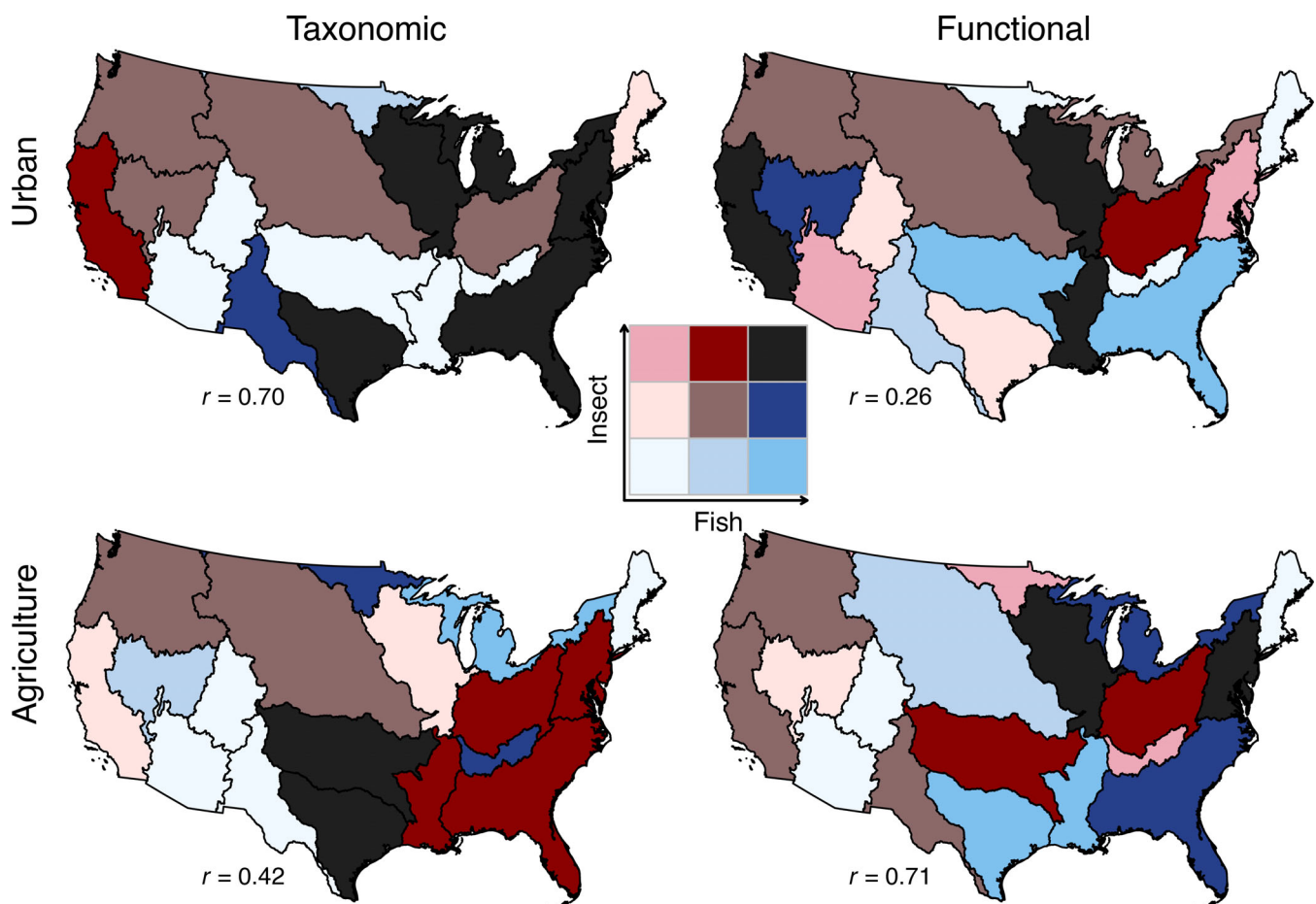


FIGURE 4 Spatial patterns of threshold values (in percentage) for taxonomic and functional compositional change between aquatic fish and insect communities in response to watershed urban and agricultural land use for major hydrological regions. Bivariate chloropleth maps display tertile values (≤ 33 th percentile; 34th–66th percentile; 67th–100th percentile) for fish and aquatic insect communities, where the lower left indicate low thresholds for both taxonomic groups and the upper right indicate high thresholds for both groups. The r values indicate Pearson correlation coefficients between the threshold values for fish and aquatic insect communities.

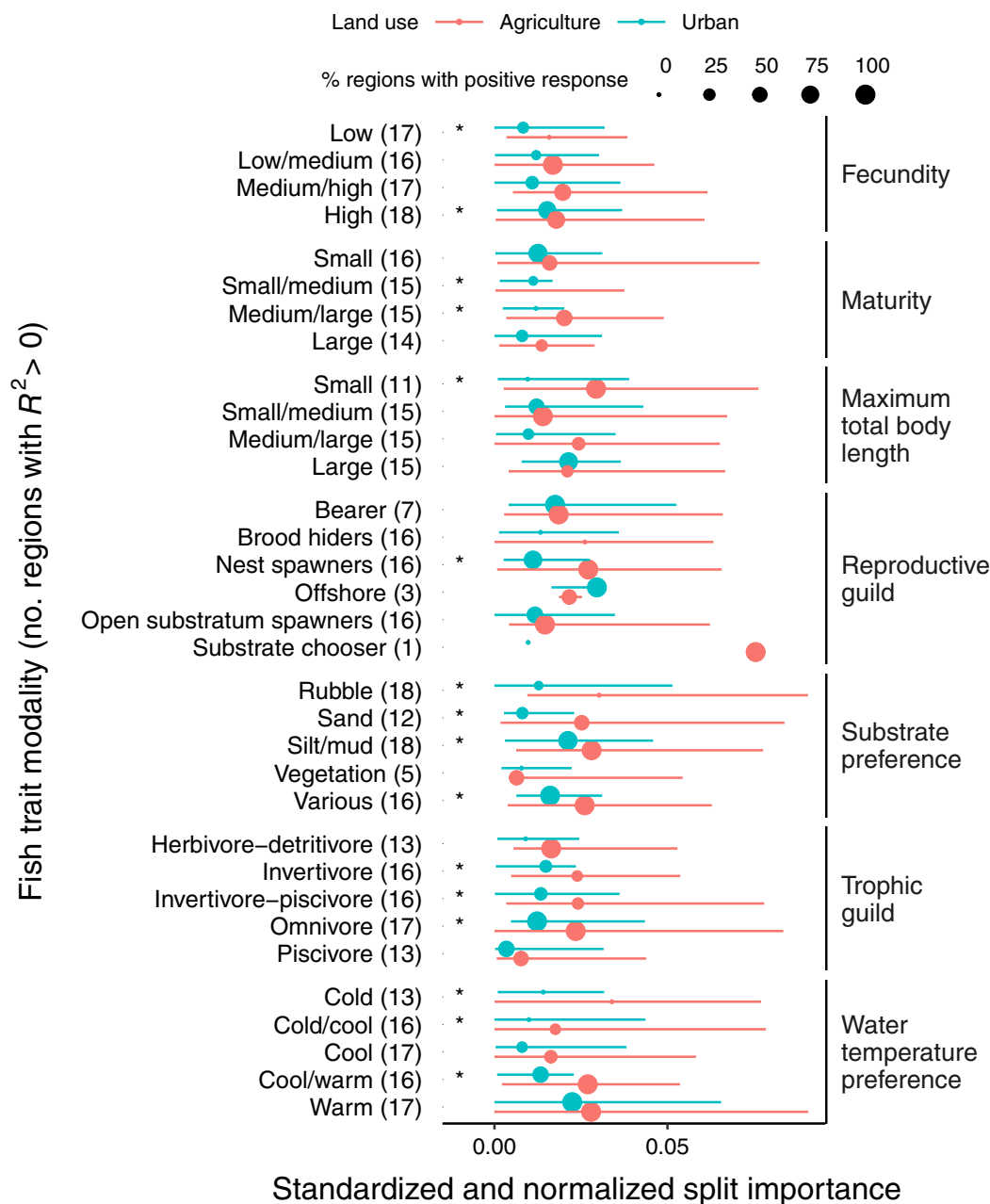


FIGURE 5 Trait modality importance for fish functional compositional threshold response to increasing urbanization and agricultural land use for major hydrological regions with $R^2 > 0$ in the conterminous United States. Importance values were standardized and normalized for each trait modality by R^2 . Solid circles represent median and whiskers represent fifth- and 95th-quantile values of importance. Statistically significant differences between urban and agricultural land use are indicated by asterisks at significance level $p < 0.05$. Bubble size indicates the percentage of hydrological regions ($R^2 > 0$) with positive response (increasing) of trait modality values in response to increase of urban and agricultural land use (in percentage). For example, the relative abundance of cool/warm species increased with percent land use, whereas cold species demonstrated decreased relative abundance values in response to increasing land use change.

cold (negative) temperature preference, large body size (positive), invertivore trophic guild (negative), and high fecundity (positive) (Figure 5, Appendix S1: Figure S14). Similarly, silt/mud (positive) and rubble (negative) substrate preference, warm (positive) and cold (negative) thermal preference, small body size (positive), and nest spawners (positive) are the top contributing

trait modalities associated with changing agricultural land use (Figure 5, Appendix S1: Figure S15).

Traits contributing the most to threshold responses in aquatic insect functional community composition to urban and agricultural land use were much more divergent (Figure 6). Collector-filterer (positive), rare occurrence in drift (negative), high maximum crawling rate

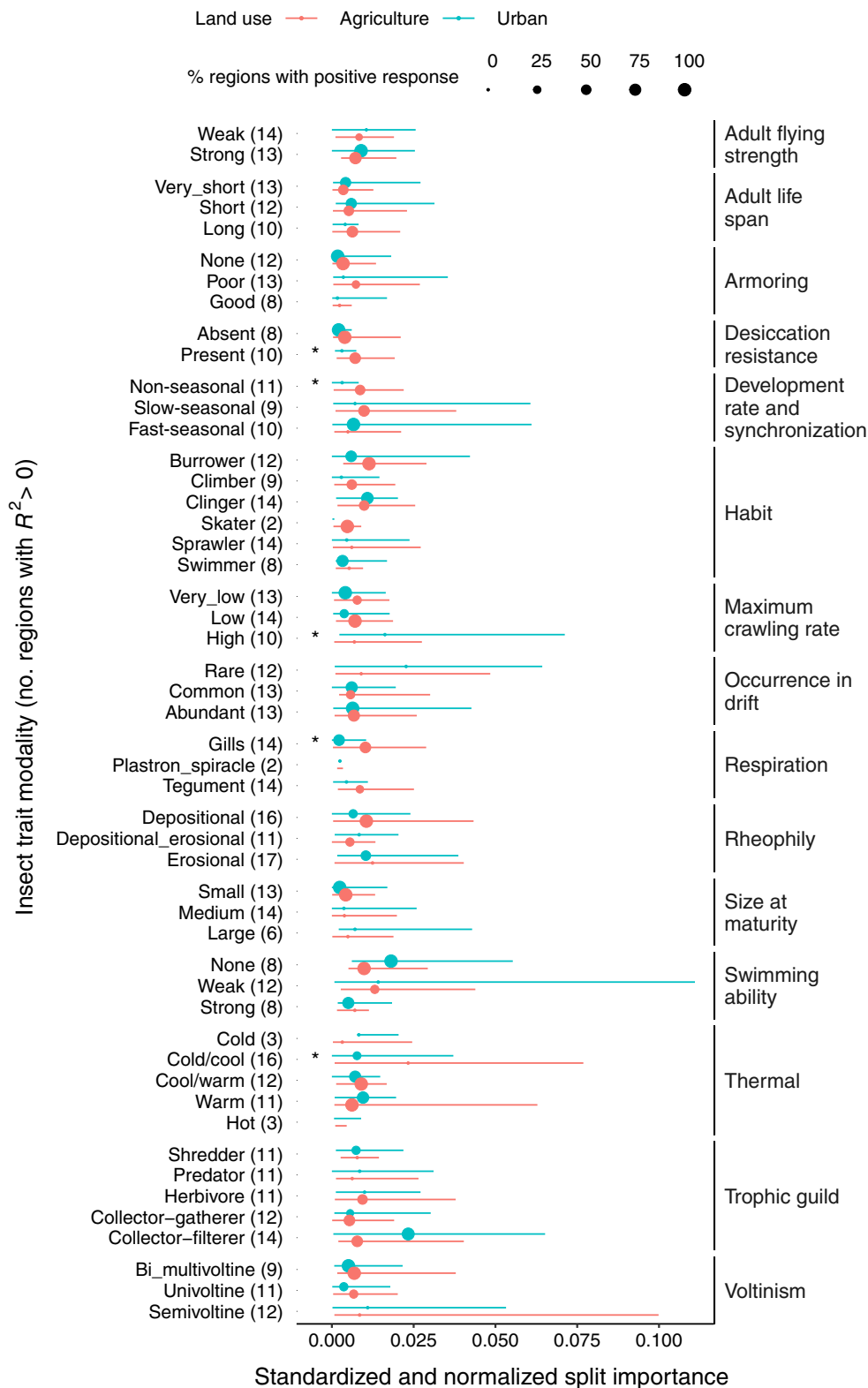


FIGURE 6 Trait modality importance for aquatic insect functional compositional threshold response to increasing urbanization and agricultural land use for major hydrological regions with $R^2 > 0$ in the conterminous United States. Importance values were standardized and normalized for each trait modality by R^2 . Solid circles represent median and whiskers represent fifth- and 95th-quantile values of importance. Statistically significant differences between urban and agricultural land use are indicated by asterisks at significance level $p < 0.05$. Bubble size indicates percentage of hydrological regions ($R^2 > 0$) with positive response (increasing) of trait modality values in response to increases in urban and agricultural land use (in percentage). For example, the relative abundance of uni/bi/multivoltine insect taxa increased with percent land use, whereas semivoltine taxa demonstrated decreased relative abundance values in response to increasing land use change.

(negative), weak swimming ability (negative), semivoltine (negative), and clinger (positive) were the most important trait modalities in functional compositional change to urban land use (Figure 6, Appendix S1: Figure S16). By contrast, trait modalities of cold/cool temperature preference (negative), weak swimming ability (negative), erosional (negative) and depositional (positive) rheophily, burrower (positive), and gill respiration (positive) contributed the most to functional changes in response to agricultural land use (Figure 6, Appendix S1: Figure S17).

DISCUSSION

Our large-scale assessment revealed strong evidence for threshold responses in taxonomic and functional composition along gradients of watershed urbanization and agricultural land use for riverine fish and aquatic insect communities across the conterminous United States. In accordance with our ecologically informed hypotheses, functional community composition consistently demonstrated abrupt shifts at lower levels of land use change when compared to taxonomic composition across taxonomic groups and geographic regions. Land use conversion has a cascading effect on freshwater habitats, altering species- and trait-sorting processes (Burcher et al., 2007), which often causes widespread replacement of specialized species with narrow ecological requirements by more broadly tolerant generalists (Chen & Olden, 2020; Davison et al., 2021; Rumschlag et al., 2023). Communities with species exhibiting specialized traits could be sensitive to even low levels of urban and agricultural land use (e.g., Larsen & Ormerod, 2010; Leitão et al., 2018). Despite the potential for certain traits to act as lower threshold signals of environmental impacts, only a limited number of traits (such as body size) have been identified as such ahead of changes in population or community demographics (Cheung et al., 2013; Clements & Ozgul, 2016). Our study confirms that changes in the frequency of particular key traits, such as body size, temperature preference, reproductive strategy, dispersal ability, and trophic ecology, could be lower threshold signals of environmental impacts that precede taxonomic community change in riverine ecosystems. These key traits can also potentially lead to early-warning thresholds indicating the effects of land use change on the disassembly of a variety of biological communities. Our findings demonstrate the value of considering threshold responses in the functional trait composition of communities in a changing world.

Land use threshold values associated with significant shifts in community composition were consistently lower for urban than agricultural practices across hydrological

regions. Urbanization has acute ecological impacts on riverine ecosystems by homogenizing physical habitat, altering flow and thermal regimes, and increasing loads of nutrients and contaminants (Paul & Meyer, 2001; Petsch et al., 2021). Although streams are also similarly impacted by agriculture (Watson et al., 2014), ecological effects are often less dramatic and more variable than those associated with urbanization (Fahrig et al., 2011; Feld, 2013). The significance of our results is amplified by the fact that many developed regions of the world, including the United States, are experiencing increasingly extensive sub/urbanization expansion and variable trends in agricultural land use as human populations continue to expand and agriculture becomes more efficient (Seto et al., 2011; Winkler et al., 2021). We also stress that identifying thresholds in functional community change is principally important in the developing Global South, where deforestation for agricultural expansion is widespread, especially in biodiverse tropical regions (Martins et al., 2012; Winkler et al., 2021).

Functional threshold responses to land use conversion were more consistent geographically than taxonomic thresholds for both fish and aquatic insects. This result underscores the empirical expectation that species traits promoting local persistence or loss along land use gradients transcend differences in regional species pools that define taxonomic community composition (Heino et al., 2013; Menezes et al., 2010). The freshwater fish fauna of the conterminous United States has been shaped by a rich history of geological and glacial events, giving rise to a phylogenetically diverse species pool (Ross, 2013). As such, threshold responses of taxonomic community composition to land use change were expected to vary geographically due to species-specific responses (Utz et al., 2010)—a prediction supported by our results. By contrast, functional community responses to land use according to specific species traits were much more similar across space. Fish communities facing intensified land use practices have been found to favor species traits associated with general physical habitat requirements, warmer thermal preference, more rapid life cycle, opportunistic feeders, and greater parental care of offspring (e.g., Comte et al., 2021; Miiller et al., 2021; Pease et al., 2015; Zeni & Casatti, 2014; also see discussion below). Increasing land use change shifts invertebrate community composition toward those species exhibiting sedentary habits, collector feeding behavior, warmer eurythermal preferences, effective dispersal capacity, multivoltine taxa, and shorter life cycle (e.g., Barnum et al., 2017; Krynak & Yates, 2018; Larsen & Ormerod, 2010). The greater geographic consistency in threshold responses found here suggests functional ecology provides a path toward identifying continental-scale generalities in community-environment relationships.

Urbanization and agricultural land use were associated with divergent functional community composition changes driven by particular trait modalities. This result emphasizes that different types of land use conversion favor, or select against, specific life-history and ecological strategies via differing underlying mechanisms (Davison et al., 2021). However, the directionality of trait responses was largely consistent with theoretical expectations and empirical findings reported at regional scales. Intense land use alteration acts as an environmental filter selecting for opportunistic life history strategists with broad, generalized niches (Barnum et al., 2017; Comte et al., 2021; Dala-Corte et al., 2016; Miiller et al., 2021). For example, bank erosion and altered flow regime degrade streambeds through excess siltation and scour, causing the loss of bottom-dwelling organisms that require clean gravel with interstitial spaces (Barnum et al., 2017; Dala-Corte et al., 2016). The replacement, reduction, or removal of riparian vegetation cover associated with urbanization and agricultural activities generally increase fine particulate organic matter inputs and changes physical habitat and hydromorphological characteristics, leading to aquatic communities with more opportunistic feeding behaviors (e.g., collector-filterers) (Barnum et al., 2017; Dala-Corte et al., 2016). Anthropogenic heat effluent or increase incoming radiation due to urbanization and removal of riparian vegetation led to stream warming that favors warmwater species (Brumm et al., 2023; Comte et al., 2021). Greater parental care increases survival and recruitment of fish species in altered urban and agricultural habitats (Miiller et al., 2021). Opportunistic life-history strategies (e.g., short life cycle, rapid maturation, high fecundity, and small body size) confer high community resilience (Townsend & Hildrew, 1994), which is advantageous in urban and agricultural habitats subjected to frequent and/or unpredictable changes (Mims & Olden, 2012; Pease et al., 2015). Our results support the notion that species traits are diagnostic of functional community change in response to land use conversion for both fish and aquatic insect.

Threshold responses of functional composition, such as those identified by our study, have the potential to introduce more nuance and rigor to prioritize biodiversity conservation strategies in light of substantial global land use changes (Gallagher et al., 2021; Rumschlag et al., 2023). Functional traits are powerful for their ability to highlight species that disproportionately enhance biodiversity and ecosystem functioning (e.g., McGill et al., 2006). Integrating functional traits into community compositional thresholds may act as a surrogate measure that ensures the conservation of not only diverse species but also resilient ecosystems to global change (Luck, 2005; Stewart et al., 2018). Diagnostic traits identified in this study also help inform adaptive management strategies seeking to sustain functional diversity and the supporting

ecosystem processes. For example, traits describing body size and trophic guild largely define species-specific nutrient excretion rates by freshwater fishes—a key ecosystem process that can control aquatic productivity—and concurrently species with these traits show variable sensitivities to land use change (Moore & Olden, 2017). Identifying functional thresholds can better inform landscape-scale conservation actions aimed at improving aquatic biodiversity, including limiting or mitigating land use change or targeting reforestation and instream restoration efforts (Gallagher et al., 2021; Miatta et al., 2021). Our research can help inform a more effective approach to the spatial planning of protected areas by considering additional dimensions of biodiversity (Brumm et al., 2021; Heino et al., 2022). We anticipate that threshold values such as those reported here can support the design of adaptive conservation goals to protect or restore freshwater biodiversity facing continued intensification of land use practices.

Functional traits define the ecosystem consequences of community change (McGill et al., 2006; Moore & Olden, 2017). As such, identifying lower land use thresholds for functional composition change has important implications to understand, predict, and mediate community resilience and ecosystem functions. Our study suggests that integrating trait information provides researchers with early-warning threshold values for land use conversion that are generally lower than those obtained by characterizing communities via taxonomic diversity. Designing conservation plans based on functional composition thresholds may lead to more protective regulations for landscape-level development affecting aquatic communities at local, regional, and continental scales (Miatta et al., 2021). This information will be particularly useful as scientists continue to develop global-scale strategies for preserving natural land cover (Allan et al., 2022). This study supports the notion that aggregating trait-specific responses may better facilitate the complex ecosystem implications of community change stemming from land use conversion, thereby enhancing the design adaptive conservation strategies seeking to protect or restore aquatic biodiversity.

AUTHOR CONTRIBUTIONS

Kai Chen and Julian D. Olden conceived and designed the study. Julian D. Olden, Brandon K. Peoples, and Stephen R. Midway assembled the data sets. Kai Chen performed the analyses and prepared figures and/or tables. Kai Chen and Julian D. Olden led the manuscript writing, with substantial edits by all authors.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.


DATA AVAILABILITY STATEMENT

Freshwater fish community data were downloaded from the USEPA National Aquatic Resource Surveys (NARS) National Rivers and Streams Assessment 2008–2009 (data and metadata files) by the survey “Rivers and Streams 2008–2009” and National Rivers and Streams Assessment 2013–2014 (data and metadata files) by the survey “Rivers and Streams 2013–2014” (available from the USEPA at <https://www.epa.gov/national-aquatic-resource-surveys/data-national-aquatic-resource-surveys>) and the USGS NAWQA (material previously obtained from USGS BioData Retrieval system <https://apps.usgs.gov/biodata/> is now available by contacting pmruhl@usgs.gov), and from Comte et al., 2020 at <https://doi.org/10.25829/ndiv.1873-10-4000>. A small proportion of fish community data is accessible through the corresponding state agency of interest. The fish community assessment data from the North Carolina Department of Environmental Quality, Division of Water Resources (NCDWR), can be directly downloaded by the survey “Fish Community Survey Results by Basin” from <https://deq.nc.gov/about/divisions/water-resources/water-sciences/biological-assessment-branch/fish-community-assessment-data>. The Pennsylvania Fish Species Occurrence Database from the Pennsylvania Fish and Boat Commission can be directly downloaded from <https://www.pasda.psu.edu/uci/DataSummary.aspx?dataset=83>. Fish Community Biomonitoring data collected by the Georgia Department of Natural Resources (DNR) Wildlife Resources Division (<https://epd.georgia.gov/fish-biomonitoring-sop>) are available to qualified researchers by

contacting the Georgia DNR at nongame.review@dnr.ga.gov at <https://georgiawildlife.com/environmental-review>. The DEEP Fish Community data are available to qualified researchers by contacting the Connecticut Department of Energy and Environmental Protection (DEEP, <https://cteco.uconn.edu/projects/fish/index.htm>) at deep.inland.fisheries@ct.gov. Freshwater invertebrate community data were downloaded from the USEPA NARS Wadeable Streams Assessment 2004 (data and metadata files) by the survey “Streams 2004,” National Rivers and Streams Assessment 2008–2009 (data and metadata files) by the survey “Rivers and Streams 2008–2009,” National Rivers and Streams Assessment 2013–2014 (data and metadata files) by the survey “Rivers and Streams 2013–2014,” and National Rivers and Streams Assessment 2018–2019 (data and metadata files) by the survey “Rivers and Streams 2018–2019” (available from the USEPA at <https://www.epa.gov/national-aquatic-resource-surveys/data-national-aquatic-resource-surveys>), and from the USGS NAWQA (material previously available from the USGS BioData Retrieval system <https://apps.usgs.gov/biodata/> is now available by contacting pmruhl@usgs.gov). All USGS NAWQA freshwater fish and invertebrate community data from USGS BioData Retrieval system were originally accessed from <https://aquatic.biodata.usgs.gov/retrievalSelect.action>, but that was closed due to security vulnerabilities. Freshwater fish and invertebrate trait data are accessible through FishTraits Database (Frimpong & Angermeier, 2008; <https://www.sciencebase.gov/catalog/item/5a7c6e8ce4b00f54eb2318c0>), FISHMORPH database (Sebastien et al., 2021; <https://doi.org/10.6084/m9.figshare.14891412.v1>), database of lotic invertebrate traits for North America (Vieira et al., 2006; <https://pubs.usgs.gov/ds/ds187/>), and from Twardochleb et al. (2021) at <https://doi.org/10.1111/geb.13257>. All environmental data are publicly available from de Colstoun et al., 2017 (<https://doi.org/10.7927/H4P55KKF>), Latifovic et al., 2016 (<http://www.ccc.org/north-american-environmental-atlas/land-cover-2010-landsat-30m/>), McKay et al., 2010, 2019 (<https://nhdplus.com/NHDPlus>), and USGS (2016, 2017) at <https://www.sciencebase.gov/catalog/item/581d0537e4b08da350d5253c> and <https://data.usgs.gov/datacatalog/data/USGS:35f9c4d4-b113-4c8d-8691-47c428c29a5b>, respectively. The R codes used for calculations of community compositional thresholds are available in Chen et al. (2023) on Figshare at <https://doi.org/10.6084/m9.figshare.21781718.v2>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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