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Identifying candidate reference reaches to assess the physical and biological integrity of wadeable streams in different ecoregions and among stream sizes

Craig P. Paukert[a,*], Ethan R. Kleekamp[b,1], Ralph W. Tingley III[b]

[a] U.S. Geological Survey, Missouri Cooperative Fish and Wildlife Research Unit, The School of Natural Resources, University of Missouri, United States
[b] Missouri Cooperative Fish and Wildlife Research Unit, The School of Natural Resources, University of Missouri, Columbia, MO 65211, United States

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ABSTRACT

Efforts to quantify disturbances to aquatic systems often use landscape-level metrics, presumably linked to ecological integrity, but fewer studies have directly linked ecological integrity to instream habitat, and applied these results to unsampled stream reaches throughout a landscape. We developed a flexible, quantitative approach that characterizes stream impairment across a landscape and identifies least-disturbed stream reaches to serve as benchmarks for high quality physical habitat and ecological integrity. Fish and macroinvertebrate community characteristics, reach-level physical habitat and water quality metrics were summarized in 891 wadeable stream reaches across two ecoregions in Missouri, USA. The influence of reach and water-quality characteristics as well as landscape-level variables on 7 fish and 3 macroinvertebrate community biological indicator metrics was then modeled using boosted regression trees (BRTs). On average, reach-level models explained more variance (25 and 27% in the two ecoregions examined) in biotic metrics than landscape-level models (18% and 20%). Abiotic and biotic associations differed among ecoregions and stream sizes, however, reach-level habitat (e.g., bankfull width/depth ratio, channel incision height) and water quality (e.g., dissolved oxygen, total chlorophyll) were consistently top predictors. At the landscape scale, fish richness in the agriculturally dominated ecoregion increased with decreased fragmentation/flow modification. Invertebrate metrics in the forested ecoregion showed community degradation apparent with crop coverage as low as 8–10% of the riparian zone, while urban impairment, most notably in the agricultural ecoregion, was best detected using invertebrate indicators of biotic integrity and measures of fish trophic ecology. Relationships among landscape-scale variables and reach characteristics identified as top predictors in BRTs also highlighted potential mechanistic relationships among landscape, habitat, and measures of ecological integrity. Using the results of the landscape-level models, estimates for overall ecological integrity were predicted for over 28,000 stream reaches throughout Missouri, and a total of 1423 candidate reference reaches were identified. The objective approach to characterizing stream impairment developed in this study offers specific advantages, including a reach and landscape-level evaluation of human disturbance as well as an inductive, multi-metric determination of ecological integrity.

1. Introduction

Stream habitat and biotic composition result from a series of complex, hierarchical interactions between broad climatic and geological conditions, anthropogenic disturbances, and finer-scale physical and ecological processes (Frissell et al., 1986; Montgomery and Buffington, 1997; Allan, 2004). Such interactions may be altered by adverse, and potentially synergistic, effects of widespread human disturbances (Allan, 2004; Kludt et al., 2017). Consequently, North American freshwater resources have grown exceedingly imperiled, and many present-day aquatic communities likely represent only a fraction of their historic constituents (Malmqvist and Rundle, 2002).

Landscape-level anthropogenic disturbances frequently alter the hydrology, geomorphology, and chemical condition of receiving

* Corresponding author at: U.S. Geological Survey, Missouri Cooperative Fish and Wildlife Research Unit, The School of Natural Resources, 302 ABNR Building, University of Missouri, Columbia, MO 65211, United States.

E-mail address: paukertc@missouri.edu (C.P. Paukert).

[1] Present address: USDA Service Center, 500 Wollard Blvd., Richmond, MO 64085.

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waters. Urbanization and watershed imperviousness can lead to changes in stream-flow regimes (Arnold and Gibbons, 1996; Booth and Jackson, 1997; Paul and Meyer, 2001; Witt and Hammill, 2018), which in turn may result in physical and ecological change (Ward and Stanford, 1995; Poff et al., 1997; Bestgen et al., 2017). Mining and agricultural activities can contribute high sediment inputs through the removal of hillslope and bank-stabilizing vegetation, resulting in unstable, highly embedded stream channels unsuitable for species reliant on clean gravel for feeding and/or spawning (Berkman and Rabeni, 1987). Similarly, stream channelization, in-stream gravel mining, and riparian deforestation all increase sedimentation while reducing woody debris critical for channel formation and maintaining habitat heterogeneity (Montgomery and Buffington, 1997; Brown et al., 1998; Harvey et al., 2017). In conjunction with these physical habitat alterations, excess nutrients, ions, heavy metals, and pesticides associated with urban and agricultural runoff, mine waste, wastewater treatment discharge, and other point-source stressors are recognized as major sources of impairment for aquatic communities (Cairns and Pratt, 1993).

Many agencies and organizations currently employ multi-metric fish and invertebrate indices to estimate biological integrity by comparing test site values to those measured at “reference reaches”, or those reaches thought to represent minimally or least disturbed conditions within an ecoregion (Karr, 1981; Stoddard et al., 2006). Initial criteria proposed for reference reach determination included the identification of relatively homogenous stream regions, evaluation of regional disturbance types and intensities, and selection of regional candidate sites with the least amount of anthropogenic disturbance (Hughes et al., 1986). Researchers have since developed landscape-scale multi-metric threat indices to characterize stream health or impairment to improve upon the qualitative techniques previously used to identify reference conditions (Annis et al., 2010; Paukert et al., 2011; Fore et al., 2014). However, such efforts often lack in-stream biological data to train and test their models, and thus may have limited ability to identify individual stressor impacts and to describe the specific ways stressors alter the physical and chemical characteristics of receiving waters (Annis et al., 2010). Studies that have incorporated biotic data to develop landscape-level indices have employed threshold analyses to characterize impairment and have been useful in portraying influences of major landscape-stresses on aquatic species, metrics, or habitat (e.g., Wang et al., 2008; Daniel et al., 2015). However, while the physiological tolerances of biota to environmental degradation may exhibit threshold or nonlinear responses (Davies and Jackson, 2006; Martinez-Fernandez et al., 2019), complex and dynamic relationships between streams and their landscapes may call for approaches that consider interactions among stressors to develop needed indicators of ecological integrity (Groffman et al., 2006). Moreover, linking coarse landscape metrics to local habitat and water quality conditions may provide practitioners with mechanistic understanding of these relationships, resulting in a greater ability to diagnose impairment and propose restoration actions (Hynes, 1994; Rabeni, 2000; Infante and Allan, 2010).

In this study, we outline a flexible, quantitative approach to characterize stream impairment and identify least-disturbed stream reaches (including areas not sampled for aquatic biota and instream habitat) based on hierarchical controls of landscape characteristics on in-stream conditions and biological integrity. The objectives of this study were to 1) assess the influence and relative importance of reach and landscape-level environmental variables on stream fish and macroinvertebrate community characteristics, 2) examine relationships between reach-level characteristics (habitat and water quality) and landscape-level environmental characteristics, and 3) predict ecoregion-wide stream biotic conditions to support the identification of candidate references reaches for Missouri, USA.

2. Methods

2.1. Spatial framework and study region

The spatial layer used in this study was a modified version of the 1:100,000-scale National Hydrography Dataset available for the entirety of Missouri (NHDPlus V1, United States Environmental Protection Agency (USEPA) & United States Geological Survey (USGS) 2005; Annis et al., 2010). Stream fish and macroinvertebrate communities were examined in two distinct size classes of wadeable streams defined in this layer, hereafter referred to as creeks (n = 19,546) and small rivers (n = 8868). These classes were delineated using Shreve-link magnitude ranges (Pflieger, 1989) and exhibit mean watershed areas of approximately 60 km^2 and 480 km^2, respectively. Fish and macroinvertebrate data (described below) were compiled and spatially referenced to the basic unit within this layer, the stream reach. Each stream reach has four defined spatial units over which landscape data were attributed and summarized; the local catchment (area draining directly into any given stream reach), the upstream network catchment (total upstream area draining to the reach) and the local and upstream network riparian zones (45 m buffer on each side for creeks, 110 m for small rivers; Annis et al., 2010).

Missouri, which encompasses about 180,500 km^2, is a physiographically diverse state near the center of the conterminous United States and exhibits three primary ecoregions, all featuring distinct geology, soils, landform, groundwater influence, and aquatic fauna (Sowa et al., 2007). The Central Till Plains (hereafter, Plains) cover the northern half of the state and contain low, rolling hills, broad river valleys, and low-gradient streams with silty or fine gravel substrates (Pflieger, 1971; Fig. 1). The Ozark Highlands (hereafter, Ozarks) encompass southern Missouri and features high local relief, deep and narrow river valleys, and much higher stream gradients than the Plains region. Stream in the Ozarks receive considerable groundwater input and typically exhibit low turbidity, high dissolved oxygen levels, and coarse gravel substrates (Sowa et al., 2007). The Mississippi Alluvial Basin (hereafter, MS Alluvial Basin) in the southeast corner of the state exists as a nearly homogenous agricultural landscape. Streams in this broad, flat valley are often highly vegetated, exhibit relatively low dissolved oxygen levels, and consist primarily of silty and fine gravel substrate (Pflieger, 1971). Due to sampling limitations and the highly homogenous nature of the region (e.g., ~75% cultivated crop), usable models for the MS Alluvial Basin were not able to be developed, and no further information will be presented in this study. Together with the two-tiered stream size classification, the Plains and Ozarks aquatic ecoregions constituted the base spatial scale for the model development and stream comparisons.

2.2. Biological data

Biotic samples from 891 stream reaches were collected by the Missouri Department of Conservation's Resource Assessment and Monitoring (RAM) Program from 2000 to 2014. The RAM program uses the U.S. Environmental Protection Agency's standardized stream fish sampling protocol, and collects macroinvertebrate community data following the Missouri Department of Natural Resources' (MDNR) semi-quantitative macroinvertebrate bioassessment protocol (Fischer and Combes, 2003; MDNR, 2012; Sievert et al., 2016). Fish community data were collected at randomly selected stream reaches (Fig. 1) between late May and early October using single-pass backpack and/or tote barge pulsed DC electrofishers and seine nets in single upstream passes. Block nets were placed at in-stream distances 40 times the mean wetted stream width to retain fish and effectively delineate the sampling reach (Sievert et al., 2016). Fish were either field-identified or preserved in formalin for later laboratory identification (Fischer and Combes, 2003). Macroinvertebrate community data were collected at fish sampling sites during return visits in September and October of the same year

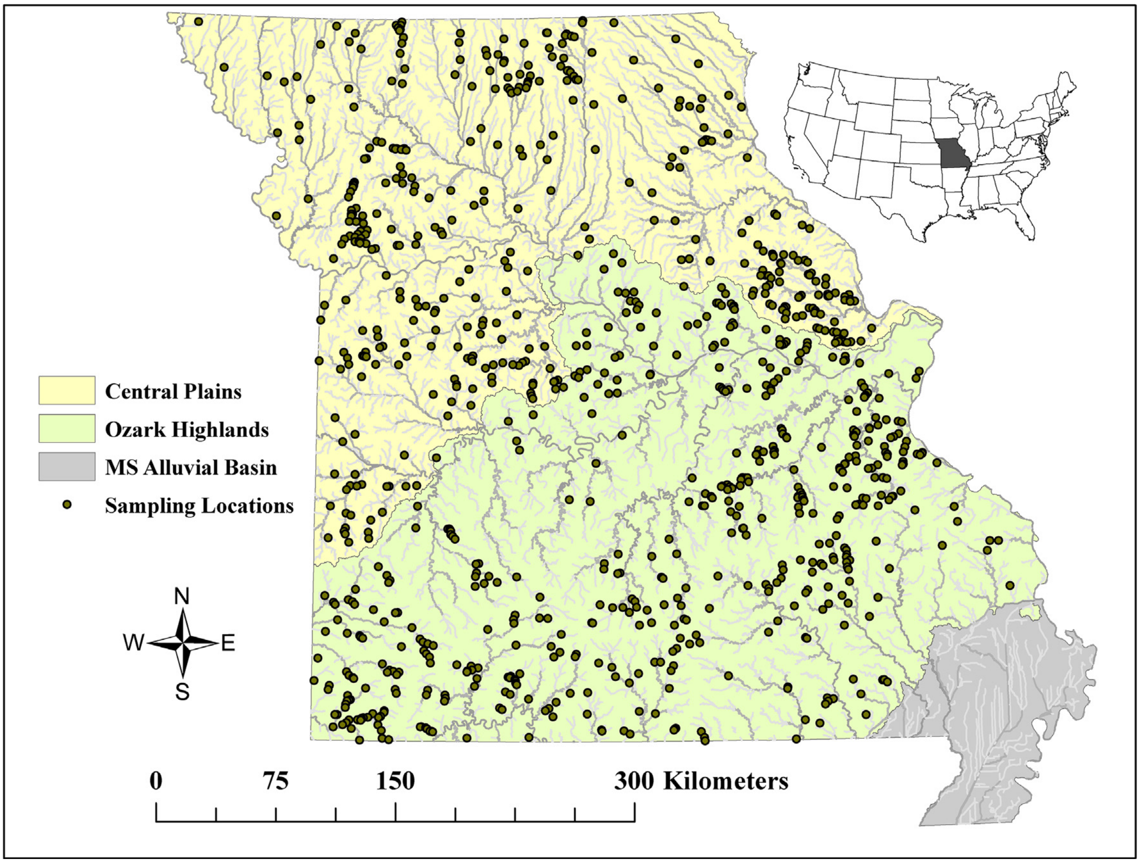

Fig. 1. Missouri's three major aquatic ecoregions and stream sampling locations used in this study. MS Alluvial Basin is the Mississippi Alluvial Basin.

(n = 578). Six kick net (500 × 500 µm mesh bag) samples were collected from each of three primary habitat types; flowing water over-coarse substrate, non-flowing water depositional substrate, and rootmat substrate (MDNR, 2012). Specimens were returned to the laboratory and identified to the genus level, and species when possible.

Ten fish and macroinvertebrate biological metrics commonly used as indicators of stream health were generated for this study (Karr, 1981; Daniel et al., 2015). Fish data were summarized into seven commonly applied metrics describing richness and diversity, habitat preference, trophic ecology, reproductive ecology, and sensitivity or tolerance to disturbance, each of which had an *a priori* hypothesized relationship with increasing anthropogenic disturbance (Table 1). The number of native fish species and benthic species typically decrease with increased sedimentation and the loss of large woody debris (Allan, 2004). Many native lithophilic spawning species spawn on or in clean gravel or cobble, and are sensitive to sedimentation (Berkman and Rabeni, 1987). Omnivorous/herbivorous species and other trophic generalists increase with anthropogenic disturbances such as riparian clearing and nutrient enrichment (Allan, 2004), while trophic specialists, such as insectivorous cyprinids, often show declines (Smogor and Angermeier, 1999). Tolerant and non-native fish species also persist in higher proportions in streams draining urbanized landscapes (Paul and Meyer, 2001). Three macroinvertebrate metrics, including Shannon's Diversity Index (SDI), the number of species occupying the orders

Table 1
Mean (standard deviation) of fish and macroinvertebrate community metrics in each aquatic ecoregion and stream size class. (±) values refer to the predicted response of each community characteristic to increasing anthropogenic disturbance. EPT Richness is the number of species in the orders Ephemeroptera, Trichoptera, or Plecoptera.

Metric	Code (±)	Central Plains		Ozark Highlands	
		Creek	Small River	Creek	Small River
Fish					
Native fish species richness	Native (−)	13.3 (4.9)	19.3 (8.3)	19.3 (7.1)	26.5 (6.7)
Number (No.) of native benthic species	Benthic (−)	2.7 (1.8)	4.9 (3.6)	6.1 (2.5)	9.1 (2.6)
No. native lithophilic species	Lith (−)	10.6 (3.8)	15.6 (6.8)	14.5 (5.4)	20.0 (5.1)
Proportion (Prop.) native insectivorous cyprinid individuals	p_cyp_insect (−)	0.13 (0.18)	0.12 (0.13)	0.15 (0.14)	0.28 (0.16)
Prop. native omnivore/herbivore individuals	p_omn/herb (+)	0.29 (0.19)	0.25 (0.18)	0.45 (0.22)	0.31 (0.17)
Prop. tolerant individuals	p_tolerant (+)	0.27 (0.24)	0.44 (0.23)	0.07 (0.12)	0.05 (0.09)
Prop. non-native individuals	p_intro (+)	0.001 (0.006)	0.006 (0.020)	0.001 (0.005)	0.001 (0.003)
Macroinvertebrate					
Shannon Diversity Index	SDI (−)	2.8 (0.4)	2.9 (0.4)	3.1 (0.5)	3.3 (0.3)
EPT Richness	EPT (−)	10.8 (5.7)	14.9 (6.8)	19.5 (8.8)	24.5 (6.9)
Hilsenhoff Biotic Index	HBI (+)	7.1 (0.7)	6.6 (0.8)	5.8 (1.1)	5.6 (0.8)
Sites with fish/invertebrate samples		278/175	111/90	383/229	121/85

Table 2
Mean (standard deviation) of in-stream physical habitat and water quality measures within each aquatic ecoregion and stream-size class. Asterisks (*) indicate variables removed from all models due to high correlations with other predictor variables. Variables denoted with "1" were included only in the Plains ecoregion and those denoted with a "2" were included only in the Ozarks ecoregion. Standard deviations for mean mobile substrate diameter, mean channel incision height, and bankfull width were also included as independent variables in models for both ecoregions.

Metric Description	Code	Central Plains		Ozark Highlands	
		Creek	Small River	Creek	Small River
Channel Morphology					
Mean bank-full width (m)	bankfull	10.1 (4.3)	19.8 (8.7)	16.8 (7.5)	28.5 (9.9)
Mean channel incision height (m)	incision	2.5 (1.4)	3.4 (1.6)	1.8 (1.0)	2.3 (1.5)
Glide habitat (%)*	glide	37.5 (34.9)	53.6 (36.3)	31.0 (22.7)	37.4 (24.6)
Riffle habitat (%)	riffle	10.5 (12.6)	5.6 (7.5)	18.1 (12.9)	14.4 (11.3)
Pool habitat (%)	pool	49.4 (34.2)	40.2 (34.7)	47.7 (25.4)	47.6 (26.4)
Channel sinuosity (m/m)	sinu	1.3 (0.7)	1.1 (0.2)	1.2 (0.5)	1.1 (0.1)
Mean width/depth ratio (m/m)	w/d	13.0 (8.0)	20.1 (11.9)	15.6 (6.4)	21.4 (7.3)
Mean depth (cm)	m_depth	30.5 (15.9)	49.5 (25.7)	36.3 (16.2)	57.4 (16.8)
Mean residual pool depth (cm)*	pool_depth	19.7 (11.2)	24.6 (12.9)	23.3 (11.4)	31.9 (12.9)
Maximum residual pool depth (cm)	max_pool_dep	71.3 (35.3)	84.7 (44.1)	82.0 (36.6)	104.5 (45.4)
Substrate					
Mean mobile substrate diameter (mm)*	sub_dia	41.2 (58.5)	38.8 (61.0)	97.8 (82.9)	79.6 (60.1)
Fine substrate: silt, clay, muck (%)	fines	24.1 (24.8)	22.2 (21.7)	5.8 (9.1)	8.7 (9.4)
Sand and fine substrate (% < 2 mm)*	sand	48.2 (30.9)	61.5 (28.5)	12.8 (16.2)	18.8 (15.9)
Fine gravel (% 2–16 mm)	gravel	11.4 (12.0)	5.2 (6.7)	12.6 (10.0)	13.6 (11.2)
Coarse substrate (% > 16 mm)[1]	coarse	26.8 (26.7)	21.5 (24.6)	60.6 (22.0)	58.8 (20.7)
Bedrock substrate (%)	bedrock	3.8 (10.0)	3.0 (8.3)	10.7 (16.9)	6.1 (9.8)
Wood or detrital substrate (%)	organic	1.4 (3.0)	2.3 (4.6)	0.7 (1.8)	0.7 (1.2)
Mean channel embeddedness (%)[2]	embed	63.0 (28.5)	75.5 (23.5)	27.1 (20.2)	33.5 (21.5)
Cover and Shading					
Proportion (Prop.) algal cover	algae	0.03 (0.06)	0.06 (0.10)	0.06 (0.10)	0.07 (0.10)
Prop. aquatic macrophytes	veg	0.03 (0.07)	0.02 (0.04)	0.08 (0.10)	0.10 (0.10)
Prop. brushy and small debris	brush	0.10 (0.10)	0.10 (0.10)	0.07 (0.07)	0.08 (0.07)
Prop. large woody debris*	LWD	0.06 (0.07)	0.08 (0.10)	0.04 (0.05)	0.06 (0.06)
Large woody debris count (No./100 m)[1]	ct_LWD	10.2 (13.7)	11.1 (14.9)	8.5 (19.1)	6.4 (6.6)
Large woody debris volume (m^3/100 m)	vol_LWD	6.3 (11.8)	11.8 (15.8)	5.0 (12.0)	6.0 (8.6)
Prop. undercut banks	undercut_bk	0.03 (0.04)	0.04 (0.06)	0.05 (0.08)	0.04 (0.06)
Prop. riparian canopy cover[2]	canopy	0.9 (0.1)	0.8 (0.1)	0.8 (0.1)	0.8 (0.1)
Prop. riparian mid-layer cover	rip_mid	0.9 (0.1)	0.9 (0.1)	0.9 (0.1)	0.9 (0.1)
Prop. riparian ground vegetation cover	grd_veg	0.9 (< 0.1)	0.9 (0.1)	0.9 (0.1)	0.9 (0.1)
Mean bank canopy density (%)*	bk_canopy	84.5 (14.5)	74 (19.7)	80.5 (17.4)	74.9 (18.0)
Mean mid-channel canopy density (%)	canopy_dens	72.2 (20.1)	45.1 (22.9)	60.6 (22.4)	38.6 (19.4)
Water Quality					
Dissolved Oxygen (mg/L)	DO	5.5 (2.1)	6.2 (2.0)	6.7 (2.2)	6.7 (1.7)
pH	pH	7.6 (0.7)	7.7 (0.9)	7.8 (0.5)	7.8 (0.3)
Turbidity (NTU)	turbid	68 (163)	812 (6589)	9 (9)	9 (11)
Conductivity (μS/cm)	cond	356 (247)	410 (169)	321 (222)	283 (216)
Total Chlorophyll (μg/L)	chl	15.2 (22.0)	20.6 (29.3)	4.7 (6.9)	7.8 (16.8)

Ephemeroptera, Trichoptera, or Plecoptera (EPT richness), and the Hilsenhoff Biotic Index (HBI), were also summarized given their potential relationships with agricultural disturbance. Both SDI and EPT richness indicate community sensitivity, and decrease with increasing anthropogenic disturbance (Paul and Meyer, 2001; Sponseller et al., 2001). HBI is a measure of community tolerance, and increases with point-source pollution and other water quality impairments (Hilsenhoff, 1988; Sarver et al., 2002).

2.3. Physical habitat and water quality data

Physical habitat characteristics were measured at eleven cross-channel transects and at intervals along the thalweg in each stream reach (n = 891) using methods described by Fischer and Combes (2003). Measured habitat characteristics described channel morphology (e.g., sinuosity, width/depth ratio, channel incision height), substrate characteristics (e.g., substrate size and variability, embeddedness), habitat complexity and cover (e.g., large woody debris, macrophytic plant cover), and vegetation composition and canopy cover in the riparian zone (Kaufmann et al., 1999; Fischer and Combes, 2003; Table 2). Water quality parameters (e.g. dissolved oxygen, pH, conductivity) were recorded on-site using hand-held water quality meters.

2.4. Landscape data

Landscape-level natural environmental and anthropogenic disturbance metrics were calculated for every creek and small river reach in Missouri using best-available landscape datasets. Landcover metrics were generated for each reach's local and network catchments and riparian zones using ArcGIS 10.2 (Environmental Systems Research Institute, Redlands CA, USA) and the stream network topology tool, RivEX (Hornby, 2013). Specific landscape and landcover metrics were selected to represent known natural controls on stream systems and environmental stressors linked to stream impairment, including measures of stream fragmentation and flow modification, urban and agricultural impairment, and point source pollution (Table S1; Ostrande and Wilde, 2002, Allan, 2004, Thornbrugh and Gido, 2009, Annis et al., 2010, Infante and Allan, 2010, Roberts and Hitt, 2010; Thornbrugh and Infante, 2019). Landcover metrics were calculated from the 2011 National Land Use/Land Cover Dataset (NLCD) as catchment percentages (e.g. agricultural cover, imperviousness; Homer et al., 2015), and point-stressors (e.g. stream crossings, mining operations, landfills) were converted to watershed densities (no./km^2). When possible, we used new datasets to update existing anthropogenic disturbance variables (i.e., point stressors; see Table S1 for additional details). Means within

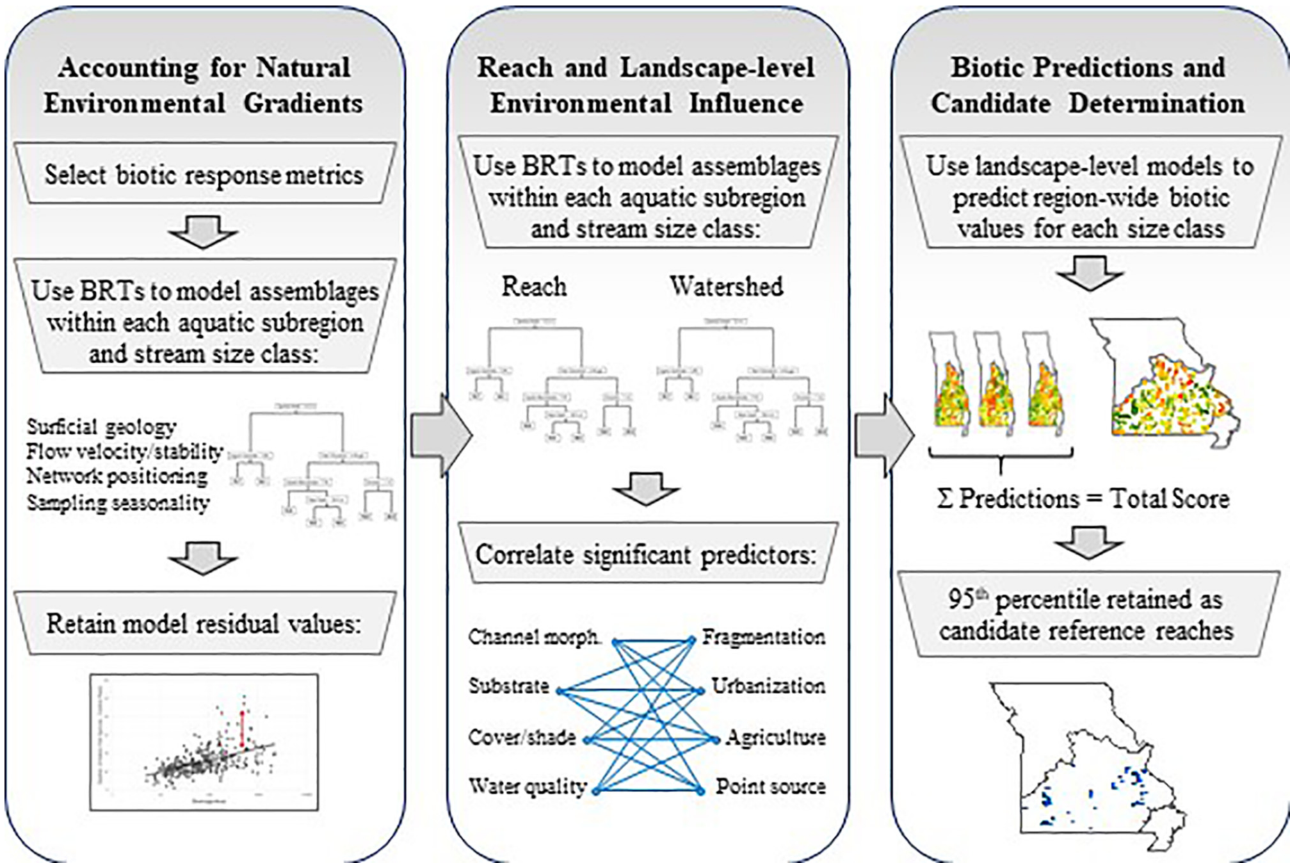

Fig. 2. Conceptual framework detailing the process of identifying regional candidate reference stream reaches.

network catchments and riparian zones were calculated as area-weighted averages.

2.5. Relating reach and landscape variables with biotic metrics

Prior to modeling the influence of reach-scale variables and landscape-level anthropogenic disturbance, the effect of natural environmental gradients known to influence fish and invertebrate community structure (drainage area, drainage density, reach gradient, spring density, surficial geology, distance to mainstem, and sampling month) were accounted for using boosted regression trees (BRTs; Fig. 2, left pane). Boosted regression trees are well-suited for this study because they are designed to maximize predictive performance, making them valuable for predicting stream condition in unsampled stream reaches (Leathwick et al., 2006; Elith et al., 2008). The selected natural variables were used to fit BRT models to each fish and invertebrate community metric, and model residual values were used as dependent variables in subsequent analyses. The use of residual values in further models reduced each biotic metric to a value relative to other streams occurring under similar natural characteristics, thus allowing us to control for the effect of natural variation across streams and more directly model biological integrity (Smogor and Angermeier, 1999; Stoddard et al., 2008; Daniel et al., 2015). Models were fit using the '*dismo*' package (Hijmans et al., 2017) in R (R Development Core Team, 2015), which is specifically designed to enhance the ecological interpretability of BRT results (Elith and Leathwick, 2011). Tree complexity was set to 5 and bag ratio to 0.5, with learning rate adjusted to minimize prediction error after completing no < 1,000 iterations (following Elith et al., 2008). Ten-fold cross validation was used to identify the optimal number of trees in each, and to estimate cross-validated residual deviance. Cross-validation is particularly useful for predictive models, as it allows models to be built with all available data while still allowing for unbiased estimates of predictive performance (Elith et al., 2008). To safeguard against overfitting, a randomly generated predictor variable (values ranging from 0 to 100) was included as a stopping criterion; only predictor variables that were of greater importance than the randomly generated predictor were included in final models (Soykan et al., 2014).

Before developing reach and landscape-level models, Pearson's pairwise correlations were used to examine the correlation structure of both predictor sets. For variable pairs exhibiting high correlations ($r > |0.70|$), only the variable exhibiting the strongest relationship with in-stream community metrics was retained in an effort to improve model performance by reducing collinearity among predictors (Dormann et al., 2013). Following predictor variable reduction, suites of BRTs (De'ath, 2007; Elith et al., 2008; Soykan, et al., 2014) were developed to evaluate the relationships between reach and landscape-level environmental variables and fish and invertebrate responses within each aquatic ecoregion and stream-size class. Model performance was evaluated by calculating the proportion of total deviance explained, which can be interpreted in a similar manner to R^2 in regression analysis (D^2; Leathwick et al., 2006; Soykan et al., 2014).

After modeling the relationship between stream biota and environmental predictors, Spearman's rank correlation was used to examine the strength and directionality of relationships between reach-level variables and landscape-level anthropogenic disturbances included in final models (hereafter "Top predictors"; Fig. 2, center pane). This allowed for the identification of potential pathways of impairment and an assessment of redundancies and gaps in the predictor sets' abilities to describe stream impairment. Next, results of the landscape-based models were used to extrapolate the biotic predictions to unsampled stream reaches throughout the state (Fig. 2, right pane). After rescaling each fish and invertebrate metrics' predicted value from 0 to 10, all values for each reach were summed to generate an estimate of overall ecological integrity, thus ensuring that the final suite of candidate least-disturbed sites met the habitat and water quality requirements of numerous components of the biotic community. Reaches with the highest predicted biological integrity (overall scores in the 95th percentile within each ecoregion and stream size class) were deemed candidate reference reaches (Fig. 2, right pane).

3. Results

3.1. Summary of biological metrics and landscape variables

Biological metrics had considerable variation within and across aquatic ecoregions and stream sizes (Table 1). Fish species richness was greater in small rivers than in creeks, and was highest in the Ozarks. The proportion of native omnivorous/herbivorous individuals was higher in creeks than small rivers, while the proportion of native insectivorous cyprinids was higher in Ozarks small rivers, but varied little between stream size classes in the Plains. EPT richness was consistently higher in larger streams, and, along with SDI, was higher in the Ozarks. The proportions of tolerant individuals and HBI values were higher in the Plains. While the proportion of non-native individuals appeared slightly higher in small rivers than in creeks, but values were extremely low in both regions (< 0.01).

Landscape-level environmental variables differed between ecoregions, and reach-level physical habitat and water quality parameters showed considerable differences between both ecoregions and stream size classes (Tables 2 and S1). Network catchments within the Plains ecoregion had greater row-crop agriculture ($\bar{x} = 31.2\%$ vs. 4.0%) and pasturelands ($\bar{x} = 42.3\%$ vs. 31.8%) as well as densities of headwater impoundments ($\bar{x} = 0.64/\text{km}^2$ vs. $0.41/\text{km}^2$) and coal mining operations ($\bar{x} = 0.014/\text{km}^2$ vs. $0.004/\text{km}^2$) than Ozarks watersheds (Table S1). On average, Plains streams consisted of narrower and more highly incised channels with higher levels of substrate embeddedness, turbidity, and total chlorophyll relative to streams in the Ozarks region (Table 2). Conversely, Ozarks streams had more forested watersheds ($\bar{x}$ = 54.6% vs 16.2%), although they did generally exhibit denser human populations, and greater densities of lead mining operations and other point-source pollution sources (Table S1). Streams within the Ozarks region tended to be wider and more riffle-dominated than those in the Plains, exhibited coarser substrate and higher dissolved oxygen levels, and tended to have less mid-channel canopy cover and woody debris than did Plains streams (Table 2).

3.2. Reach-level environmental influence on biotic metrics

Models were successfully constructed for nine of ten biotic metrics for at least one stream size classification (Tables 3 and 4) using 30 reach-level predictors in both the Ozarks and Plains ecoregions (Table 2). The model deviance was unable to be reduced for all models predicting the proportion of non-native individuals, as well as for Plains creek SDI values and Ozarks small river SDI values. On average, reach-level models explained ~25% of the variation in fish and invertebrate metrics in the Plains region, with the proportion of native insectivorous cyprinids in small rivers as the lowest (8%), and the number of native benthic fish species in small rivers the highest (40%). In the Ozarks region, reach-level models on average explained ~27% of the variation in biotic metrics, with the proportion of tolerant individuals in creeks as the lowest (13%), and HBI values in small rivers the highest (46%).

Measures of fish richness (native fish species richness, number of native benthic species, number of native lithophilic species) were most related to measures of channel morphology, which accounted for between 40 and 50% of the explained variation in each metric (Fig. 3). In addition, top predictors for richness metrics consistently included measures of channel morphology (e.g., mean depth, bank-full width/depth ratio, and standard deviation of channel incision height; Tables 3 and 4). Native fish species richness was also positively related to dissolved oxygen in all streams except Plains small rivers, while aquatic macrophytes and coarse gravel substrate were top predictors in Ozarks creeks and small rivers of the Plains region, respectively.

Proportional fish metrics (proportion native insectivorous cyprinid individuals, native omnivores/herbivore individuals, and tolerant individuals) varied considerably in predictability between ecoregion and stream size, and their relationship with reach-level variables. For example, the proportion of native insectivorous cyprinids was negatively associated with mean depth in the Plains region, and positively associated with bank-full width/depth ratio and dissolved oxygen. In the Ozarks region, available cover and riparian characteristics had a strong influence on native insectivorous cyprinids, as seen by an increase with woody debris, undercut banks, and riparian canopy presence in creeks, and a negative association with macrophyte cover and mid-channel canopy density in small rivers (Table 4). Overall, the proportion of native tolerant individuals increased with measures of smaller substrate (e.g., fine substrate, channel embeddedness) and total chlorophyll, and decreased with increased gravel substrate and bank-full width/depth ratio (Tables 3 and 4). The proportion of omnivorous/herbivorous individuals in creeks was negatively associated with dissolved oxygen, and positively associated with conductivity.

Macroinvertebrate metrics (SDI, EPT, and HBI), were generally more strongly related to water quality parameters than fish metrics, with total chlorophyll, dissolved oxygen, and conductivity accounting for an average of 30–40% of the explained variation in each metric (Fig. 3). In the small rivers of the Plains region, SDI increased with coarse substrate, woody debris, and riffle percentage. In the Ozarks region, SDI was also highest in riffle-dominated creeks and was also negatively associated with increased total chlorophyll. Invertebrate EPT richness was most strongly related to reach-level environmental conditions and responded to metrics consistently across stream size and aquatic ecoregion, and was positively related to bank-full width, width/depth ratios, dissolved oxygen, and woody debris volume, and negatively related to total chlorophyll, conductivity, and mid-channel canopy cover. Conversely, HBI values were negatively related to dissolved oxygen, bank-full width, and percent riffle, and positively related to total chlorophyll and channel embeddedness (Tables 3 and 4).

3.3. Landscape-level environmental influence on biotic metrics

Models were constructed successfully for nine of ten biotic metrics for at least one stream size classification using the 29 (Plains) and 28 (Ozarks) landscape-level predictors retained for analysis (Table S1). The model deviance was unable to be reduced for the proportion of non-native individuals, as well as for Plains creek Shannon Diversity Index (SDI) values, Ozarks small river SDI values, Plains Hilsenhoff Biotic Index (HBI) values in small rivers, and Ozark small river values of the proportion of native insectivorous cyprinids (Tables 3 and 4). On average, landscape-level models explained about 18% of the variation in fish and invertebrate metrics in the Plains region, with the number of native lithophilic species in creeks having the lowest explained variation (4%), and the number of native lithophilic species in small rivers having the highest (31%). In the Ozark region, landscape-level models on average explained about 20% of the variation in biotic metrics, with the SDI value in creeks being the lowest (7%), and HBI values in small rivers being the highest (51%).

Percent forest, together with fragmentation and flow modification metrics, were commonly among the top predictors of fish and invertebrate community characteristics (Tables 3 and 4). Together, natural landcover and fragmentation and flow modification metrics accounted for about 50–75% of the explained variation in each metric (Fig. 4). Conversely, metrics representing point-source pollution consistently showed the weakest relationship with biotic metrics within both ecoregions, on average accounting for $< 10\%$ of the explained variation in fish and invertebrate metrics (Fig. 4). Agricultural and urbanization metrics typically accounted for 20–30% of the explained

Table 3
Reach and landscape-level boosted regression tree model results for each biotic response within creeks and small rivers of the Plains aquatic ecoregions of Missouri. K – number of model parameters, D^2 – proportion of deviance explained, LC – Local Catchment, NC – Network Catchment, LR – Local Riparian, NR – Network Riparian. Refer to Tables 1, 2 and S1 for metric and variable abbreviations.

Metric/scale	Plains Creeks			Plains Small Rivers		
	K	D^2	Top Predictors	K	D^2	Top Predictors
Native						
Reach	7	0.14	m_depth(+) w/d(+) DO(+) bankfull(+)	12	0.36	coarse(+) cond(−) sdincision(+) w/d(+)
Landscape	16	0.05	NC_hw_imps(−) LR_forest(+) LC_pasture(−)	18	0.29	LR_forest(+) NC_hw_imps(−) LR_pasture(−)
Benthic						
Reach	13	0.15	m_depth(+) fines(−) bankfull(+) coarse(+)	15	0.40	cond(−) coarse(+) riffle(+) w/d(+)
Landscape	15	0.16	LC_pasture(−) LR_forest(+) NC_hw_imps(−)	18	0.26	NC_hw_imps(−) LR_forest(+) LC_grass(−)
Lith						
Reach	11	0.16	w/d(+) DO(+) cond(+) m_depth(+)	17	0.31	w/d(+) coarse(+) cond(−) incision(−)
Landscape	9	0.04	NC_hw_imps(−) LR_forest(+) LR_imperv(+)	18	0.31	NC_hw_imps(−) LR_forest(+) LC_grass(−)
p_cyp_insect						
Reach	16	0.32	w/d(+) DO(+) m_depth(−) max_pool_dep(−)	15	0.08	w/d(+) m_depth(−) brush(−) pH(−)
Landscape	11	0.21	LC_pop_dens(−) LC_pasture(−) NC_hw_imps(−)	9	0.14	NC_cafo(+) LC_dev_low(−) LC_grass(−)
p_omn/herb						
Reach	16	0.21	cond(+) DO(−) pool(+) max_pool_dep(+)	13	0.17	DO(+) coarse(+) pH(+) undercut_bk(+)
Landscape	13	0.16	LC_pop_dens(+) NC_hw_imps(+)LC_forest(+)	4	0.10	NC_dams(−) NC_npdes(+) LR_imperv(+)
p_tolerant						
Reach	8	0.29	fines(+) cond(−) max_pool_dep(+) w/d(−)	11	0.34	w/d(−) DO(+) coarse(−) m_depth(+)
Landscape	12	0.20	NC_hw_imps(+) LC_forest(−) NC_rd_crs(+)	4	0.20	LR_forest(−) NC_cafo(−) LC_grass(+)
SDI						
Reach	–	–	–	13	0.20	vol_LWD(+) DO(−) riffle(+) coarse(+)
Landscape	–	–	–	13	0.26	LR_crop(−) LC_pasture(−) LC_forest(+)
EPT						
Reach	18	0.28	bankfull(+) canopy_dens(−) chl(−) DO(+)	5	0.26	w/d(+) vol_LWD(+) canopy_dens(−)
Landscape	13	0.11	LC_forest(+) LR_crop(+) NR_pasture(−)	11	0.14	LR_crop(−) LC_pop_dens(−) NC_hw_imps(−)
HBI						
Reach	13	0.23	DO(−) max_pool_dep(+) pH(−) sinu(−)	17	0.17	bankfull(−) incision(−) max_pool_dep(−) pH(−)
Landscape	9	0.17	LC_grass(−) LC_forest(−) LC_pop_dens(+)	–	–	–

variation, but their influence varied among biotic response and between aquatic ecoregion (Fig. 4). Within the Plains ecoregion, the density of headwater impoundments and pasture landcover within the local and network catchments had the strongest negative influence on the fish richness metrics (Table 3). Fish richness metrics in Ozarks creeks were negatively related to road crossing density. The relationship of the density of headwater impoundments differed between ecoregions, as it was positively associated with native fish species richness and the number of native lithophilic species in Ozarks small rivers. Fish richness metrics also increased with higher percentages of forested landcover in Ozarks creeks, and showed some sensitivity to urban impairment (Table 4 and Fig. 4).

Fish metrics related to trophic ecology (proportion of native insectivorous cyprinid individuals, proportion of native omnivore/herbivore individuals) generally showed stronger relationships to urban impairment than did species richness metrics, although in some cases responded to point-source pollution sources counter to what was predicted (Table 3 and Table 4). For example, in the Plains ecoregion, the proportion of native insectivorous cyprinids was negatively associated with pastures, grasslands, population density and low-intensity development in the local catchment. However, the proportion of native insectivorous cyprinids increased with increased the density of confined animal feeding operations (CAFO) in the network catchment in Plains small rivers and with lead-mining density in the network catchment of Ozarks creeks. Average densities of both stressors were relatively low, at $0.013/km^2$ and $0.038/km^2$, respectively. In contrast to insectivorous cyprinids, the proportion of native omnivorous/herbivorous individuals increased with local catchment population density and local riparian imperviousness in the Plains region, and decreased with increased forest cover in the network catchments of Ozarks creeks and small rivers.

Within both aquatic ecoregions, invertebrate metrics (SDI, EPT, HBI) typically showed strong relationships with agricultural disturbance (Fig. 4). Within the Plains region, SDI was negatively related to crop and pasture landcover, and positively related to forested area. Similarly, EPT values in creeks had a negative relationship with pasture in the network riparian zone, and local riparian crop in small rivers, although they had a positive relationship with local riparian crop in creeks (Table 3). Invertebrate community tolerance, as measured by HBI, was negatively related to forest and grassland in the local catchment, and was positively associated with local population density. In general, invertebrate metrics responded to agricultural disturbances in Ozarks creeks (Table 4).

3.4. Linking reach and landscape-level environmental variables

Each of the 15 top reach-level predictors were significantly correlated ($P < 0.05$) to at least 5 of the top 14 landscape-level predictors (Kleekamp, 2016). Increased headwater impoundment density in the network catchment was associated with narrower, incised stream channels with lower percentages of coarse substrate, and lower dissolved oxygen levels. Similarly, increased row crop agriculture in the local and riparian network was linked with deeper, more incised streams, fewer aquatic macrophytes and lower dissolved oxygen, and higher levels of fine sediment and total chlorophyll. In contrast, the percentage of low intensity development manifested in the fewest measurable habitat and water quality metrics, with higher conductivity levels being the most significant indicator of that source of impairment.

3.5. Predicting statewide biological integrity

Biotic metric values for all small river and creek reaches across the

Table 4
Reach and landscape-level boosted regression tree model results for each biotic response within creeks and small rivers of the Ozarks aquatic ecoregion of Missouri. K – number of model parameters, D^2 – proportion of deviance explained, LC – Local Catchment, NC – Network Catchment, LR – Local Riparian, NR – Network Riparian. Refer to Tables 1, 2 and S1 for metric and variable abbreviations.

Metric/scale	Ozarks Creeks			Ozarks Small Rivers		
	K	D^2	Top Predictors	K	D^2	Top Predictors
Native						
Reach	15	0.21	veg(+) w/d(+) DO(+) pool(+)	16	0.43	w/d(+) sdincision(+) pool(+) DO(+)
Landscape	8	0.16	NC_forest(+) NC_rd_crs(−) LR_forest(+)	15	0.15	NC_hw_imp(+) NR_crop(+) NC_dev_low(−)
Benthic						
Reach	17	0.18	veg(+) max_pool_dep(−) bankfull(+)	16	0.19	w/d(+) incision(+) sdincision(+) canopy(−)
Landscape	9	0.15	NC_dev_low(−) NC_rd_crs(−)	10	0.20	NC_wells(+) LC_grass(−) NC_npdes(−)
Lith						
Reach	18	0.22	veg(+) pool(+) w/d(+)	14	0.44	turbid(+) w/d(+) canopy_dens(−)
Landscape	10	0.15	NC_forest(+) NC_rd_crs(−) LR_forest(+)	13	0.16	NC_hw_imps(+) LR_forest(−) LC_grass(−)
p_cyp_insect						
Reach	16	0.15	vol_LWD(+) pH(+) undercut_bk(+) canopy(+)	11	0.16	w/d(+) canopy_dens(−) veg(−)
Landscape	11	0.11	NC_forest(+) NC_lead(+) LC_grass(−)	–	–	–
p_omn/herb						
Reach	17	0.17	max_pool_dep(−) cond(+) pH(−) DO(−)	12	0.31	gravel(−) pH(−) bankfull(−) embed(−)
Landscape	14	0.15	NC_forest(−) NC_dams(−) NR_grass(−)	9	0.13	NR_grass(−) NC_dev_low(+) NC_forest(−)
p_tolerant						
Reach	15	0.13	chl(+) embed(+) gravel(−) cond(+)	12	0.24	embed(+) fines(+) incision(+)
Landscape	9	0.08	LR_forest(−) NR_crop(+) LR_crop(+)	8	0.16	NR_crop(+) NC_lndfl(+) NC_npdes(+)
SDI						
Reach	6	0.22	riffle(+) chl(−) m_depth(+) cond(−)	–	–	–
Landscape	10	0.07	NR_crop(−) NC_forest(+) NC_dev_low(−)	–	–	–
EPT						
Reach	18	0.42	chl(−) DO(+) cond(−) veg(+)	17	0.27	chl(−) DO(+) riffle(+) bankfull(+)
Landscape	8	0.38	NC_forest(+) NR_crop(−) NC_wells(−)	15	0.30	NC_wells(+) NC_forest(+) NC_coal(−)
HBI						
Reach	16	0.37	chl(+) incision(+) DO(−) riffle(−)	12	0.46	chl(+) riffle(−) embed(+) DO(−)
Landscape	9	0.37	NR_crop(+) NC_forest(−) NC_hw_imps(+)	9	0.51	NC_dams(+) NC_dev_low(+) NR_crop(+)

Plains and Ozarks aquatic ecoregions were predicted using the BRT results and the landscape-level variables. Cumulative biological integrity scores ranged from 0 to 80 within both Plains stream size classes, 0–90 for Ozarks creeks, and 0–70 for Ozarks small rivers. Maximum values were based on the number of biotic metrics related to landscape-level anthropogenic disturbance variables as described in Tables 3 and 4 (e.g., seven of the biotic metrics within the Ozarks small rivers spatial scale). Streams scoring at the high end of the continuum reflect least-disturbed landscape conditions relative to other reaches within the same aquatic ecoregion and stream size class. Conversely, streams scoring on the lower end of the spectrum reflect heightened impairment, and thus are estimated to exhibit degraded conditions (Fig. 5).

No stream reaches received maximum scores for all 7–9 biotic metrics. The median score for Plains creeks was 38.6/80, with the maximum score of 63.4/80 (Table 5). Plains small river scores were only slightly lower, with median and maximum scores of 34.2/80 and 61.8/80, respectively. Ozarks creeks had the highest concentration of least-impaired stream reaches, as indicated by median and maximum biological integrity scores of 52.0/90 and 77.4/90, respectively. Similar to the Plains region, high quality small river reaches in the Ozarks were fewer, with a median biological integrity score of 37.7/70, and with a maximum score of 51.8/70 (Table 5).

Sites scoring in the 95th percentile within each aquatic ecoregion and stream size classification were retained in support of identifying candidate reference reaches. Within the Plains region, 447 creek and 236 small river reaches were retained and in the Ozarks region, 532 creek and 208 small river reaches were selected (Fig. 6). Reference reach candidates varied considerably between and within aquatic ecoregions in terms of landcover/landuse within their landscapes, although several patterns were evident. Within the Plains region, candidate creek reference reaches had above average forested landcover (31.3%), below average pasture cover (29.8%), slightly below average cultivated crop (27.1%), and near average imperviousness (2.3%; Table 5). Small river candidates in the Plains region showed a similar pattern with forest (18.3%), pasture (38.9%), and imperviousness (1.5%), although exhibited slightly above average levels of cultivated crop (38.9%). Candidate reference reaches within the Ozarks region exhibited 88.9% forested local catchments, with low levels of pasture (5.2%) and imperviousness (0.8%), and extremely low levels of cultivated crop (< 0.1%). On average, Ozarks small rivers had local catchments that were 54.5% forested, 36.9% pasture land, 1.5% impervious, and 0.4% cultivated crop.

4. Discussion

This study is one of the first efforts to estimate biological integrity of wadeable streams using predicted values of both fish and invertebrate community characteristics. Additionally, this study represents a novel framework for relating landscape-level anthropogenic disturbances to in-stream physical habitat and biotic condition, and for applying results to un-sampled streams. Together, these results may be useful to practitioners to prioritize streams reaches for conservation effort, and the described approach may help support the identification of candidate reference reaches in other systems that are directly linked to biological integrity.

Reach-level physical habitat and water quality variables consistently explained greater proportions of variation in biotic metrics (26%) than landscape-level variables (19%). This finding corroborates previous work showing the importance of reach-level environmental characteristics on fish and invertebrate communities (Richards et al., 1997; Wang et al., 2003; Kautza and Sullivan, 2012), but does differ

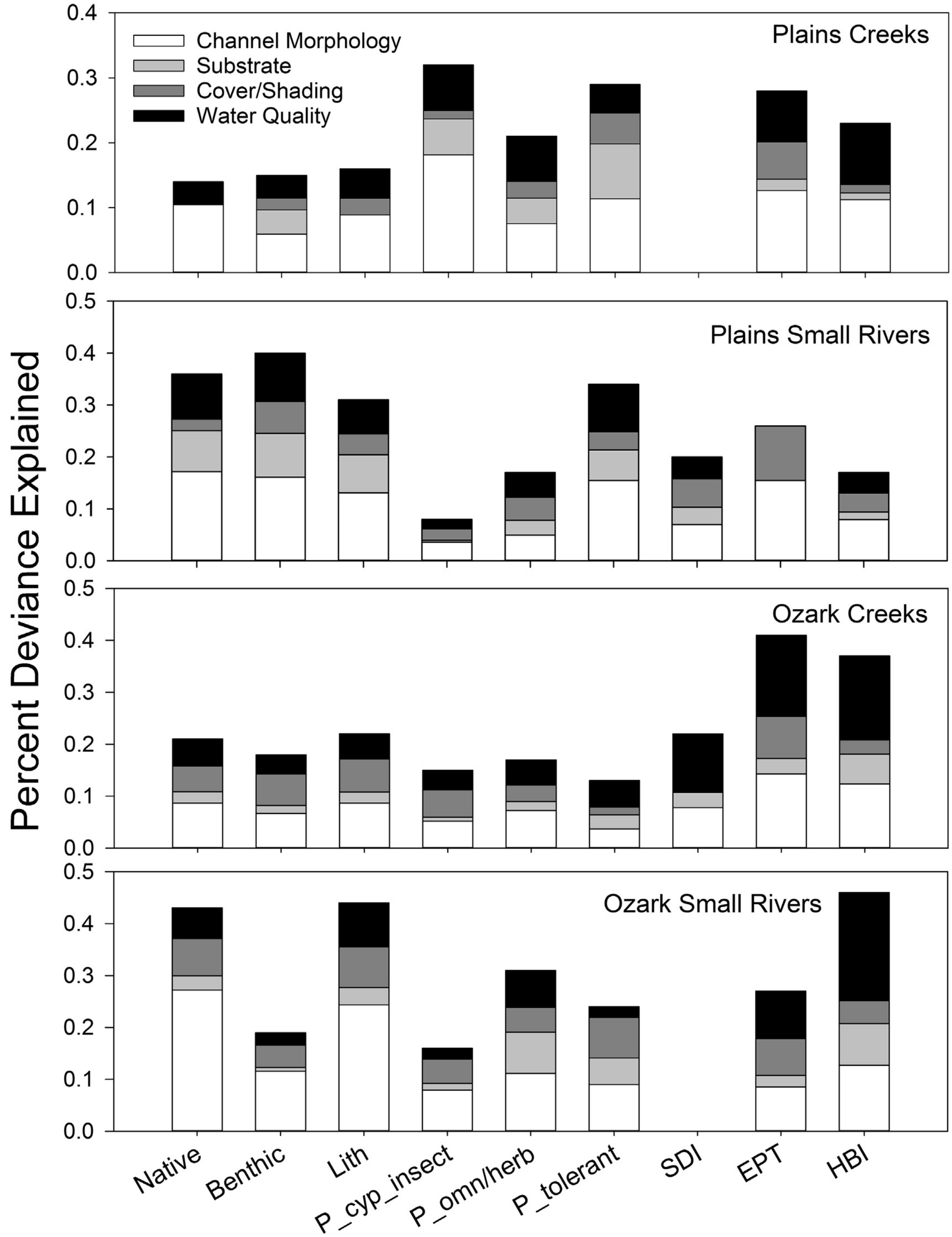

Fig. 3. Bar graphs depicting the relative influence of channel morphology, substrate, cover/shading, and water quality metrics (see Table 2 for additional details) on stream fish and macroinvertebrate community characteristics within creeks and small rivers of the Plains and Ozarks. Refer to Table 1 for an explanation of biotic metric codes. Blank columns refer to metrics where BRT model deviance was unable to be reduced, and therefore biotic metrics were unexplained by reach-level predictors. Model deviance was unable to be reduced for proportion of non-native individuals in all models, and was therefore excluded from the figure.

from some studies that indicate landscape characteristics were greater determinants of stream biota than reach-level habitat and water quality (Roth et al., 1996; Allan et al., 1997). This discrepancy is scale dependent, as landscape factors are likely to have stronger relationships with response metrics than local factors over larger spatial extents and over areas with greater heterogeneity in condition (Infante et al., 2009). For example, two studies documenting predictors of biotic integrity in the same Michigan river system over differing spatial extents found differences in main drivers of biotic integrity, with catchment landcover being the dominant predictor at the larger spatial extent and habitat variables and local landcover at the smaller extent (Roth et al., 1996; Lammert and Allan, 1999). In our study, modeling environmental influences within aquatic ecoregions and accounting for natural controls on stream biota prior to additional analyses likely reduced the potential

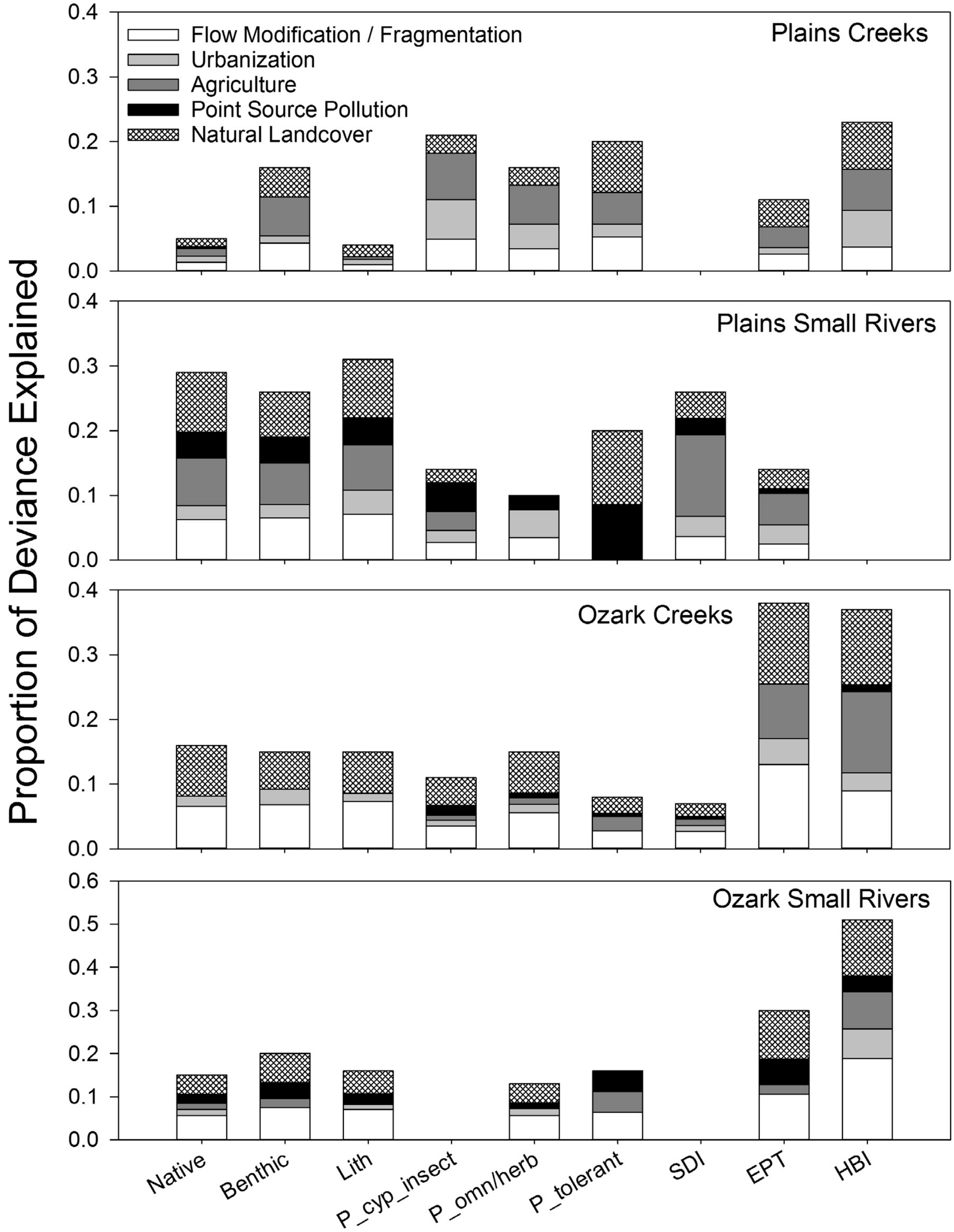

Fig. 4. Bar graphs depicting the relative influence of landscape-level predictors (flow modification/fragmentation, urbanization, agriculture, point source pollution, natural landcover) on stream fish and macroinvertebrate community characteristics within creeks and small rivers of the Plains and Ozarks (see Table S1 for more details). Refer to Table 1 for an explanation of biotic metric codes. Blank columns refer to metrics where BRT model deviance was unable to be reduced, and therefore biotic metrics were unexplained by landscape-level predictors. Model deviance was unable to be reduced for proportion of non-native individuals in all models, and was therefore excluded from the figure.

variation explained by landscape predictors. Without these steps, it is plausible that more extreme gradients in natural landscape characteristics and anthropogenic disturbances would have resulted in a stronger landscape signal.

In general, channel morphological characteristics were the most influential predictors of fish richness measures at the reach-level, and routinely accounted for about 40 to 50% of the explained variation in the total number of native species, the number of native benthic species, and the number of native lithophilic species. Even after controlling for the effect of drainage area, these richness measures still showed strong positive associations with increasing bank-full width, bank-full width/depth ratio, mean depth and standard deviation of channel

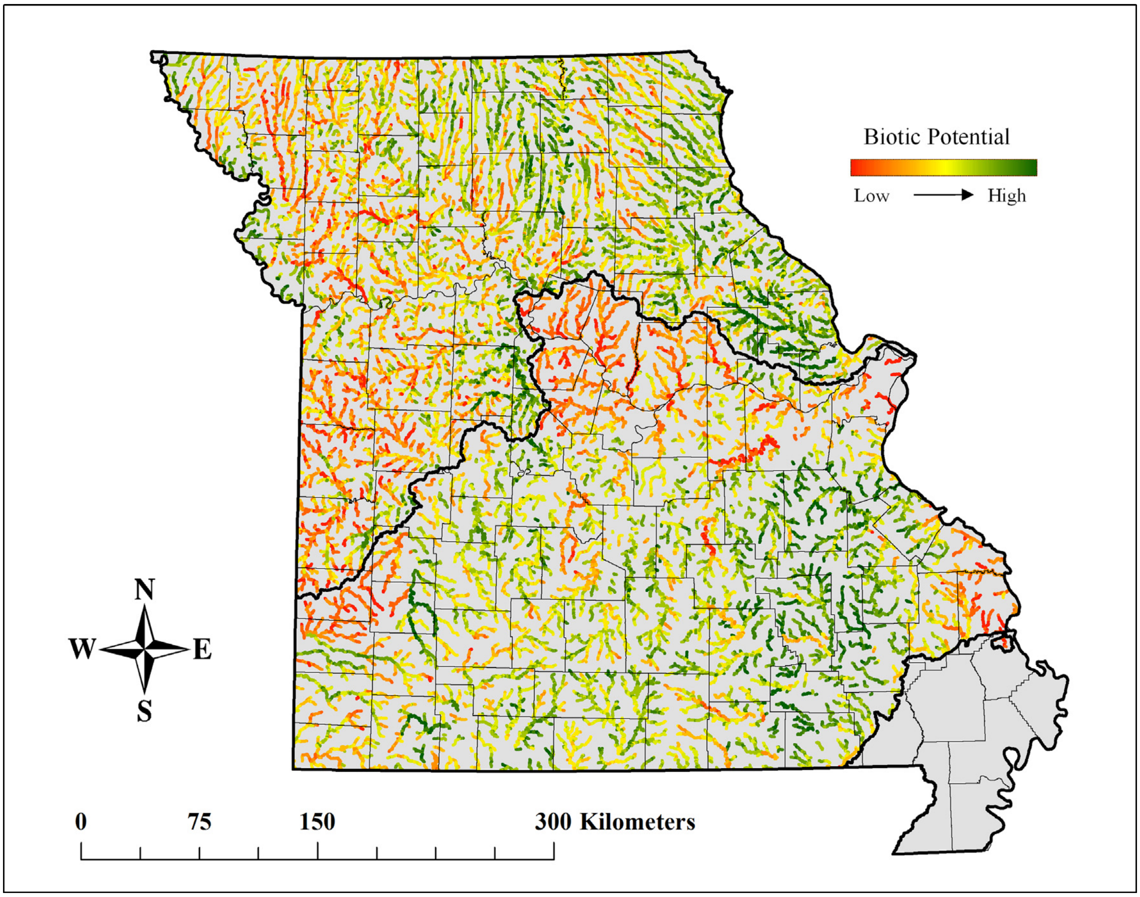

Fig. 5. The predicted biological integrity of creek and small-river reaches in the Plains and Ozarks aquatic ecoregions of Missouri. Biological integrity was based on cumulative rescaled biotic metric scores for each stream size in each ecoregion. Reaches with the highest biotic potential, indicated in green, are least-disturbed systems, while reaches with the lowest biotic potential, indicated in red, likely exhibit degraded conditions.

incision, highlighting the importance of wider and more variable channel conditions in maintaining habitat heterogeneity and species richness (Gorman and Karr, 1978). In contrast, invertebrate metrics and proportional fish metrics typically exhibited stronger relationships with water quality parameters (e.g., DO, total chlorophyll, conductivity), and to a lesser extent, substrate characteristics (e.g., channel embeddedness). These results align with existing evidence of non-concordance of fish and invertebrate responses to disturbance (Infante et al., 2009; Backus-Freer and Pyron, 2015; Kimmel and Argent, 2016), highlighting the need to incorporate both into an overall biological integrity assessment. Further, our results broadly support previous findings that fish metrics may be effective indicators of habitat degradation while invertebrate metrics may be more useful as indicators of water quality impairment (Rabeni et al., 1997; Wang et al., 1997; Bramblett et al., 2005; Piliere et al., 2014). These results also indicate that increased percentages of fine sediment and substrate embeddedness, linked to riparian agricultural and urban development, result in increased invertebrate community tolerance (HBI), greater proportions of tolerant fish species, and lower fish species richness. This finding is similar to others who have documented the loss of interstitial benthic habitat and spawning substrate as a result of excess sedimentation, resulting in degraded fish and invertebrate communities (Berkman and Rabeni, 1987; Berry et al., 2003; Kemp et al., 2011; Descloux et al., 2013). However, substrate characteristics accounted for small amounts of explained variation for the majority of biotic metrics (Fig. 3). The limited exploratory power of substrate characteristics overall may be attributable to lower precision of particle size and embeddedness measurements in relation to more precisely measured features, such as stream widths and depths (Kaufmann et al., 1999).

The relationships between landscape-level environmental variables

Table 5
Summary of cumulative biological integrity scores (IQR = interquartile range), and mean (standard deviation) values of general landcover/landuse metrics within the local landscapes of creek and small river candidate reference reaches within the Central Plains and Ozark Highlands aquatic ecoregions of Missouri.

Ecoregion/scale	Biological Integrity			Landcover and Landuse (%)			
	Max Score	Median (IQR)	95th Percentile	Forest	Crop	Pasture	Impervious Surface
Plains							
Creeks	63.4/80	38.6 (32.6–45.2)	52.5	31.3 (15.9)	27.1 (19.6)	29.8 (18.6)	2.3 (3.1)
Small rivers	61.8/80	34.2 (28.1–40.6)	50.6	18.3 (9.4)	38.9 (16.6)	27.6 (9.8)	1.5 (0.6)
Ozarks							
Creeks	77.4/90	52.0 (43.9–58.3)	65.8	88.9 (6.0)	< 0.1 (0.3)	5.2 (4.5)	0.8 (0.5)
Small rivers	51.8/70	37.7 (32.7–41.2)	45.3	54.5 (26.4)	0.4 (0.6)	36.9 (25.4)	1.5 (0.7)

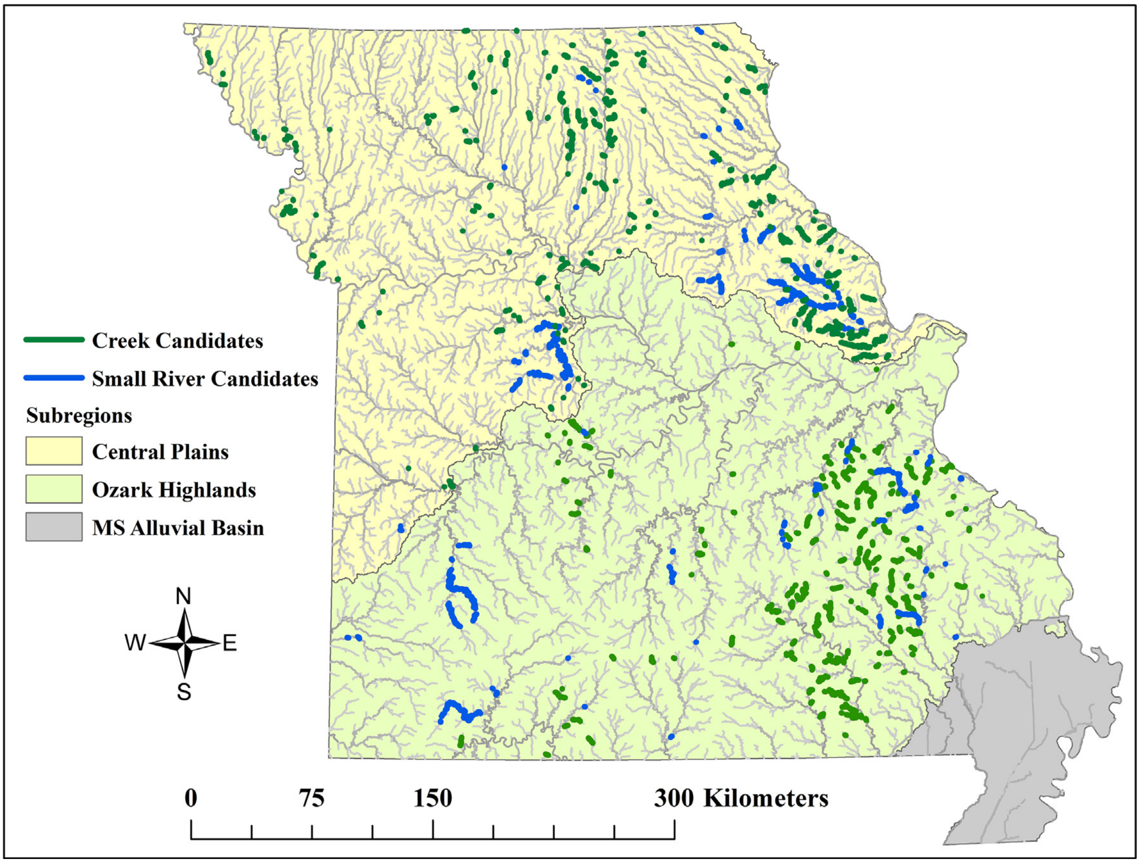

Fig. 6. Potential candidate creek and small river reference reaches in the Central Plains and Ozarks Highlands aquatic ecoregions of Missouri. Reaches within the MS Alluvial Basin were excluded from this study. Candidate reference reaches were those that scored in the 95th percentile within each aquatic ecoregion and stream size classification. A total of 447 creek and 236 small river reaches were retained as candidates in the Plains ecoregion, while 532 creek and 208 small river reaches were identified as candidates in the Ozarks Highlands aquatic ecoregion.

and biotic metrics differed between stream size class and aquatic ecoregion, although several patterns were evident. Forested landcover, together with measures of fragmentation and flow modification, were consistently among the top landscape predictors, frequently accounting for between 50 and 75% of the total explained variation in biotic metrics. This largely consisted of decreased fish richness as headwater impoundment densities in the Plains and road crossing densities in the Ozarks increased, and increased fish richness and invertebrate metric values with increased forested landcover, particularly at the local catchment and local riparian scale. The strength of these relationships is further evidence that fish species of the Plains are strongly influenced by flow conditions and water availability (Matthews, 1988; Dodds et al., 2004; Perkin et al., 2015). The amount of pastureland in the local catchment and riparian zone also may be a source of fish community impairment, corroborating studies documenting the negative influence of riparian cattle grazing, including dramatically increased phosphorous contributions and destabilized stream bank conditions (Quinn et al., 1992; James et al., 2007). However, row-crop agriculture in the local and network riparian zones across ecoregions had a stronger influence on invertebrate metrics than fish richness metrics, likely due to increased sedimentation and nutrient contributions, as measured by channel embeddedness and total chlorophyll. Invertebrates are sensitive to row-crop agriculture and the resultant channel and water quality degradation (Lenat and Crawford, 1994; Lammert and Allan, 1999; Allan, 2004) and even within the agriculturally-dominated Plains region, invertebrate community metrics could differentiate streams along a continuum of agricultural impairment. Invertebrate metrics of the Ozarks region showed greater degradation with agricultural landcover even at values as low as 8–10% within the network riparian zone (see Kleekamp, 2016 for additional details), which were much lower than previously found in the Midwest using fish community data (Wang et al., 1997).

Urban sources of impairment (i.e. population density, imperviousness, etc.) showed little influence on fish richness measures in the Plains ecoregion but had stronger relationships with invertebrate metrics and fish metrics related to trophic ecology. The proportion of native insectivorous cyprinids decreased with increased population density and low intensity development, while the proportion of omnivorous/herbivorous individuals increased with population density and local riparian imperviousness. These metrics are often linked to urbanization, and fish community integrity typically decreased with increased urbanization (Wang et al., 2001; Morgan and Cushman, 2005; Martínez-Fernández et al., 2019) of about 3–10% of the landscape, depending on the metric used (Yoder et al., 1999; Paul and Meyer, 2001; Wang et al., 2001; Morgan and Cushman, 2005; Edge et al., 2017).

Despite its history as a major source of stream impairment (Cairns and Pratt, 1993), point-source pollution consistently proved to be a weak predictor of fish and invertebrate characteristics, and when present, tended to influence biotic metrics contrary to what was expected. For instance, the proportion of native insectivorous cyprinids in the Plains region showed a positive relationship with the density of CAFOs, and increased with lead mine density in Ozarks creeks. This discrepancy could be the result of average densities for these stressors being low within the study area (0.013/km^2 and 0.038/km^2). Given that point-source stressors were concentrated in remote, largely forested areas within the network catchments of reaches across each ecoregion, it is possible that the surrounding natural landcover characteristics are largely responsible for the resulting biotic community characteristics.

Still, fish metrics have been shown to respond to low densities of point-source pollution in multiple ecoregions of the United States (< 0.05 mines/km^2; Daniel et al., 2015), and further investigation may therefore be warranted.

By correlating influential variables from both the reach and landscape-level predictor sets, a mechanistic view of the specific ways human landscape alterations impact the physical and chemical condition of receiving waters can be developed (Rabeni, 2000; Infante and Allan, 2010). In our study, increased headwater impoundment density appeared to be influential on multiple aspects of in-stream habitat in predictable ways, resulting in narrower, more incised stream channels with less coarse substrate, and lower dissolved oxygen levels. Row crop agriculture was linked to deep, heavily incised streams, fewer aquatic macrophytes and lower dissolved oxygen, and much higher levels of fine sediment and total chlorophyll, which correspond with anticipated effects of agriculture on habitat (Allan, 2004). The percentage of low intensity development, which has been found to be detrimental to both fish and invertebrates (Thornbrugh and Infante, 2019), was only strongly linked to higher conductivity. Similarly, Wang et al. (1997) found urbanization to be more weakly tied to physical habitat integrity than to biotic integrity, suggesting the limited ability to identify urban impairment using common habitat and water quality metrics.

The index of biological integrity provides a comprehensive view of stream condition in all reaches of the Ozarks and Plains ecoregions that has multiple advantages over other approaches. First, rather than simply assigning impaired and unimpaired status to stream reaches, the scoring system reflects a continuum of degraded conditions, allowing for increased conceptualization of major threats to these systems. Second, by focusing on predicted scores, the full complexity of landscape conditions was retained, but did not sacrifice any ability to describe biotic conditions (Leathwick et al., 2006; Elith et al., 2008; Thompson et al., 2012). This approach also increases the likelihood that landscape characteristics are accurately portraying in-stream condition in unsampled reaches, an improvement over cumulative index approaches that are based on theoretical landscape controls on stream habitat and biota. Further, by incorporating multiple ecological indicators into the estimate, this study identified a wider range of disturbances than detectable using single indicators, a noted advantage (Dale and Beyeler, 2001). The continuum of scores for up to 9 different biological metrics can be used in concert, or parsed into the specific biological metric of interest. Finally, the index of biological integrity may be a valuable tool in assessing where to target on-the-ground investigation for the identification of candidate stream reference reaches. We used the 95th percentile within each stream size class and aquatic ecoregion to demonstrate how such an approach could result in the identification of reference reaches with limited additional resource investment.

4.1. Conclusions

Conservation practitioners require tools and datasets that can be used to determine where action is required and how to measure the success of restoration or preservation initiatives. The approach outlined in this manuscript can support the identification of candidate reference reaches at unsampled stream sites at large spatial scales, and is scalable to particular stream sizes, ecoregions, and biotic responses. Moreover, these results can be used to designate areas of high conservation value, and restoration need. By taking additional steps to understand mechanistic relationships between landscape, habitat and biological integrity, our approach can also provide practitioners with a conceptual understanding of how landscape degradation impacts stream systems. Finally, by replacing previous best-professional judgment techniques (Hughes et al., 1986; Rabeni et al., 1997) with a stepwise, data-based approach, we ensure repeatability and lower bias in identifying high and low quality stream reaches (Doisy et al., 2008).

While the results and approach described in this study are robust, there are several potential limitations to be noted. First, the identified relationships between landscape characteristics and biotic metrics, as well as subsequent biological integrity scores, are dependent on the landscape datasets included and the specific biotic metrics and landscape variables generated. It is possible the use of different landscape datasets, variables, or biotic metrics could result in differing relationships and interpretations of integrity. However, as noted throughout, we used common biotic metrics and developed landscape variables based on relationships identified in other studies, therefore limiting the potential for obtuse results. Second, the selection of least-disturbed streams using the 95th percentile cutoff is not synonymous with the selection of reaches in pristine conditions. Biological integrity scores across the Plains and Ozarks ecoregions indicate that the Plains, for instance, are more heavily degraded than Ozark streams, and it is certain that many of those with high biological integrity scores in both regions are still impacted by landscape disturbance to various degrees. However, in instances where widespread degradation occurs across a region, restoration and conservation initiatives still require the identification of sites to be viewed as benchmarks. Therefore, the outlined approach will be increasingly valuable in other regions as large-scale datasets of landscape characteristics are released and can be paired with existing biological data to help direct conservation action and support the identification of candidate reference reaches.

CRediT authorship contribution statement

Craig P. Paukert: Conceptualization, Methodology, Resources, Investigation, Writing - original draft, Visualization, Writing - review & editing, Supervision. **Ethan R. Kleekamp:** Methodology, Formal analysis, Investigation, Writing - original draft. **Ralph W. Tingley III:** Visualization, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2019.105966.

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