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Predicting community–environment relationships of stream fishes across multiple drainage basins: Insights into model generality and the effect of spatial extent

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A B S T R A C T

Resource managers increasingly rely on predictive models to understand species–environment relationships. Stream fish communities are influenced by longitudinal position within the stream network as well as local environmental characteristics that are constrained by catchment characteristics. Despite an abundance of studies quantifying species–environment relationships, few studies have evaluated the generality of these relationships among basins and spatial extents. We modeled community composition of stream fishes in thirteen sub-basins, nested within three basins in Kansas, USA using constrained ordination and environmental predictor variables representing (1) longitudinal network position, (2) local habitat, and (3) catchment characteristics. We tested the generality of species–environment relationships by quantifying the variation in model performance and the importance of environmental variables among the thirteen sub-basins and among three spatial extents (sub-basin, basin, state). Model performance was variable across the thirteen sub-basins, with adjusted constrained inertia ranging from 0.13 to 0.36. The importance of environmental variables was also variable among sub-basins, but longitudinal network position consistently predicted more variation in community composition than local or catchment variables. Model performance did not differ among spatial extents, but the importance of longitudinal network position decreased at broader spatial extents whereas local and catchment variables increased in importance. Results of this study support the longstanding frameworks of the river continuum and hierarchically-structured habitat. We show that (1) the relative importance of longitudinal network position, local characteristics, and catchment characteristics can vary from one region to another and (2) the spatial extent at which predictive habitat models are developed can influence the perceived importance of different environmental predictor variables. Resource managers should consider physiographic context and spatial extent when developing predictive habitat models for management and conservation purposes.

1. Introduction

Understanding species–environment relationships is a fundamental step in the conservation of aquatic biodiversity. Resource managers increasingly rely on predictive models to assess impacts of habitat alteration (Oberdorff et al., 2001), evaluate the spatial hierarchical nature of stream habitat (Allan et al., 1997), estimate habitat suitability for native species reintroductions (Harig and Fausch, 2002), forecast non-native species invasions (Vander Zanden et al., 2004), and predict impacts of climate change on species distributions (Lyons et al., 2010). Additionally, natural resources agencies use species distribution models to make informed management decisions and identify priority areas of conservation. Such predictive modeling tools are particularly important in regions that are highly modified by human activities and harbor endemic and imperiled species such as the Great Plains of the central United States (Dodds et al., 2004; Gido et al., 2010; Hoagstrom et al., 2011).

Early conceptual models provided a framework for understanding stream communities based on the hierarchical structure of stream habitats (Frissell et al., 1986; Allan et al., 1997). That is, natural and anthropogenic characteristics of the catchment influence habitat characteristics at the spatial resolution of the stream reach, mesohabitat, and microhabitat. For example, models of stream fish community composition in the Great Plains found environmental predictor variables measured at the catchment-, reach-, and site-resolutions to be correlated with one another (Gido et al., 2006). In these streams, soil erodibility in the catchment was correlated with channel gradient, a reach-scale variable, and turbidity, a

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site-scale variable. Although environmental variables measured at the catchment resolution may be adequate predictors of community composition, it is through the hierarchical structure of lotic habitat that these variables are causatively linked to population vital rates (i.e., birth, death, emigration, and immigration) and consequent spatial variation in the distribution and abundance of species (Frissell et al., 1986). Consequently, the relationship between community composition and catchment characteristics may vary among drainage basins, depending on the interactions among environmental conditions at different levels of the hierarchy. Understanding how these hierarchical relationships may differ among basins poses a challenge to resource managers in interpreting and applying predictive habitat models.

Few studies have evaluated the generality of species–environment relationships among drainage basins (but see Wang et al., 2003; Wenger and Olden, 2012), resulting in limited understanding of how the relative importance of local and catchment variables differs among drainage basins. Regardless, inferences of among-basin differences have been made by comparing the results of multiple, independent studies. For example, Wang et al. (2006) asserted that fish communities responded most strongly to catchment variables in basins with extensive anthropogenic land cover changes (e.g., Roth et al., 1996; Allan et al., 1997; Wang et al., 1997, 2001) whereas assemblages in more pristine basins responded more strongly to local variables (e.g., Lammert and Allan, 1999; Wang et al., 2003). Natural catchment characteristics such as geology and soil properties can also scale down and constrain local habitat and stream communities (Frissell et al., 1986; Gido et al., 2006; Neff and Jackson, 2011), but the consistency of multi-scale linkages of these natural catchment characteristics among basins is also poorly understood.

Several factors may lead to inconsistent species–environment relationships among basins. First, consistent importance of local or catchment variables between regions (e.g., drainage basins) may change if their correlation with causative environmental variables differs in strength or direction between two regions. For example, water temperature may be a proximal variable that varies with stream size, but the strength of the relationship between these two variables may depend on riparian canopy cover which may differ among regions. This relationship between such distal and proximal predictor variables is referred to as environmental correlation structure (Jiménez-Valverde et al., 2009; Saupe et al., 2012). It is likely that catchment variables are distal to population vital rates of stream fishes and constrain proximal variables such as disturbance regime, water chemistry, temperature, or local habitat that directly affect population vital rates (Poff and Allan, 1995; Poff, 1997). Second, differences in the length of an environmental gradient between regions may affect the importance of that environmental variable between those regions. For example, Sundblad et al. (2009) showed that niche models for estuarine fishes transferred inaccurately between two regions when the range of values for a key environmental variable (salinity) observed within each region differed between those regions. Similarly, in a study of stream macroinvertebrate communities, Mykra et al. (2007) demonstrated that the importance of environmental variables was positively correlated with their range of variation (i.e., gradient length) within the study region. Lastly, the spatial extent at which predictive habitat models are developed may also affect the importance of environmental variables by altering environmental correlation structure or the length of environmental gradients (Ohmann and Spies, 1998).

Longitudinal network position is a ubiquitous predictor of community composition of stream fishes. Changes in the type and diversity of local habitat as well as increased colonization and decreased extinction rates are factors that may contribute to the observed change in community composition from headwaters to large rivers (Schlosser, 1987; Taylor and Warren, 2001; Roberts and Hitt, 2010). Previous studies assessing the relative importance of local and catchment variables on community composition frequently included measures of network position at several spatial resolutions. For example, investigators often include channel width and catchment area as measures of network position representing local and catchment categories, respectively (e.g., Gido et al., 2006; Esselman and Allan, 2010; Saly et al., 2011). Given the ubiquitous importance of network position in predicting community composition, it is likely that network position directly (via colonization and extinction dynamics) or indirectly (via strong correlation with important abiotic variables such as local habitat) increases the perceived importance of local or catchment variables assessed in these studies. Thus, assessing the relative roles of local and catchment variables, independent of network position, may improve understanding of the hierarchical nature of stream habitat as well as the generality of species–environment relationships.

1.1. Objectives and hypotheses

In this study, we used constrained ordination to relate environmental variables to community composition of stream fishes in thirteen sub-basins and across three spatial extents of the Central Great Plains, USA. Our first objective was to assess variation in model performance and the importance of network position, local, and catchment predictor variables among thirteen sub-basins. We hypothesized that the importance of network position would be consistently greater than the importance of catchment and local variables across the thirteen sub-basins, given the thoroughly documented change in community composition along the river continuum (Schlosser, 1987; Taylor and Warren, 2001; Roberts and Hitt, 2010). By contrast, we hypothesized that correlation structure between catchment predictors and the causative environmental variables that drive variation in population vital rates would differ among the thirteen sub-basins, resulting in reduced concordance of these environmental variables among sub-basins. Because sub-basins differ in physiography associated with ecoregions and annual precipitation associated with an east–west aridity gradient, we expected inconsistent environmental correlation structure among sub-basins. Second, we hypothesized that models would perform better in sub-basins draining multiple ecoregions that have longer environmental gradients. Greater environmental variation within a sub-basin that drives variation in community composition will likely improve model performance.

Our second objective was to compare model performance and the importance of local, catchment, and network position across three spatial extents (sub-basins, basins, and the state of Kansas). We predicted that broadening the spatial extent would increase the length of environmental gradients, but the rate of increase in gradient length would differ among network position, local, and catchment variables. Specifically, we predicted that all stream sizes would be represented at all three spatial extents (i.e., sub-basins, basins, and state), whereas variation in local and catchment variables associated with ecoregional transitions and an east–west aridity gradient would be apparent only at broader spatial extents (i.e., basins and state). Accordingly, we hypothesized that network position would decrease in importance whereas local and catchment variables would increase in importance at broader spatial extents.

2. Methods

2.1. Study area and datasets

We modeled community composition within the Great Plains of the central United States at three nested spatial extents: thirteen sub-basins, three basins, and the state of Kansas (hereafter