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Under siege: Isolated tributaries are threatened by regionally impaired metacommunities

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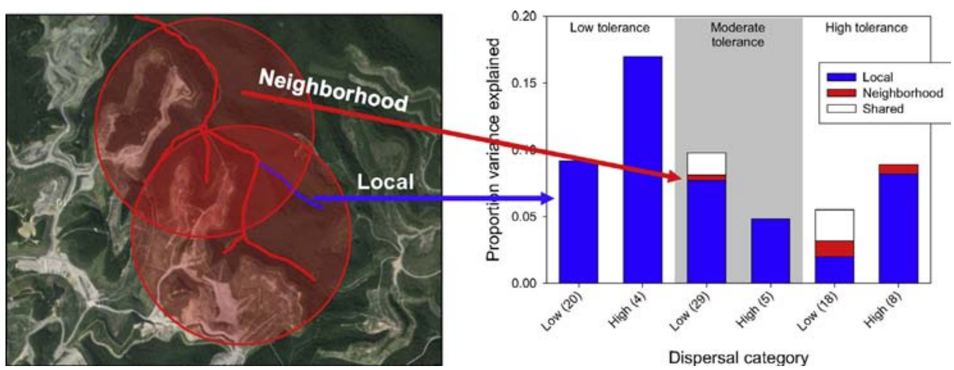
HIGHLIGHTS

- Isolation affects the ability of pristine streams to preserve regional biodiversity.
- Local condition explained the majority of variation in local communities.
- Isolation results in decreased mass and rescue effects of key low dispersing taxa.
- Increasing isolation also results in a regional proliferation of tolerant taxa.
- Protection of regional species' pools will require more than headwater conservation.

GRAPHICAL ABSTRACT



In heavily degraded regions, even the most pristine headwater streams are at risk due to the simultaneous decrease in mass and rescue effects of key low-dispersing taxa and proliferation of regionally dominant tolerant taxa.

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ABSTRACT

Pristine streams are often targeted as conservation priorities because of their ability to preserve regional biodiversity. However, isolation within heavily degraded regions likely alters important metapopulation and metacommunity processes (e.g., rescue and mass effects), affecting the ability of in-tact communities to boost regional conditions. To test this hypothesis, we sampled invertebrate communities and physicochemical conditions from 168 streams within the mountaintop removal-valley fill mining region of West Virginia. We used redundancy analysis to first test for significant effects of local (observed physicochemical conditions) and neighborhood (streams within a 5 km buffer) degradation on assemblage structure across all taxa and stress tolerance (low, moderate, high) and dispersal (low, high) categories. We then used generalized linear and hurdle models to characterize changes in community metrics and individual taxa, respectively. Local condition consistently explained the majority of variation (partial R^2 up to 5× those of neighborhood condition) in community structure and was the only factor affecting sensitive taxa. Neighborhood condition explained significant variation in moderately tolerant taxa with low dispersal capacity and highly tolerant taxa, regardless of dispersal. Decreased occurrence (*Baetis*) and abundance (*Maccaffertium*) of key taxa and corresponding metrics (%E, %EPT) suggest decreased dispersal and associated mass and rescue effects within degraded neighborhoods. Decreased neighborhood conditions also resulted in the proliferation of tolerant taxa (Chironomidae, *Chimarra*, *Hemerodromia*). Our results suggest communities within even the most pristine streams are at risk when isolated within heavily impacted regions. Consequently, protection of regional species' pools in heavily impacted regions will require more than simply conserving un-impacted streams.

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1. Introduction

Advances in metacommunity ecology have led to an emerging paradigm recognizing the importance of regional factors (e.g., species pool and location within dispersal networks) and processes (e.g., dispersal and mass effects) in structuring local assemblages (Heino et al., 2003; Leibold et al., 2004; Brown and Swan, 2010; Hitt and Angermeier, 2011). An important avenue of continued research concerns applying metacommunity theory to the management of disturbed ecosystems (Brown et al., 2011; Heino, 2013). For example, preservation of undisturbed headwater catchments has become an important component of freshwater conservation efforts within actively developing watersheds (Lowe and Likens, 2005). A major motivation for their preservation is the understanding that headwater streams contribute disproportionately to regional biodiversity and serve as critical habitat for the preservation of regionally rare and endangered taxa (Lowe and Likens, 2005; Meyer et al., 2007; Finn et al., 2011).

However, extensive local disturbances occurring across larger spatial scales have the potential to alter communities within undisturbed streams through disruption of regional metapopulation and metacommunity structure and processes. Increasing isolation of intact tributaries through expanding human activity may result in dispersal limitation and decreased mass and rescue effects (i.e., dispersal of a taxa from suitable habitats to suboptimal or extirpated habitats), particularly for regionally sensitive taxa and/or taxa with low dispersal ability (Astorga et al., 2012; Vanschoenwinkel et al., 2013; Radkova et al., 2014; Heino et al., 2015). Moreover, extensive disturbance may also facilitate establishment and proliferation of subdominant competitors and disturbance tolerant specialists via mass effects from degraded surrounding streams (Pandit et al., 2009; Vanschoenwinkel et al., 2013). Consequently, the ability of intact communities to preserve regional biodiversity may be limited as they become increasingly isolated within heavily impacted systems (Campbell and McIntosh, 2013; Heino, 2013). To our knowledge, however, this has never been demonstrated.

We provide such an assessment by analyzing macroinvertebrate communities from the central Appalachian region in relation to their influence from local and regional (i.e., neighborhood, *sensu* Merovich et al., 2013) drivers of environmental degradation. We focus on the primary mountaintop removal-valley fill (MTR-VF) mining region because stream networks within this region offer a relevant opportunity to demonstrate regional metacommunity processes in an actively developing landscape with important current and future socioeconomic implications. Extensive contemporary and historic coal mining and residential development activities within this region have resulted in widespread ecological impacts (Bernhardt et al., 2012; Merriam et al., 2015a, 2015b). However, the geography of land use activities within this region creates a unique juxtaposition of severely degraded streams within otherwise pristine stream networks and high quality streams within otherwise severely degraded networks (Merovich et al., 2013). Consequently, we had the rare opportunity to collect an un-confounded dataset with respect to local and regional controls over community composition across a large spatial scale (see Ewers and Didham, 2006).

Previous efforts to quantify spatial constraints over community structure and processes (i.e., dispersal) have used spatial location and distance among sites to represent spatial structuring. However, inferences regarding the importance of metacommunity processes (i.e., mass effects and dispersal) from such studies are limited by the spatial extent encompassing the sampling sites (Heino et al., 2015). Herein, we constructed an index of neighborhood condition that describes the extent to which each study site is isolated by surrounding land use activity and aquatic degradation (*sensu* Merovich et al., 2013). Consequently, we were able to directly test the hypothesis that both local physicochemical conditions and the degree of isolation (i.e., neighborhood condition) significantly influence local community composition. We further hypothesized that the effects of isolation are mediated by tolerance and dispersal characteristics. More specifically, we expect increasing isolation will have a strong negative effect on sensitive taxa with low dispersal abilities owing to decreased mass and rescue effects. We further expect that increasing isolation will have a strong positive effect on tolerant taxa, regardless of dispersal capacity, via increased mass effects from nearby degraded streams. It is important to note that our use of the term 'isolation' refers to the extent to which a site is surrounded by degraded aquatic conditions and does not imply jurisdiction under the Clean Water Act.

2. Materials and methods

2.1. Study area and site selection

The study region is comprised of the eight 8-digit hydrologic unit code watersheds intersecting the mountaintop mining region within West Virginia (Fig. 1). These watersheds drain approximately 20,795 km^2 and include the Tug Fork, Twelvepole Creek, and Elk, Gauley, Upper Kanawha, Upper and Lower Guyandotte, and Coal Rivers. We selected 168 streams as study sites (Fig. 1). Sites were selected to be evenly distributed across drainage basins and to represent the full gradient of combined local and network (neighborhood) conditions [i.e., streams with high and low quality local conditions located within intact and degraded stream networks]. All study sites had basin areas <40 km^2 and were independent of one another with respect to upstream-to-downstream flow (Petty et al., 2010).

2.2. Local physicochemical condition

We sampled physicochemical attributes once at each site during the summers (July–August) of 2010, 2011, or 2012. A detailed description of our physicochemical sampling protocol is provided by Merriam et al. (2015a). Briefly, reaches were defined as 40× mean stream width, with minimum and maximum reach lengths of 150 and 300 m. We measured overall habitat quality with US Environmental Protection Agency (EPA) rapid visual habitat assessments (RVHA; Barbour et al., 1999). We obtained in-situ measures of specific conductance, dissolved oxygen, pH, and temperature. We obtained filtered samples for determination of dissolved Al, Ba, Ca, Cd, Cr, Fe, K, Mg, Mn, Na, Ni, Se, and Zn and unfiltered samples for determination of NO_3, NO_2, total P, alkalinity, Cl, SO_4, and total dissolved solids. The current study uses previously described chemical signatures (i.e., principal components) to describe patterns in local chemical conditions related to contemporary surface mining [Ca^{2+}, K^+, Mg^{2+}, SO_4^{2-}, and HCO_3^-, and Se; henceforth referred to as mining water quality (mWQ)] and residential development [Na^+, Cl^-, and Ba; residential water quality (rWQ)] – the dominant land use activities within the study region (Merriam et al., 2015b).

2.3. Macroinvertebrate community data

We sampled benthic macroinvertebrate communities immediately following physicochemical sampling with procedures established by the West Virginia Department of Environmental Protection (WV DEP) Watershed Assessment Program (WV DEP, 2009). We obtained kick samples (net dimensions 335 × 508 mm with 500-μm mesh) from 4 targeted riffles distributed throughout the reach and combined organisms and debris into a single composite sample for each site. Samples were immediately preserved with 95% ethanol. In the laboratory, we sub-sampled macroinvertebrate communities following the 200 count method (WV DEP, 2009). We identified organisms to genus, except Mollusca (family), Chironomidae, Hydracarina, Oligochaeta, and Nematoda, with keys in Merritt and Cummins (2008).

We categorized taxa based on WV DEP-defined tolerance values that reflect relative sensitivity to anthropogenic influence [low (0–2), moderate (3–5), and high (6–10)]. We categorized taxa with respect to dispersal capacity (high, low) using 2 traits characterizing adult dispersal

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