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RESEARCH ARTICLE

# Habitat alteration and habitat fragmentation differentially affect beta diversity of stream fish communities

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**Abstract**

*Context* The cumulative impact of broad scale environmental change includes altered land-cover and fragmentation. Both altered land-cover and fragmentation have a negative effect on species diversity, but the scale they act on may differ because land-cover alters environmental characteristics, whereas fragmentation alters movement among sites.

*Objectives* We evaluated the scale specific effects of land-cover, fragmentation, and habitat size on alpha and beta diversity (total, turnover, and nestedness).

*Methods* Stream fish communities were sampled across five urbanizing watersheds. Generalized mixed linear models were used to test how diversity (alpha and beta) is affected by land-cover, connectivity, and habitat size. Indices of land-cover were calculated from correspondence analyses on land-cover data, fragmentation was estimated with the dendritic connectivity index, and habitat size was calculated as the length of the stream segment (alpha diversity) or the length of the stream network (beta diversity).

*Results* Alpha diversity was most strongly related to land-cover variables associated with urban development and agriculture (negative relationship with urbanization). Whereas, beta diversity was most strongly influenced by habitat size (positive relationship) and fragmentation (positive relationship). Turnover was positively correlated with fragmentation and habitat size, whereas species loss was negatively correlated with habitat size.

*Conclusions* Land-cover has a larger effect on alpha diversity because it alters the environmental conditions at a site, whereas fragmentation has a larger effect on beta diversity because it affects the movement of individuals among sites. Assessing the cumulative impact of environmental change requires a multiscale approach that simultaneously considers alpha and beta diversity.

**Keywords** Stream fragmentation · Freshwater fish · Dendritic ecological network · Urbanization · Agriculture · Community response · Meta-community

## Introduction

In much of the world, terrestrial and aquatic ecosystems are undergoing unprecedented rapid change.

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Change includes habitat loss, habitat conversion, fragmentation, pollution, and invasion by non-native species (among others). All of these changes can occur simultaneously and have a large effect on biodiversity and community composition (Fahrig 2003; Altermatt 2013; Carrara et al. 2014). The conversion of natural land-cover to agricultural fields and urban development simultaneously alter the characteristics of habitats and the structure of habitat networks. A consequence habitat conversion is the loss of species because they are unable to persist in the new, altered, environmental conditions (Fahrig 1997; Leibold et al. 2004; Strecker et al. 2011). Changing the structure of a habitat network generally results in habitat fragmentation (i.e. loss of connectivity) which impedes or prevents the movement of individuals among habitat patches, interfering with meta-population and meta-community dynamics, and reducing the total amount of habitat available to individuals (Hanski 1999; Pardini et al. 2010; Fahrig 2013). The alteration, reduction, and fragmentation of habitat networks, are major drivers of the global decline in biodiversity (Devictor and Robert 2009; Isaac et al. 2009).

Overall, both habitat alteration and fragmentation result in a decline in diversity (Fagan 2002; Pardini et al. 2010; Perkin and Gido 2012; Mahlum et al. 2014a). However, impacts due to habitat alteration interact with those due to fragmentation resulting in diversity declining at different spatial scales (Angermeier and Winston 1998; Leibold et al. 2004; Padgham and Webb 2010). Habitat alteration affects the abundance of species at the scale of individual habitat patches, the local scale (Fahrig 1997; Devictor and Robert 2009; Isaac et al. 2009), whereas habitat fragmentation affects the abundance of species at the scale of the habitat network, the regional scale (Hanski 1999; Labonne et al. 2008; Padgham and Webb 2010; Banks-Leite et al. 2012; Henriques-Silva et al. 2013). Thus, when simultaneously considering the effects of habitat alteration and fragmentation, there is a need to explore effects on alpha diversity (e.g. species richness) at the level of individual habitat patches and beta diversity among patches at the level of entire habitat networks. If both alpha and beta diversity are not considered simultaneously conclusions drawn on the importance of land-cover and fragmentation may be misleading due to scale specific effects of each.

Alpha diversity is measured within individual habitat patches whereas beta diversity is a measure of the amount of variation in species composition among patches (Whittaker 1960; Tuomisto 2010) that can be broken down into two components; turnover, and nestedness. Species turnover occurs in a habitat network when species are lost and replaced in habitat patches with different environmental conditions, and nestedness occurs when species are lost and not replaced, leading to a hierarchical pattern in species presence (Baselga 2008, 2010). Overall the differential replacement of species across patches leads to increased beta diversity (Baselga et al. 2007). Connectivity can play and important role in maintaining alpha and beta diversity in habitat networks which are being altered. In well-connected networks a decline in alpha diversity is offset by the presence of new species that can persist in the different environmental conditions, leading to turnover in beta diversity (Andrén 1994; Devictor and Robert 2009; Pardini et al. 2010). In fragmented habitat networks, the movement of individuals among the habitat patches can be disrupted (Labonne et al. 2008), leading to a pattern of nestedness in beta diversity within a habitat network (Ulrich et al. 2009). Both nestedness and turnover result in increased in beta diversity, however, distinguishing between them allows for a more thorough understanding of the cumulative impacts of habitat alteration and habitat fragmentation which is essential to fully evaluate the consequences of anthropogenic habitat change.

The effects of habitat alteration and habitat fragmentation are thought to be particularly strong in dendritic ecological networks, such as streams, where there is only one pathway between any two points on the network (Grant et al. 2007; Cote et al. 2009; Padgham and Webb 2010; Erős et al. 2012). Within dendritic networks, stream fish communities are broadly structured by local biotic and abiotic factors that characterize geographic regions (Jackson and Harvey 1989; Mandrak 1995; see Jackson et al. 2001 for a review). Within a stream, fish communities are structured due to geology, longitudinal position, habitat size, temperature, current speed, substrate composition, and interactions with other species (Angermeier and Winston 1998; Taniguchi et al. 1998; Allan 2004; Neff and Jackson 2012). Urbanization and agriculture impact fish communities because they alter some of the environmental variables (e.g. current speed and temperature) that determine which species can persist where (Booth and Jackson 1998; Fausch et al. 2002; Walsh et al. 2005; Pease et al. 2011), although the magnitude of impact on the environmental characteristics is often less than the within stream variation in the characteristic. In general, urbanization and agriculture lead to a reduction in alpha diversity when habitat specialist species are lost (Booth and Jackson 1998; Stanfield and Kilgour 2013). The reduction in alpha diversity directly affects beta diversity within the network as the community at a particular site changes, and in well-connected networks the major component of beta diversity will be turnover because species are able to colonize altered habitat patches (Walsh et al. 2005; Wenger et al. 2008; Johnson and Angeler 2014).

Many stream fish can disperse over large distances within stream networks (Fausch 2010). Dams, weirs, and road crossings are the major sources of habitat fragmentation in streams (Falke and Gido 2006; Rolls et al. 2013). As fragmentation impedes movement among habitat patches in a habitat network, it impacts meta-population/meta-community dynamics and is a serious threat to population stability. Within streams, fragmentation results in a decline in species richness at individual habitat patches (Nislow et al. 2011), and an increase in beta diversity in a habitat network (Perkin and Gido 2012; Perkin et al. 2015). The increase in beta diversity is due to a combination of species loss at individual sites and the prevention of recolonization by barriers which leads to an overall pattern of nestedness in beta diversity. When habitat change occurs simultaneously with fragmentation, changes to habitat quality are likely the major driver of community composition at particular sites with fragmentation playing a lessor role (Perkin and Gido 2012; Mahlum et al. 2014a).

The overall goal of our work is to evaluate the relative influence of agricultural and urban land-cover and fragmentation on alpha and beta diversity at different spatial scales. Our first objective was to evaluate the relative importance of anthropogenic land-cover (at the local and regional scales) and connectivity on alpha diversity and the abundance of the most common species at each individual stream segment. Our second objective was to determine the relative importance of land-cover and connectivity on patterns of beta diversity, and to partition beta diversity in turnover and nestedness. For alpha diversity it is expected that land-cover will be more strongly correlated than connectivity, and for beta diversity it is expected that connectivity will be more strongly correlated that land-cover. Lastly, it is expected that anthropogenic land-cover will be positively correlated with turnover, and connectivity will be negatively correlated with nestedness.

## Methods

### Study site

The five watersheds in this study are within a 250,000 ha region centered on Toronto (Ontario, Canada) in the Lake Ontario watershed (Table 1; Fig. 1). There are two major types of landscape disturbance within the watersheds in the Toronto region: (1) urban development; and (2) agriculture. Each of the five watersheds is fragmented to various degrees by road crossings, dams, fish weirs, and other structures. We investigated the structure of fish assemblages and the factors that influence them at two scales; (1) Alpha diversity (i.e. individual sites) and (2) Beta diversity (i.e. among multiple sites).

### Fish assemblage sampling

In each of the watersheds, the fish assemblage was sampled at multiple sites between 1996 and 2011 by the Toronto and Region Conservation Authority (TRCA) and the Ontario Ministry of Natural Resources and Forestry (OMNRF) according to the Ontario Stream Assessment Protocol (OSAP—Stanfield 2010) (Fig. 2a) as part of a broad scale monitoring program. For the monitoring program a random stratified design was used to select sites to characterize conditions within streams. Sites were at least 40 m in length and included 5–10 bankfull widths. All fish sampling was conducted during periods of baseflow in July or August. Within a watershed, sites were sampled during different years and as such some among year (temporal) variation in fish assemblage is expected to occur. There was no systematic bias in the spatial location of fish sampling sites with a year. Fish sampling was conducted with single-pass electrofishing (7–15 s/m$^2$), and all captured individuals were identified to species and counted. All species were retained in the analyses because our interest is on the differential effects of land-cover and connectivity on overall diversity and rare species likely make up a large proportion on changes in beta diversity among sites (Poos and Jackson 2012).

A site was defined as a stream segment that a fish sampling event occurred on. Stream segments were

**Table 1** General characteristics of the five watersheds in southern Ontario

| Stream | Total length of river (km) | Area of watershed (ha) | Forest and wetland (ha) | Number of fish sampling sites | Species richness | Mean richness (SD) | Number of barriers | Number of subnetworks |
|---|---|---|---|---|---|---|---|---|
| East Don | 194.2 | 35,806 | 2918 | 33 | 27 | 4.78 (2.62) | 81 | 9 |
| Etobicoke | 279.8 | 21,165 | 1262 | 24 | 24 | 7.88 (3.57) | 146 | 6 |
| Highland | 78.1 | 10,158 | 621 | 16 | 23 | 4.44 (1.79) | 142 | 4 |
| Mimico | 68.9 | 7709 | 173 | 11 | 15 | 3 (2.41) | 119 | 3 |
| Rouge | 541.8 | 33,288 | 4625 | 75 | 37 | 6.97 (3.54) | 343 | 24 |

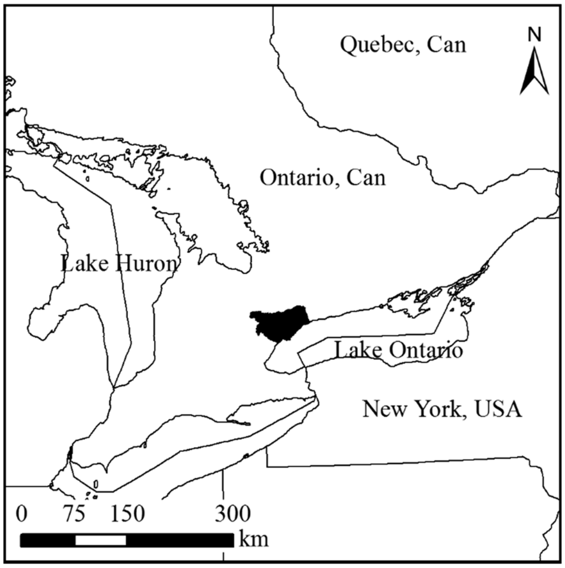

**Fig. 1** Map indicating the location of the study area (*in black*) in the Toronto region of Ontario, Canada

defined as the continuous length of stream between confluences, barriers, and terminal points.

## Diversity indexes

Alpha diversity at each sampling site was measured as: (1) species richness, (2) Shannon's diversity index, and (3) Pielou's evenness index. To investigate individual species level responses, the abundance of common species (found in all watersheds and at 25% of all sites) was also analyzed.

Beta diversity within each of the individual stream networks was measured as network species richness, defined as the total number of species captured in each network. The multi-site dissimilarity index, $\beta_{SOR}$, was used to estimate total beta diversity and total beta diversity was partitioned into $\beta_{SIM}$ to estimate turnover and $\beta_{SNE}$ to estimate nestedness (Baselga 2010). Within each watershed, individual hierarchical stream networks were created for every confluence where two tributaries joined together and fish sampling occurred

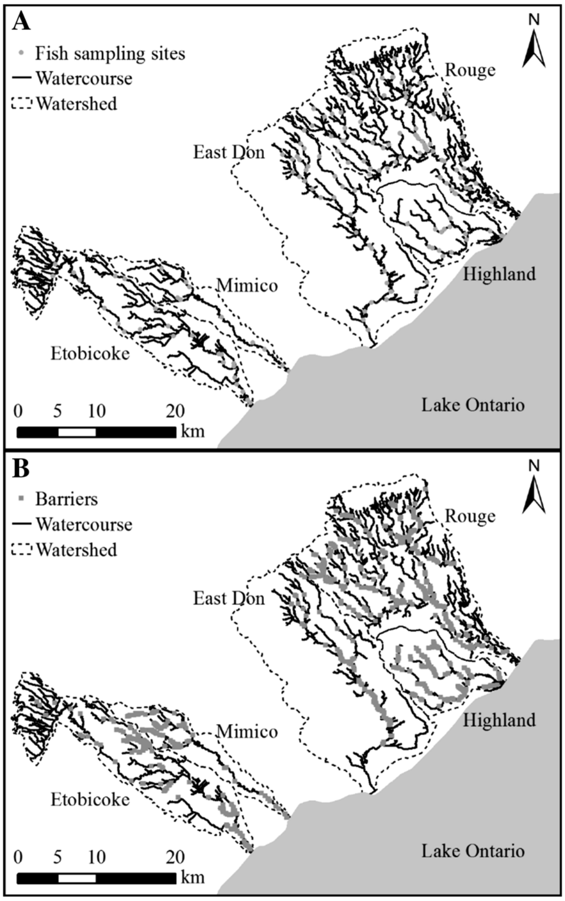

**Fig. 2** Location of fish sampling sites within the five watersheds (**a**) and the location of all barriers in the five watersheds (**b**)

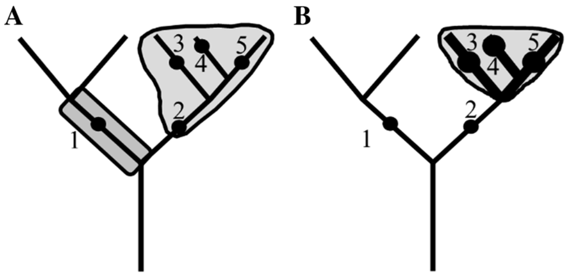

**Fig. 3** **a** To investigate patterns in alpha diversity, land-cover disturbance was calculated as the percent land-cover in each of the categories (Table 2) at the local and the regional scale. The local scale was defined as land-cover within 100 m buffers of stream segments with fish sampling sites (e.g. site 1) and the regional scale was defined as land-cover within drainage basins created for each fish sampling site (e.g. site 2). **b** To investigate patterns in beta diversity, individual stream networks were created for each confluence that had fish sampling sites on both sides of the confluence. e.g. Sites 3, 4, and 5 create one network. Land-cover disturbance was calculated at the sub-catchment scale; the percent of land-cover in each category within the sub-catchment of each confluence

on both sides. The individual stream networks contained all connected stream habitat upstream of the confluence (Fig. 3b).

## Land-cover

Land-cover data for all of the watersheds were obtained from the Southern Ontario Land Resource Information System (SOLRIS—Ontario Ministry of Natural Resources 2002) at a resolution of 0.5 ha. Land-cover categories within SOLRIS were condensed into six land-cover types (Table 2) and used to create indices of disturbance.

To quantify land-cover disturbance for each site, the percent land-cover in each of the categories (Table 2) was calculated at the local and the regional scale. Local land-cover was calculated within a 100 m buffer on each stream segment (Fig. 3a) and a correspondence analysis (hereafter CA) was performed. Scores on the first two axes (LocCA1 and LocCA2 respectively) were extracted for each site and used as an index of disturbance at the local scale. Then regional land-cover was calculated within a drainage basin for each site (Fig. 3a). Drainage basins were created using ArcHydro and a 10 m digital elevation map in ArcGIS 10.2 (ESRI, Redlands, CA) using the site as the pour point. A CA was performed on the percent land-cover data and scores on the first two axes were extracted for each site and used as an index of disturbance at the regional scale (RegCA1 and RegCA2 respectively, Table 3).

To quantify network land-cover disturbance, a sub-catchment was created for the confluence of each individual stream network created to measure beta diversity. A CA was performed on the percentage of land-cover in the six categories (Table 2) within the sub-catchment, constructed with ArcHydro and a 10 m digital elevation map in ArcGIS 10.2, of each individual stream network and the first and second axis scores were extracted (SubCatCA1 and SubCatCA2 respectively) and used as an index of disturbance within the sub-catchment (Table 4).

## Connectivity

A complete stream-barrier assessment was performed on each of the watersheds. Barrier assessments consisted of walking the entire stream network and recording the location and type of every potential barrier to fish passage (Fig. 2b). Barrier characterization included identifying the type of barrier (e.g. dam, weir, road crossing) and measuring the depth of the

**Table 2** Land-cover types used in the correspondence analyses to create an index of habitat disturbance at the local, regional, and sub-catchment scales from the Southern Ontario Land Resource Information System (SOLRIS)

| Name | Abbreviation | SOLRIS category/categories |
|---|---|---|
| Forest | For | Sum of forest, coniferous forest, mixed forest, deciduous forest, and hedgerow |
| Wetland | Wet | Sum of swamp, fen, bog, marsh |
| Agriculture | Agri | Tilled agriculture |
| Built-up impervious | Imperv | Built-up impervious |
| Built-up pervious | Perv | Built-up pervious (i.e. urban recreation areas) |
| Road | Road | Transportation |

**Table 3** Environmental predictors used for analysis of alpha diversity and the abundance of individual species

| Predictor: definition | Abbreviation |
|---|---|
| *Segment length* Length of segment on which the fish sampling location is located | SegL |
| *Segment connectivity* The probability that an individual in a habitat patch can reach any other habitat patch on the network | DCIs |
| *Local-CA index 1* First axis of correspondence analysis conducted on proportion of land-cover in each category (Table 2) within 100 m buffers of stream segment | LocCA1 |
| *Local-CA index 2* Second axis of correspondence analysis conducted on proportion of land-cover in each category (Table 2) within 100 m buffers of stream segment | LocCA2 |
| *Regional-CA index* First axis of correspondence analysis conducted on proportion of land-cover in each category (Table 2) within the drainage basins of the fish sampling site | RegCA1 |
| *Strahler stream order* Strahler stream order of the segment the site was located on | Strahl1…5 |
| *Watershed* Watershed in which the segment is located | WShed |

pool downstream and the height of the bottom of the barrier. The pool depth and barrier height were used to determine whether the bottom of the crossing structure was above the surface of the water (i.e. "perched" structures). The number and type of barriers varied among the five streams (Table 1).

Structural connectivity was measured with the dendritic connectivity index (DCI; Cote et al. 2009). The DCI Index estimates the probability that any two organisms placed randomly in two habitat patches on a network are in patches that are structurally connected to one another and can be calculated for diadromous and potadromous species. In our study, we are interested in species that can move within the habitat network in both directions, so the potadramous (DCIp) metric was calculated. DCI can be compared among watersheds because it represents the percent of natural connectivity remaining in the network (Cote et al. 2009). In addition to the network-level metric, we calculated a connectivity score for each stream segment that estimates the probability that any particular stream segment is connected to the rest of the network (DCIs).

The DCI metrics rely on two variables: an attribute for each segment that determines quality (set as the length of the segment), and the permeability of the connection between any two segments on the network. The permeability was set at 1 for segments that connect to one another and do not have a barrier

**Table 5** Categories used to estimate the permeability of each barrier

| Outlet drop (m) | Baseflow (m/s) | Permeability |
|---|---|---|
| 0 | <0.25 | 1 |
| 0 | 0.25–0.40 | 0.80 |
| 0 | >0.40 | 0.50 |
| 0–0.15 | Any | 0.25 |
| >0.15 | Any | 0 |

Categories are from Anderson et al. (2012)

**Table 4** Environmental predictors used for analysis of Beta diversity

| Predictor: definition | Abbreviation |
|---|---|
| *Network length* The length of the stream network | Length |
| *Dendritic connectivity index* Potadromous: the potadromous dendritic connectivity index was calculated for each network. This value is the probability that any two individuals placed randomly on the network are in patches which are connected to one another | DCIp |
| *Sub-catchment land-cover* The first axis of correspondence analysis conducted on proportion of land-cover in each category (Table 2) within sub-catchments for each individual stream network | SubCatCA1 |
| *Watershed* Watershed in which the network is located | WShed |

separating them. For segments with complete barriers separating them (e.g. dams), the permeability was set as 0. The majority of barriers in the watersheds studied herein are partial barriers associated with road crossings (e.g. culverts) which are semi-permeable barriers to a large number of species. The permeability of crossings was estimated using two variables, the height of the outflow and baseflow rate (Table 5). Outflow height (barrier height—pool depth) was measured during the barrier assessments and indicated "perched" structures. The most recent baseflow measurement at the first downstream station from June, July, or August was used to calculate permeability. Using categories to determine the permeability of a crossing is not ideal, and other methods such as estimating permeability of crossings using modelling techniques such as FishXing (Furniss et al. 2006) or using Bayesian belief networks (e.g. Anderson et al. 2012) have been developed. However, models such as FishXing have been shown to be very conservative and do not accurately predict fish passage in actual streams (Mahlum et al. 2014b), and Bayesian belief networks require extensive knowledge of the probability of passage for all fish species, which is not available for most of the species in this study.

For alpha diversity (local scale, the individual patch), the entire watercourses were used to calculated connectivity and the DCIs fraction for each segment was used as an estimate of how well each stream segment was connected to the rest of the network. For beta diversity (regional scale), each individual stream network was used as the input and the overall DCIp index for that individual stream network was used as an estimate of connectivity for that network.

### Statistical analyses

To determine which predictors (Table 3) affect alpha diversity (species richness, Shannon's diversity index, Pielou's evenness index, and the abundance of the most common species at each site), generalized linear mixed-effects modelling (GLMM) was used (Pinheiro and Bates 2000; Zuur et al. 2009). Watershed was included as a random effect in all models. The full model contained all predictors listed in Table 3, and model fitting was conducted with single term deletions and log likelihood ratio tests. A reduced model was created by including all fixed factors with $p < 0.1$ in single term deletions and compared to the full model using a Chi square test. In the final models the significance of fixed factors was determined with 95% confidence intervals estimated by boot-strapping for non-count data and profile likelihood for count data; if the confidence interval did not overlap 0 the predictor had a significant effect on the response variable. The amount of variation in the response variable explained by the complete model $\left(R^2_{GLMM(C)}\right)$ and the random factors $\left(R^2_{GLMM(M)}\right)$ was calculated using the method outlined in Nakagawa and Schielzeth (2013). A similar model-fitting procedure was carried out for beta diversity (total species richness, $\beta_{SOR}$, $\beta_{SIM}$, and $\beta_{SNE}$), the only difference was the set of predictors used (Table 4).

All predictors were standardized to *z*-scores prior to the statistical analyses. A negative binomial distribution was used for analyses on the abundance of individual species. Alpha diversity measures were calculated with the *vegan* package (Oksanen et al. 2015), beta diversity measures with the *Betafor* package (Baselga and Orme 2012), and generalized linear modelling was conducted with the *lme4* package (Bates et al. 2015) in R v3.2.1 (R Core Team 2015). All spatial analyses were conducted with ArcGIS 10.2 (ESRI, Redlands, CA).

## Results

A total of 44 species (Supplementary Material S1) were found in the five watersheds, species richness within a watershed ranged between 15 and 37 species and mean species richness at sites ranged between 3 and 7.9 species (Table 1).

### Alpha diversity

The first two axes (LocCA1 and LocCA2) of the local land-cover CA explained 36.7 and 27.8% of the land-cover variation respectively and both axes were retained as indices of land-cover disturbance (Fig. 4). LocCA1 contrasted sites along a gradient from high agriculture to high urban lands, whereas the LocCA2 contrasted sites along a gradient of increasing amount of pervious and impervious cover which is associated with urbanization. Sites from each of the streams represented the variation in local land-cover

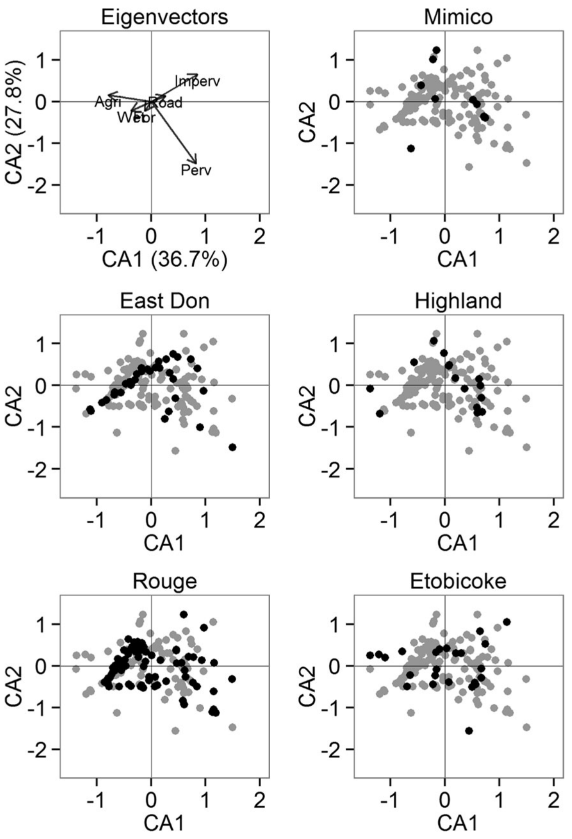

**Fig. 4** Biplots for a correspondence analysis conducted on local land-cover for all watersheds together. Each watershed is displayed on a separated biplot, *gray points* represent all sampling locations and *black points* representing sampling locations from that watershed

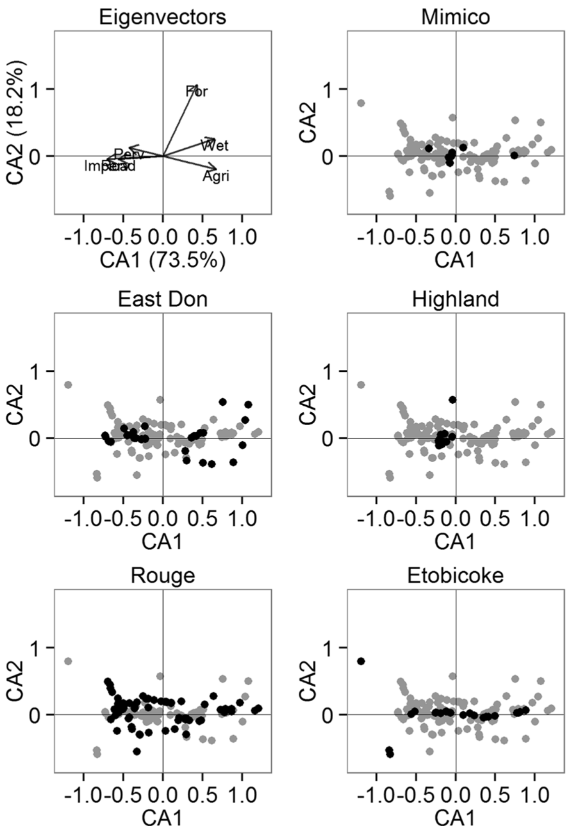

**Fig. 5** Biplots for a correspondence analysis conducted on regional land-cover for all watersheds together. Each watershed is displayed on a separated biplot, *gray points* represent all sampling locations and *black points* representing sampling locations from that watershed

among the streams (Fig. 4). Only the first axis of the regional land-cover CA (RegCA1) was retained as an index of land-cover disturbance because it explained 73.5% of the variation in regional land-cover (Fig. 5), the second axis (RegCA2) of the CA explained 18.2%. RegCA1 contrasted sites along a gradient of high urban development to agriculture. Regional land-cover within three of the watersheds, East Don, Rouge, and Etobicoke, represented the variation in land-cover among all the watersheds, but the regional land-cover within the Mimico and Highland watersheds was biased towards high urban development (Fig. 5). Due to these biases additional analyses were conducted by calculating the land-cover indices for each of the watersheds individually (Supplementary Material S2).

The reduced model for species richness contained LocCA1, and the first, second, and third Strahler stream order (Table 6). The full model was not superior to the reduced model ($X^2 = 5.20$; $df = 6$; $p = 0.52$). The reduced model explained 48.7% $\left(R^2_{GLMM(M)}\right)$, watershed as random effect explained 29.4% $\left(R^2_{GLMM(C)}\right)$, and the fixed factors explained 19.3% of the variation in species richness. The negative association with LocCA1 indicates that species richness was lower in stream segments in urban areas and higher in agricultural regions (Fig. 4).

The final model for Shannon's diversity contained LocCA1, RegCA1, and the first and third Strahler stream orders (Table 6). The complete model was not superior to the reduced model ($X^2 = 9.91$; $df = 6$; $p = 0.13$). The reduced model accounted for 28.0% $\left(R^2_{GLMM(M)}\right)$, the watershed random effect accounted for 18.4% $\left(R^2_{GLMM(C)}\right)$, and the fixed factors

**Table 6** Model coefficient and confidence intervals for significant variables included in reduced general linear mixed effect models for each of the response variables

| Response | Variable | Estimate | Lower CI | Upper CI |
|---|---|---|---|---|
| Alpha diversity | | | | |
| Species richness | LocCA1 | −0.60 | −1.028 | −0.159 |
| $n = 159$ | Strahl1 | −4.78 | −6.294 | −3.368 |
| | Strahl2 | −3.00 | −4.187 | −1.834 |
| | Strahl3 | −3.48 | −4.455 | −2.442 |
| Shannon's diversity index | LocCA1 | −0.11 | −0.198 | −0.0129 |
| $n = 159$ | RegCA1 | 0.11 | 0.0078 | 0.219 |
| | Strahl1 | −0.52 | −0.815 | −0.238 |
| | Strahl3 | −0.28 | −0.454 | −0.108 |
| Pielou's evenness index | RegCA1 | 0.034 | 0.00254 | 0.0621 |
| $n = 159$ | | | | |
| Individual species | | | | |
| Brook Stickleback | LocCA1 | −0.56 | −1.0617 | −0.103 |
| (*Culaea inconstans*) | Strahl2 | 1.91 | 0.907 | 3.0285 |
| $n = 159$ | | | | |
| Fathead Minnow | Strahl1 | −0.95 | −2.309 | 0.169 |
| (*Pimephales promelas*) | | | | |
| $n = 159$ | | | | |
| Longnose Dace | DCIs | −0.62 | −1.146 | −0.156 |
| (*Rhinichthys cataractae*) | LocCA1 | −0.55 | −1.081 | −0.0610 |
| $n = 159$ | RegCA1 | −0.87 | −1.494 | −0.301 |
| | Strahl1 | −3.21 | −4.884 | −1.742 |
| | Strahl2 | −2.82 | −4.164 | −1.636 |
| | Strahl3 | −2.79 | −4.0375 | −1.685 |
| Creek Chub | Strahl4 | 1.35 | 0.213 | 2.837 |
| (*Semotilus atromaculatus*) | Strahl5 | 1.43 | 0.296 | 2.911 |
| $n = 159$ | | | | |
| Beta diversity | | | | |
| Total species richness | Length | 4.57 | 3.178 | 5.981 |
| $n = 46$ | DCIp | −3.43 | −5.200 | −1.657 |
| | SubCatCA1 | −3.03 | −5.552 | −0.604 |
| $\beta_{SOR}$ | Length | 0.057 | 0.0149 | 0.0959 |
| $n = 46$ | DCIp | −0.13 | −0.178 | −0.0926 |
| $\beta_{SIM}$ | Length | 0.091 | 0.0371 | 0.146 |
| $n = 46$ | DCIp | −0.12 | −0.177 | −0.0603 |
| $\beta_{SNE}$ | Length | −0.028 | −0.0529 | −0.00,308 |
| $n = 46$ | | | | |

See Tables 3 and 4 for acronym definitions

$n$ = number of samples included in the analyses, where 159 indicates number of individual sites and 46 indicates number of habitat networks

accounted for 9.6% of the variation in the data. The association with LocCA1 (negative) and RegCA1 (positive) indicate that Shannon's diversity was lower in urban areas and higher in agricultural regions (Figs. 3, 4). The Strahler stream order of the sampling site was also important, as Shannon's diversity was lower in first and third order streams.

The reduced model for Pielou's evenness contained RegCA1. The complete model was not superior to the reduced model ($X^2 = 0.68$; df = 9; $p = 0.69$). The inclusion of watershed as a random effect did not account for any additional variation in Pielou's evenness index that was not explained by the fixed factors $\left(R^2_{\mathrm{GLMM(C)}} = R^2_{\mathrm{GLMM(M)}} = 0.0356\right)$. RegCA1 was positively correlated with Pielou's evenness index (Table 6) indicating that Pielou's evenness index was positively correlated with the amount of agriculture and negatively correlated with the amount of urban development (Fig. 5).

### Abundance of individual species

Only four species were captured in each of the watersheds and at least 25% of all sites (Supplemental Material S1); Brook Stickleback (*Culaea inconstans*), Fathead Minnow (*Pimephales promelas*), Longnose Dace (*Rhinichthys cataractae*), and Creek Chub (*Semotilus atromaculatus*). Therefore, we built models for the abundance of each of the four species.

The reduced model for Brook Stickleback contained LocCA1 and the second Strahler stream order as fixed effects. The complete model was not superior to the reduced model ($X^2 = 7.35$; df = 7; $p = 0.39$) and the reduced model explained 68.2% $\left(R^2_{\mathrm{GLMM(M)}}\right)$, the random effect watershed explained 28.9% $\left(R^2_{\mathrm{GLMM(C)}}\right)$, and the fixed factors explained 39.3% of the variation in the abundance of Brook Stickleback. LocCA1 was negatively correlated with the abundance of Brook Stickleback, indicating that abundance was higher in stream segments in agricultural areas than urban, and abundance was higher in second order stream segments (Table 6).

For Fathead Minnow, the reduced model contained Strahler stream order as a fixed effect, and the full model was not superior to it ($X^2 = 12.61$; df = 8; $p = 0.12$). The abundance of Fathead Minnow was lower in first order streams, but the confidence interval overlapped 0 (Table 6). The reduced model explained 17.1% $\left(R^2_{\mathrm{GLMM(M)}}\right)$, the random effect watershed explained 6.8% $\left(R^2_{\mathrm{GLMM(C)}}\right)$, and the Strahler stream order explained 10.3% of the variation in Fathead Minnow abundance.

Model fitting for the abundance of Longnose Dace found that the reduced model contained the fixed effects of DCIs, LocCA1, RegCA1, as well as the first, second, and third Strahler stream orders (Table 6). The complete model was not superior to the reduced model ($X^2 = 6.24$; df = 4; $p = 0.18$). The reduced model explained 83.3% $\left(R^2_{\mathrm{GLMM(M)}}\right)$, the random effect watershed explained 37.2% $\left(R^2_{\mathrm{GLMM(C)}}\right)$, and the fixed factors explained 46.1% of the variation in the abundance of Longnose Dace. DCIs was negatively correlated with the abundance of Longnose Dace. Correlations between LocCA1 and abundance indicated that Longnose Dace were more abundant in streams in agricultural areas, results which conflict with the correlation with RegCA1 which found that Longnose Dace were more abundant in urban areas. Longnose Dace were least abundant in first, second, and third order stream (Table 6).

The reduced model for Creek Chub contained the fixed effects Strahler stream order 4 and 5 and the complete model was not superior to the reduced model ($X^2 = 4.70$; df = 8; $p = 0.79$). The reduced model explained 31.1% $\left(R^2_{\mathrm{GLMM(M)}}\right)$ of the variation in the abundance of Creek Chub, which can be attributed to

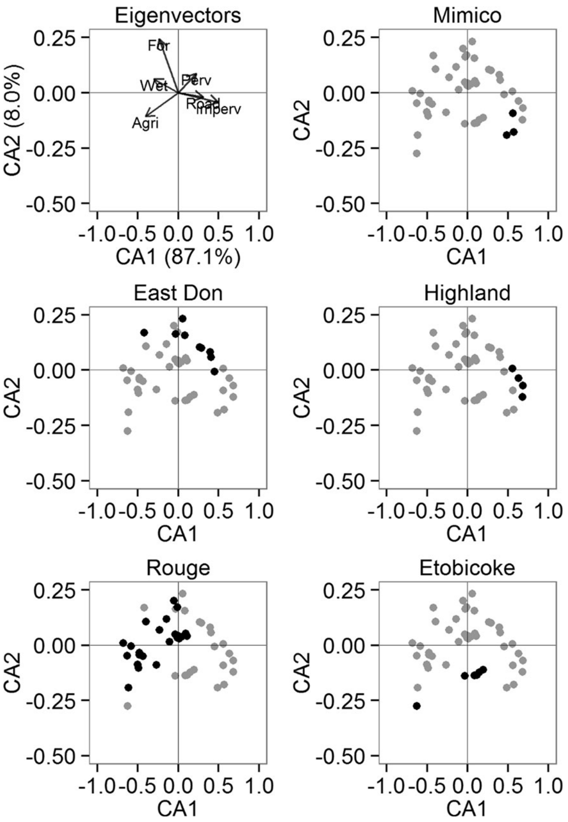

**Fig. 6** Biplots for a correspondence analysis conducted on land-cover within drainage basins of each habitat network for all watersheds together. Each watershed is displayed on a separated biplot, *gray points* represent all sampling locations and *black points* representing sampling locations from that watershed

the fixed factors as the random effect watershed did not explain any of the variation. The abundance of Creek Chub was highest in fourth and fifth order stream segments (Table 6).

### Beta diversity

Only the first axis of the sub-catchment land-cover CA (SubCatCA1) was used as an index of land-cover disturbance because it explained 87.1% of the variation in land-cover among drainage basins created for each habitat network (Fig. 6). The reduced model for total species richness contained all of the fixed effects and it explained 77.4% $\left(R^2_{\mathrm{GLMM(M)}}\right)$, the random effect watershed explained 60.9% $\left(R^2_{\mathrm{GLMM(C)}}\right)$, and the fixed factors explained 16.5% of the variation in total species richness. Total species richness was positively correlated with the length of the habitat network, negatively correlated with network connectivity, and negatively correlated with SubCatCA1 (Table 6). The negative correlation with SubCatCA1 indicates that species richness is higher in habitat networks in agricultural regions with wetlands than in urban developed areas (Fig. 6).

The reduced model for total beta diversity ($\beta_{\mathrm{SOR}}$) contained the length of the habitat network and DCIp as fixed factors. The complete model was not superior to the reduced model ($X^2 = 2.76$; df = 1; $p = 0.096$). The reduced model explained 76.1% $\left(R^2_{\mathrm{GLMM(M)}}\right)$, the random effect watershed explained 45.5% $\left(R^2_{\mathrm{GLMM(C)}}\right)$, and the fixed factors explained 30.6% of the variation in $\beta_{\mathrm{SOR}}$. Overall total beta diversity was positively correlated with the size of the habitat network and was negatively correlated with connectivity (Table 6).

For turnover ($\beta_{\mathrm{SIM}}$) the reduced model contained the length of the habitat network and DCIp as fixed factors, and the complete model was not superior ($X^2 = 2.88$; df = 1; $p = 0.089$). The reduced model explained 68.4% $\left(R^2_{\mathrm{GLMM(M)}}\right)$, the random effect watershed explained 38.5% $\left(R^2_{\mathrm{GLMM(C)}}\right)$, and the fixed factors explained 29.9% of the variation in turnover. Turnover was positively correlated with the length of the habitat network and negatively correlated with connectivity (Table 6).

Only the length of the habitat network was retained in the reduced model for nestedness ($\beta_{\mathrm{SNE}}$). The reduced model explained 45.1% $\left(R^2_{\mathrm{GLMM(M)}}\right)$, the random effect watershed explained 33.8% $\left(R^2_{\mathrm{GLMM(C)}}\right)$, and the fixed factors explained 11.3% of the variation in nestedness. The complete model was not superior ($X^2 = 3.067$; df = 2; $p = 0.22$) to the reduced model. The length of the habitat network was negatively correlated with nestedness (Table 6).

## Discussion

Habitat alteration and habitat fragmentation occur simultaneously and are both thought to be major drivers of stream fish community composition (Allan 2004; Perkin and Gido 2012; Cooper et al. 2015). Understanding the cumulative effects of anthropogenic land-cover and fragmentation requires studies that span multiple spatial scales because their effects are most evident at different scales. For instance, in our study, axes from CA's that represented variability in land-cover at the local and regional scale were correlated with various measures of alpha diversity, whereas connectivity and the length of the habitat network were correlated with measures of beta diversity. Thus, there is a need to consider the scale specific effects of habitat alteration and habitat fragmentation when studying the cumulative effects of both types of environmental change.

### Alpha diversity

Land-cover, at the local and regional scale, were the variables most commonly correlated with all measures of alpha diversity. This result corroborates earlier work by Mahlum et al. (2014a) who found land-cover variables were superior explanatory variables relative to connectivity for alpha diversity of stream fish assemblages. Land-cover at both scales can have site specific effect on water temperature, nutrient loading, flow rates, turbidity, dissolved oxygen, and other environmental variables that can determine what species are found at which sites (Angermeier and Winston 1998; Booth and Jackson 1998; Fausch et al. 2002; Pease et al. 2011). The lack of a correlation between the connectivity of each site DCIs and measures of alpha diversity indicate that the local abiotic or biotic conditions of a habitat patch determine which species can persist at a particular site, highlighting the need to consider how development alters habitat conditions at particular sites (Booth and Jackson 1998; Fausch et al. 2002; Pease et al. 2011). Stream order was correlated with species richness and Shannon's diversity, and the pattern of lower richness and diversity in low ordered streams. This result was expected because within streams there is a gradient of increasing temperature, stream width, and habitat heterogeneity when moving from the headwaters to the mouth, which leads to a corresponding increase in diversity and richness (Angermeier and Winston 1998; Taniguchi et al. 1998).

Species richness, Shannon's diversity index, and Pielou's evenness index were negatively correlated with the amount of urban land-cover (pervious and impervious) and positively correlated with the amount of agricultural land-cover at the local and regional scale. The positive correlation with agriculture is likely due to the history of land-cover change in the area, natural areas were transformed into agricultural fields beginning in the early 1800s, and more recently agricultural fields were and are being transformed into urban development (Butt et al. 2005; Puric-Mladenovic et al. 2011). Historic land-cover can play an important role in determining community composition because at the time of sampling the community may still be responding to prior disturbance (Wenger et al. 2008; Neff and Jackson 2013). Furthermore, agricultural development results in the removal of specialist species and an increase in the prevalence and abundance of species that are able to persist in altered conditions (e.g. increased nutrients and increased temperature), which can result in higher species richness (Stanfield and Kilgour 2013). For these reasons, it is likely that while both agriculture and urban development have a negative effect on alpha diversity, the effect of urban development is likely larger than the effect of agriculture (Wenger et al. 2008). Our study streams had the greatest amount of urban development at the mouth and mid reaches, corresponding to locations where species richness and diversity is highest. As development intensification increases in the head waters, there is potential for negative cumulative effects in lower reaches where species richness and diversity are highest. Furthermore, streams at mid reaches may be more susceptible to cumulative effects of habitat change and fragmentation because they are structured by both habitat characteristics and dispersal, whereas headwater streams are structured by habitat characteristics (Brown and Swan 2010).

The four most common species in the watersheds are known to be able to tolerate significant habitat alteration (Stanfield and Kilgour 2013), but can be affected by within stream habitat fragmentation (Nislow et al. 2011). Neither land-cover nor connectivity was significantly associated with the abundance of Fathead Minnow or Creek Chub, rather the abundance of these two species was associated with Strahler stream order. The abundance of Longnose Dace was negatively correlated with connectivity (DCIs) and urban land-cover, and positively correlated with agriculture and wetlands at both spatial scales. Results presented herein match the known habitat associations of Longnose Dace, which include gravel riffles of fast-moving creeks and small to medium rivers (Page and Burr 1991) that are uncommon in urban streams. The abundance of Brook Stickleback was negatively correlated with urban development and positively correlated with agriculture at the local scale, again matching known habitat associations such as cool water in pools and backwaters of creeks and small rivers (Scott and Crossman 1973; Etnier and Starnes 1993). Overall results for individual species demonstrate the difficulty in predicting associations between the abundance of common species and land-cover or fragmentation. Land-cover data and connectivity indices may be better suited to determining community level impacts, and inferences for individual species will have to be made on a case by case basis.

## Beta diversity

Patterns in beta diversity were largely determined by the size of the habitat network; in larger networks species richness was higher, total beta diversity ($\beta_{SOR}$) was higher, turnover ($\beta_{SIM}$) was higher, and nestedness ($\beta_{SNE}$) was lower. These results were expected due to the increase in the amount of habitat and increase in habitat heterogeneity associated with larger networks. It was expected that overall beta diversity ($\beta_{SOR}$) would be correlated with land-cover variables and connectivity, the portion of total beta diversity that was attributed to turnover ($\beta_{SIM}$) would be positively correlated with land-cover, and the portion of total beta diversity attributed to nestedness ($\beta_{SNE}$) would be positively correlated with connectivity. Patterns in overall beta diversity matched expectations as overall beta diversity was negatively correlated with DCIp, demonstrating that lack of connectivity results in increased community dissimilarity (Nislow et al. 2011; Perkin and Gido 2012; Perkin et al. 2015), likely because fragmentation prevents the movement of organisms with the habitat network. Interestingly, predictions for turnover and nestedness were not upheld as turnover was negatively correlated with DCIp and nestedness was not correlated with DCIp. The negative correlation between turnover and connectivity indicates that turnover is may be more likely to occur in poorly connected networks. In all networks, rare species are most likely to be lost due to stochasticity (Fahrig 1997; Fagan 2002; Grant 2011), and in fragmented networks recolonization after local extinction is unlikely to occur. Thus, turnover could be expected in poorly connected networks. The effects of fragmentation may be strongest in the mid reaches of streams because dispersal is asymmetrical in dendritic networks, with populations in lower order headwater segments producing more emigrants than immigrants and populations in mid reaches producing fewer emigrants than immigrants (Morrissey and de Kerckhove 2009).

Patterns in alpha diversity presented herein clearly show the negative effects of habitat alteration, as measured by land-cover, on stream fish communities. The negative effects of habitat alteration could be exacerbated in small stream networks that have been fragmented, because small stream networks are unlikely to support large number of species and the communities are unlikely to turnover. Therefore, our results provide further evidence that a regional approach that considers both connectivity and land use is necessary to understand the structure of fish communities in stream ecosystems (Fagan 2002; Labonne et al. 2008; Padgham and Webb 2010; Perkin and Gido 2012).

### Among watershed variation

Inspection of watershed specific biplots for regional land-cover, and land-cover within drainage basins for habitat networks (Figs. 4, 5) indicate that not all watersheds represented the considerable among watershed variation in land-cover, and some were biased towards being more heavily urbanized. The large amount of variation explained by the watershed random factor (alpha diversity: 7–37%; beta diversity: 33–61%) in the GLMMs demonstrate the strong biases. Due to the potential biased results, the land-cover index calculated with correspondence analyses were carried out on each watershed individually (see Supplemental Material S2). There were some major differences in the results between the two analyses. If land-cover indices are calculated for each of the watersheds individually, land-cover at the local and regional scale is correlated with patterns in alpha diversity. Similar inferences are drawn for the effect of the different types of land-cover between the two methods; species richness and Shannon's diversity index were positively correlated with the amount of agriculture, forest, and wetlands. The relationships between measures of beta diversity and network length and connectivity remain the same, but land-cover is no longer associated with total species richness. Finally, relationships between the abundance of individual species and predictor variables were different for all species. Most notably, none of the predictor variables were correlated with the abundance of Creek Chub and Longnose Dace. The abundance of Brook Stickleback was correlated with land-cover at both spatial scales rather than only local land-cover. Creating an index of land-cover for each watershed individually provides a better estimate of local factors that influence species abundance and community composition for each of the watersheds, but results in a decrease in the ability to generalize the results because results are watershed or site specific.

## Conclusions

Using a multi-scale approach and considering alpha and beta diversity simultaneously allows for the cumulative effects of environmental change to be understood. Urbanization results in an overall loss of species and reduction in alpha diversity at particular sites due to alterations of the abiotic and biotic structure of habitats. The overall loss of species at individual sites could be offset by dispersal of individuals from other areas within the habitat network. However, urbanization also results in fragmentation which prevents the movement of organisms within a habitat network and leads to an increase in community dissimilarity. Thus, when habitat alteration and fragmentation occur simultaneously, species that are lost from altered sites are not replaced, leading to a simultaneous reduction in species richness and an increase in community dissimilarity. In dendritic networks, such as streams, the combined effects of habitat change and fragmentation are likely to be greatest in mid reaches, where diversity is highest, the impacts of habitat change are greatest, and communities are structured by both habitat characteristics and dispersal (Brown and Swan 2010). The effects of habitat change on communities can be both scale and species specific, such that effective conservation and management of stream ecosystems in urbanized and urbanizing watersheds requires both a local approach focused on ensuring that habitat conditions can support species of interest and a regional approach to ensure that habitat networks are well connected to facilitate dispersal.

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