

Habitat filtering and adult dispersal determine the taxonomic composition of stream insects in an urbanizing landscape

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SUMMARY

1. Suitability of the local habitat ('habitat filtering') and dispersal between stream reaches determines the composition of insect communities, and urban land use may affect both processes. While urban streams are often poor habitats for insects and dispersal between them is often hindered, conservation and restoration activities generally focus solely on the local (in-stream) environment.
2. We determined whether in-stream habitat filtering (a 'local' process) or dispersal between reaches (a 'regional' process) controlled assemblage composition in a landscape subject to ongoing urban development ('urbanizing'). We compared models incorporating geographic distance between sites, environmental dissimilarity, and land-use/land-cover attributes of dispersal pathways in an attempt to explain the dissimilarity of stream insect assemblages. Distance and land-use/land-cover attributes were characterised along both overland (straight line) and corridor pathways.
3. Both in-stream habitat filtering and dispersal affected assemblage composition, but habitat had a stronger influence. Overland distance was a better predictor of assemblage dissimilarity than corridor distance, implying stream insect dispersal occurs across catchment boundaries as well as along stream corridors. The best model incorporated land-use/land-cover attributes along dispersal pathways, which supported the idea that urban land-use in the terrestrial environment mediates dispersal.
4. Conservation and restoration strategies for streams in urbanizing landscapes that focus on local habitat quality and ignore dispersal are missing a potentially important mechanism affecting insect assemblage composition. While the primary focus should be on maintaining or improving the local habitat, potential dispersal pathways should also be considered.

Keywords: Stream insects, urbanisation, dispersal, habitat filtering, connectivity

Introduction

Current views of the link between landscape urbanisation and the composition of stream communities have generally stressed the poor quality of in-stream environments resulting from catchment land use and direct alterations to the stream (e.g. channelisation, point source chemical inputs, etc.; Paul & Meyer, 2001; Walsh *et al.*, 2005; Wenger *et al.*, 2009). Stream insects, however,

interact with both aquatic and terrestrial environments during their life cycle. The larval stage of most stream insects is aquatic, and thus, conditions in the stream control survival and fitness at this stage. Many (but not all) adult stream insects interact with the terrestrial environment for at least a short time and can potentially fly long distances across the landscape (Bunn & Hughes, 1997; Bilton, Freeland & Okamura, 2001). The natural and anthropogenic characteristics of terrestrial landscapes at

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small and broad spatial scales can affect survival, fitness and dispersal of the adult stage (Wilcock, Hildrew & Nichols, 2001; Macneale, Peckarsky & Likens, 2005; Finn *et al.*, 2006; Smith, Alexander & Lamp, 2009). Thus, a focus on in-stream conditions probably does not represent all the effects on stream insects resulting from urban development (Brown *et al.*, 2011).

Niche-based (i.e. local) processes operating within stream reaches include species interactions and responses to habitat conditions that 'filter' species with suitable traits from the regional species pool (Ricklefs, 1987; Poff, 1997; Brown *et al.*, 2011). Dispersal-based processes operating at spatial scales broader than individual reaches are controlled by the interaction of landscape characteristics, habitat patch characteristics, species- and gender-based morphological and behavioural traits related to movement and the regional species pool (Ricklefs, 1987; Loreau, 2000; Hoffsten, 2004; Petersen *et al.*, 2006). Recent research examining stream macroinvertebrate metacommunities has indicated that habitat filtering is more important than dispersal for determining assemblage composition and that the importance of dispersal generally decreases with decreasing stream size (Heino & Mykrä, 2008; Brown & Swan, 2010; Finn & Poff, 2011; Campbell & McIntosh, 2013; Göthe, Angeler & Sandin, 2013).

The use of terrestrial habitats by the adult stage of many species suggests that stream insects are affected by fragmentation and habitat loss that can occur across urbanizing landscapes (Delettre & Morvan, 2000; Urban *et al.*, 2006; Becker *et al.*, 2007). Fragmentation and habitat loss typically lower taxon richness and increase community homogenisation for terrestrial assemblages (McKinney, 2002; Fahrig, 2003) and should have similar effects on stream insects. The filling of stream channels or the conversion of streams into storm water systems can increase the distance between suitable aquatic habitats (Elmore & Kaushal, 2008). Additionally, the absence of oviposition structures (e.g. large rocks, wood, etc.) may further decrease the amount of suitable stream reaches across urbanizing landscapes (Alp, Indermaur & Robinson, 2013; Lancaster & Downes, 2013). Intervening stream reaches, riparian corridors of poor habitat quality and dispersal barriers (e.g. culverts; Blakely *et al.*, 2006) may also limit dispersal (Fagan, 2002; Fahrig, 2007; Smith *et al.*, 2009).

Analysis of the taxonomic similarity of communities among locations in the stream network, in relation to intervening geographic distance and environmental dissimilarity of their habitats, can indicate whether in-stream habitat filtering, dispersal or a combination of

both is controlling their species composition (Chase *et al.*, 2005). The notion is that (i) communities become more dissimilar when dispersal between them decreases with increasing distance; and (ii) community composition diverges as environmental differences increase (Nekola & White, 1999). Thus, the strength of correlations between community dissimilarity and either geographic distance or environmental dissimilarity can indicate the relative importance of dispersal versus in-stream habitat filtering, respectively. Geographic distance alone, however, may not fully represent the amount of dispersal occurring between habitat patches. Urban land use along dispersal pathways is likely to decrease connectivity among patches compared with those in undeveloped landscapes separated by otherwise similar distances. Thus, characteristics of dispersal pathways should be considered when relating community dissimilarity to geographic distance (Urban *et al.*, 2006; Fahrig, 2007; Moritz *et al.*, 2013).

We used a model selection approach to compare the effects of factors representing in-stream habitat filtering and dispersal on the composition of a stream insect assemblage. We explore the hypothesis that urbanisation represents a functional impediment to dispersal between streams. Using a distance-decay framework, we examined relationships between dissimilarity of stream communities in 'non-nested' reaches (i.e. no sample locations are found directly downstream of another sample location) and both geographic distance and environmental dissimilarity. Our primary objective was to determine whether the relative effect of in-stream habitat filtering and dispersal on assemblage composition are consistent with patterns found across less-affected landscapes and sites nested within the stream network (e.g. Heino & Mykrä, 2008; Brown & Swan, 2010; Finn & Poff, 2011; Campbell & McIntosh, 2013; Göthe *et al.*, 2013). The examination of the assemblage of only flying insects in non-nested reaches meant that assemblages in this study were not connected through drift but were connected primarily via adult flight along overland or corridor pathways. Urban land use could enhance in-stream habitat filtering, through degradation of the in-stream environment. Alternatively, fragmentation of aquatic habitats and dispersal barriers may strengthen the importance of dispersal limitations. We predicted that the relative effect of in-stream habitat filtering and dispersal on assemblage composition will not differ from stream systems in less-affected landscapes. We asked three general questions: (i) Does in-stream habitat filtering dominate dispersal for determining insect assemblage composition? (ii) Are pathways along the stream corridor or

across catchments more important for the dispersal of stream insects between non-nested reaches? (iii) Does land-use/land-cover along dispersal pathways affect the connectivity of insect assemblages?

Methods

We used data on insect assemblages and the environment from the Maryland Department of Natural Resources (MD-DNR) Maryland Biological Stream Survey (MBSS) biomonitoring programme to analyse relationships between (i) geographic distance and (ii) environmental dissimilarity with assemblage dissimilarity (Fig. 1). The MBSS is a probability-based stream biomonitoring programme that examines biotic and abiotic

components of stream ecosystems (see Klauda *et al.*, 1998 for more details).

Site selection

Geographic location, habitat and biological data were used as criteria for selecting MBSS sites for inclusion in this study. The data included sites from five sub-catchments of the Chesapeake Bay in Maryland's Piedmont physiographic province (Fig. 2). The sub-catchments are Maryland Department of the Environment 6 digit (MDE6) drainage units, which are aggregates of smaller drainage areas used for water quality monitoring and a modification of similar units delineated by the United States Geological Survey (USGS). The total area within

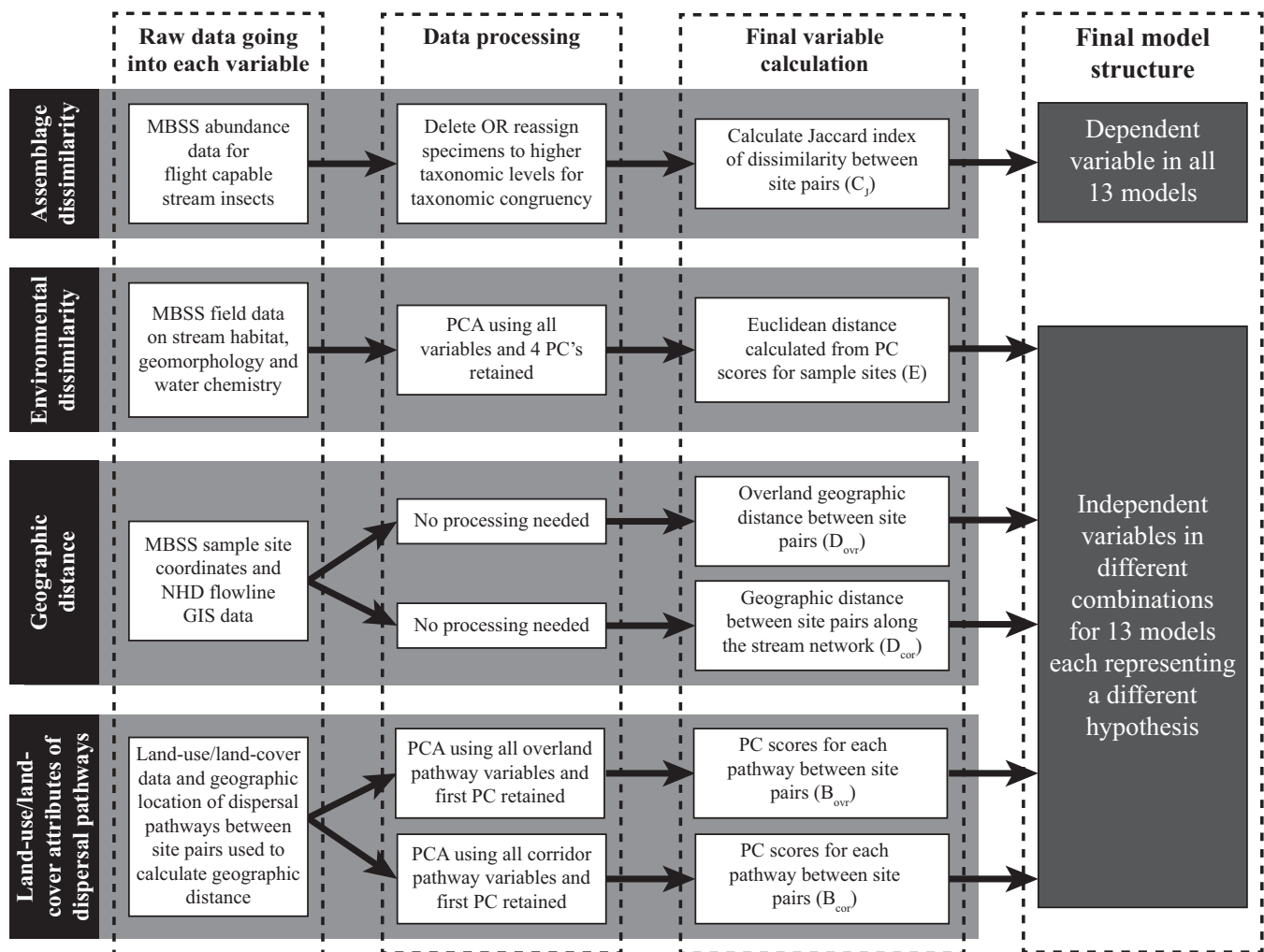


Fig. 1 Conceptual diagram of the model selection procedure for hypothesis testing. For each variable, the diagram lists raw data sources, processing steps and calculated variables. Assemblage dissimilarity was used as the dependent variable in all models, and all other variables were used as independent variables in some combination to form the 13 different models compared in the analysis. The value representing the paired environmental dissimilarity was calculated in the final variable calculation, but the values representing land-use/land-cover attributes of dispersal pathways between site pairs were determined directly from GIS data in the data processing step prior to use in the PCA.

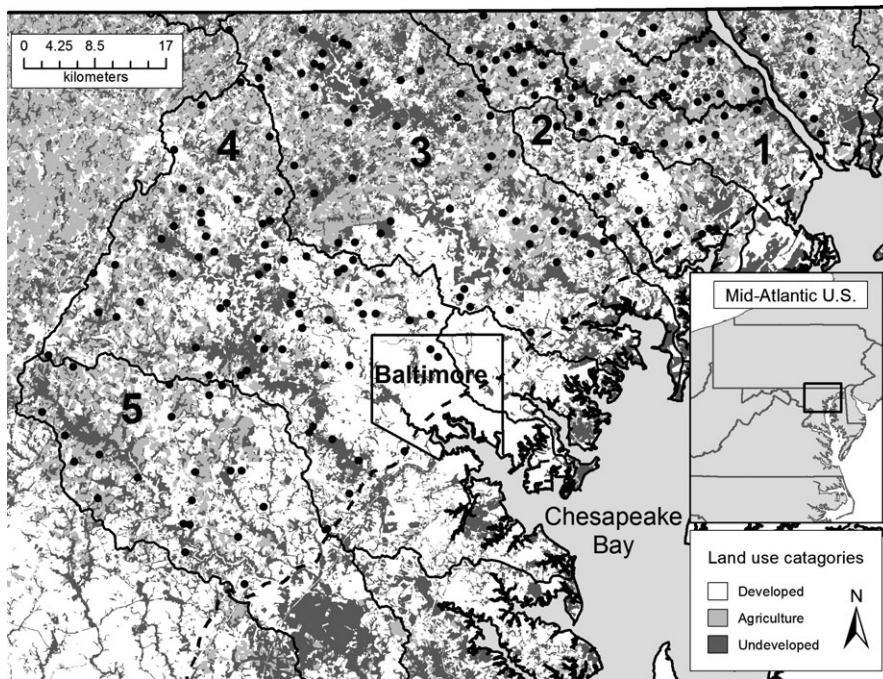


Fig. 2 Map of the study region showing location of MBSS sample sites (black dots) within each of five MDE6 drainage units in Maryland, U.S.A. (labelled 1 = Susquehanna, 2 = Bush, 3 = Gunpowder, 4 = Patapsco, 5 = Patuxent). The black dashed line traces the fall line between the Piedmont (to the northwest) and the Coastal Plain physiographic provinces. Land-use data derived from National Land Cover Data (NLCD) were summarised as developed (commercial, urban and residential classes), agricultural (crops and pasture) and undeveloped (forest, wetland, and fresh water). The map insert indicates the location of the study area within the Mid-Atlantic region of the United States.

Maryland's boundaries and the piedmont physiographic province for the five drainage areas used for this study ranged from 30 254 (Bush) to 125 351 ha (Patapsco). Analysis was restricted to the Piedmont to minimise the effect of habitat and community differences that can occur naturally or as a result of human impacts in different physiographic provinces (Utz, Hilderbrand & Boward, 2009). Data from a particular location represented a single sampling event from that reach collected between 2000 and 2009.

Sample site locations were checked against metadata descriptions and repositioned to align with USGS 1:24 000 National Hydrology Dataset (NHD; Simley & Carswell, 2009) flow lines using ArcGIS v10.1 (Esri, Redlands, CA) to correct for minor differences between field-measured coordinates and GIS data. Stream order was determined by visual inspection of NHD maps and only sites on first- and second-order streams were retained for analysis. Our final data set included 189 MBSS sample sites across all five MDE6 drainage units (Bush = 17, Gunpowder = 51, Patapsco = 58, Patuxent = 20, Susquehanna = 43). Sample sites were only compared within MDE6 drainage units, which led to a total of 4157 pairwise comparisons.

Stream insect assemblages and dissimilarity

Stream insect data used in this study were exclusively from collections made for the MBSS programme. Field collections and laboratory subsampling and

identifications were performed using standard MBSS protocols (Stranko *et al.*, 2007; Boward & Friedman, 2011). In summary, 'kick', 'jab' or 'sweep' samples were collected from different habitats (riffles, pools, runs, snags and other coarser substrata) within a 75-m reach using a D-framed net. Data provided from the MD-DNR represented subsamples of 100 benthic invertebrates that were identified to the lowest practical taxonomic level (no finer than genus). We removed all non-Insecta individuals and other selected insect taxa from the benthic invertebrate data set to isolate aquatic taxa with flying stages for analysis (see Appendix S1 in Supporting Information). Additionally, taxonomic resolution must be identical between sample sites to measure dissimilarity between communities (Cao & Hawkins, 2011). The original data included specimens identified to genus that were also identified to order, family, subfamily or tribe in the same or other samples. Taxonomic congruency was reached by coalescing some genera to family or deleting specimens from the data set using a method that minimised information lost (Cao & Hawkins, 2011; Appendix S1). The resulting data set consisted of taxa consistently identified to the same taxonomic level (i.e. genus or species) across all samples. The data set used in the analysis of assemblage dissimilarity retained 19 821 individuals of the 22 093 individuals in the original data set (89.7%) from 193 distinct taxonomic units.

We calculated Jaccard dissimilarity based on presence/absence data using R v2.14.1 (*vegan* package v2.0-2):

$$C_J = (A + B - 2 * J) / (A + B - J) \quad (1)$$

where A = number of taxa at sample site A , B = the number of taxa at sample site B , and J = the number of taxa shared by samples sites A and B . We did not use a measure of dissimilarity that incorporates abundance to avoid biasing the results given that the original data were from fixed count subsamples and altered to achieve taxonomic congruency. We determined which, if any, taxa were driving broad patterns of taxonomic dissimilarity across sites within each MDE6 drainage unit using the function *simper*, R v2.14.1 (*vegan* package v2.0-2). The insect assemblage for each MDE6 drainage unit was divided into two groups based on a hierarchical cluster analysis of Jaccard dissimilarity values using the Unweighted Pair Group Method with Arithmetic Mean (Legendre & Legendre, 2012). Because the function *simper* uses Bray–Curtis dissimilarities, the analysis of the proportional contribution to dissimilarity was performed using presence/absence data to match with our use of the Jaccard Index for the model selection procedure (Clarke, 1993).

Environmental dissimilarity

Habitat and stream chemistry data used for describing environmental dissimilarity between sample sites were derived from MBSS protocols (Fig. 1), described by Stranko *et al.* (2007). Variables retained for this analysis included conductivity ($\mu\text{S cm}^{-1}$), dissolved oxygen (mg L^{-1}), pH, mean stream width (m), mean thalweg depth (cm) and mean velocity (m s^{-1}). Qualitative measures of stream habitat, epifaunal substratum, velocity and depth diversity, pool quality, riffle quality, embeddedness, and shading by riparian vegetation were also included in the analysis of environmental dissimilarity (Appendix S1). Catchment land-use/land-cover represents an indirect measure of the in-stream environment, and it was considered inferior to the direct measures of in-stream habitat from the MBSS data. We also considered conductivity a better overall predictor of the characteristics controlling in-stream habitat filtering than the nutrient data available. Nutrients are an important component of water quality, but we believed that numerous confounding factors and potential indirect pathways affecting nutrient concentrations limited our ability to link nutrient data to in-stream habitat and insect assemblage composition (Roy *et al.*, 2003; King *et al.*, 2005; Yuan, 2010; Liess *et al.*, 2012). Additionally, empirical evidence suggests that conductance may better describe in-stream habitat than nutrients for Maryland Piedmont

streams (King *et al.*, 2005; Craig, 2009; see Appendix S1 for a more detailed explanation).

A principal component analysis (PCA) was used to reduce environmental variables to those components with an eigenvalue >1 (King *et al.*, 2005; Legendre & Legendre, 2012). Euclidean distance was calculated from sample scores for each retained axis from the PCA to represent a single value for the environmental dissimilarity between sample site pairs within MDE6 drainage units (Fig. 1).

Geographic distance and dispersal pathways

Movements along stream corridors (Sode & Wiberg-Larsen, 1993; Petersen *et al.*, 2004) and through upland areas (Macneale *et al.*, 2005) are both potential dispersal pathways for flying adult insects. Thus, geographic distances (km) were calculated between all site pairs along both a straight geodesic line (overland pathway) and stream flow lines (corridor pathway) within each MDE6 drainage unit. A Pearson correlation coefficient was calculated between the geographic distances for overland and corridor pathways to assess multicollinearity between the two dispersal pathway variables.

Land-use/land-cover attributes of all dispersal pathways were measured to assess the potential for dispersal constraints to affect connectivity represented by inter-site distance measures (Table 1). Percentages of commercial and residential land uses and the percentage of all impervious surfaces were used as proxy measures for light pollution (Eisenbeis, 2006) and air temperature (Yuan & Bauer, 2007; Myint *et al.*, 2010), respectively. Forested, commercial and high-density residential land cover was assessed from 2010 Maryland Department of Planning (MDP) land-cover/use data (1:12 000; MDP, 2011). The percentage of impervious surfaces was obtained from the 2006 National Land Cover Data 30 m per cent impervious surface data set (Fry *et al.*, 2011). These data sets provided the best temporal overlap with the MBSS community data. Adult insects dispersing along the stream corridor likely stay close to the stream channel (Sode & Wiberg-Larsen, 1993; Petersen *et al.*, 1999), but they are unlikely to fly in a straight line through the uplands. Thus, we calculated the percentage of forest in strips of land of different widths on both sides along the corridor and overland pathways (30 m and 100 m, respectively (Table 1). By contrast, diffuse light sources and air temperature may have spatially broader impacts than forest cover on adult insect flight behaviour and survival, so commercial and residential

Table 1 List of landscape variables that may impact dispersal, with representative citations (see Smith *et al.*, 2009 for further description). These variables are referred to as ‘geographic proxies’ because they use spatial data representing indirect measures of the mechanisms causing the potential impact to dispersal. These variables were included in the PCA to create a single variable (from PC1) representing land-use/land-cover attributes of dispersal pathways between sample site pairs. Buffer distances represent the distance to one side of the buffered object (e.g. per cent forest in 100 m on either side of the overland pathway)

Landscape variables	Potential impact to dispersal	Measure for overland pathway	Measure for corridor pathway
1. Forested area along dispersal pathway	Forested areas may encourage dispersal (Petersen <i>et al.</i> , 1999)	Per cent forested area in 100 m buffer	Per cent forested area in 30 m buffer
2. Artificial light sources	Possible environmental sink may discourage dispersal (Perkin <i>et al.</i> , 2011)	Per cent commercial and high-density residential land use in 100 m buffer	Per cent commercial and high-density residential land use in 100 m buffer
3. Temperature on land	High temperatures decrease survival, may discourage dispersal (Collier & Smith, 2000)	Per cent impervious surfaces in 100 m buffer	Per cent impervious surfaces in 100 m buffer
4. Road – stream intersections (bridges and culverts)	Bridges and culverts are a barrier to dispersal (Blakely <i>et al.</i> , 2006)	Not applicable	Number of road–corridor pathway intersections per km
5. Paved surfaces (roads)	Possible environmental sink may discourage dispersal (Kriska, Horváth & Andrikovics, 1998)	Number of road–overland dispersal pathway intersections per km	Not applicable

land uses and per cent impervious surfaces were summarised within 100 m on both sides of overland and corridor pathways. Existing road centreline maps for 2008 were obtained from Maryland State Highway Administration (MSHA) and used to calculate intersections with both stream flow lines and upland pathways (MSHA, 2009). The geographic proxies used in this analysis should be interpreted as a suite of general stressors on adult insects rather than individual mechanisms (Smith *et al.*, 2009).

Geographic proxies were summarised using a PCA, and an aggregate description of standardised estimates of land-use/land-cover along upland and corridor pathways across all sample site pairs was obtained by analysis of the first principal component (PCA; package *stats* in R v2.14.1; Fig. 1). Only the first principal component was used as it explained a large portion of the variance in the data (see Results) and allowed us to represent this component as a single term in the model, similar to geographic distance and environmental similarity.

Model selection

A model selection approach was used to evaluate the importance of geographic distance, land-use/land-cover attributes of dispersal pathways and environmental dissimilarity for explaining patterns of assemblage dissimilarity between sites (Johnson & Omland, 2004;

Anderson, 2008). Hypothesis testing by model selection requires that models representing specific competing hypotheses be developed *a priori*, so that the relative quality of the models determines which hypothesis is best supported. Thirteen models were developed that predicted assemblage dissimilarity using either single predictors or a combination of predictors (Table 3). The candidate set of models was capable of answering our research questions without including interaction terms. An interaction between geographic distance and land-use/land-cover attributes of dispersal pathways was the most sensible to include, but a *post hoc* analysis showed no increase in model fit when that interaction term was added to the best model ($\Delta_i < 2$; Anderson, 2008).

Separate models were included for overland and corridor pathways whenever geographic distance, land-use/land-cover attributes of dispersal pathways or both were included in the model. Overland and corridor pathway land-use/land-cover attributes were not included together within a single model, to avoid correlation that would confound interpretation of relative model quality. This set of candidate models allowed us to focus on comparing the two dispersal pathways individually.

Generalized linear models were created using function *glm()* (Gaussian distribution and the identity link function) within the R package *stats* (2011) and compared using package *AICcmodavg* (v 1.24; Mazerolle, 2013). A generalised linear model was used because the data did

not meet the assumptions required for a linear model. Variance inflation factors were calculated using the *car* package (2011) to check for overdispersion, which could indicate potential problems with a lack of independence or heterogeneous distributions between variables (Anderson, 2008). We measured Pearson's correlation coefficients between overland geographic distance, corridor geographic distance and environmental dissimilarity to assess any potential spatial autocorrelation. We also measured correlation between overland pathway land-use/land-cover attributes, corridor pathway land-use/land-cover attributes and environmental dissimilarity to determine whether the in-stream environment and land-use/land-cover attributes of dispersal pathways were similarly influenced by human land use surrounding the stream.

Results

Assemblage dissimilarity

Assemblage composition varied widely across samples. Jaccard dissimilarity measures across all sample site pairs from all MDE6 drainage units ranged from a maximum of 1 (i.e. no shared taxa) to a minimum of 0.478. This indicated that pairs of sample sites never approached complete similarity. Most taxa occurred infrequently across sample sites. The percentage of taxa found in greater than 50% of the samples for each MDE6 drainage unit ranged from 5% to 6.8%. *Ephemera* and *Parametriocnemus* (Diptera: Chironomidae) were the only taxa present at over 75% of sites for the Gunpowder, Patapsco, Patuxent and Susquehanna MDE6 drainage units, and *Orthocladius* (Diptera: Chironomidae), *Cheumatopsyche* (Trichoptera: Hydropsychidae) and *Parametriocnemus* were the only taxa found in over 75% of sites in the Bush MDE6 drainage unit. The widespread occurrence of these taxa probably contributed to patterns of dissimilarity across sample site pairs.

The contributions of particular taxa to Bray–Curtis dissimilarity, based on presence/absence data, were rarely greater than 2%, indicating that many taxa contributed to broad patterns of dissimilarity among sites rather than a few key taxa. Five taxa of Chironomidae, *Ephemera* (Ephemeroptera: Ephemerellidae), *Amphinemura* (Plecoptera: Nemouridae), *Chimarra* (Trichoptera: Philopotamidae), *Hydropsyche* (Trichoptera: Hydropsychidae), *Optiosevus* (Coleoptera: Elmidae), *Microcyloepus* (Coleoptera: Elmidae) and *Simulium* (Diptera: Simuliidae) were the only taxa that contributed more than 2% (maximum contribution was 2.5% by *Chimarra*).

Species traits varied widely among taxa that contributed to patterns of dissimilarity. *Eukiefferiella* (Chironomidae) was the most pollution tolerant (tolerance value = 8 out of 10, with 10 being the most tolerant), and *Ephemera* was the most intolerant (tolerance value = 2; Stribling *et al.*, 1998). In general, the group was evenly comprised of pollution-tolerant and pollution-intolerant taxa. Additionally, taxa from this group belonged to a variety of functional feeding groups, including collectors, shredders, filterers, scrapers and predators (Stribling *et al.*, 1998). This group of taxa also had a variety of dispersal abilities and was not comprised of highly dispersive taxa based on dispersal traits listed in Poff *et al.* (2006). Half of the taxa were designated as having high female dispersal, and only three were considered strong fliers (Poff *et al.*, 2006). *Hydropsyche* was the only taxon considered to have high female dispersal and be a strong flier (Poff *et al.*, 2006).

Environmental dissimilarity

A PCA on environmental variables (Appendix S2) resulted in four components (eigenvalues > 1) that accounted for 72.2% of the total variance in environmental data (Table 2; Fig. 3). In-stream habitat, mean depth, shading and pH are all measures that may reflect the stream's natural setting or human impacts to in-stream habitat through catchment land use, riparian deforestation or channel alterations. Euclidean distance calculated between sample pairs based on site scores for axes 1–4 ranged from 0.27 to 13.9 (mean = 3.86, SD = 1.92). The majority of high Euclidean distance measures (values > 10) were attributed to two sites within the Patapsco MDE6 drainage unit that had environmental measures indicating high anthropogenic impacts (i.e.

Table 2 Results of the PCA on environmental variables used to calculate environmental dissimilarity. Only the PCs with an eigenvalue >1 that were retained for further analysis are shown. Euclidean distance between sample scores extracted from the first four axes represented environmental dissimilarity between sample site pairs

Axis	Eigenvalue	Variance explained (%)	Factor loading*
1	4.794	36.9	In-stream habitat (−0.402)
2	1.888	14.5	Mean depth (0.411)
3	1.475	11.3	Shading (−0.566)
4	1.240	9.5	pH (−0.618)

*Factors listed are the single factor with the greatest (negative or positive) loading, and the loading is listed in parentheses. See Fig. 3 for biplot of first four axes.

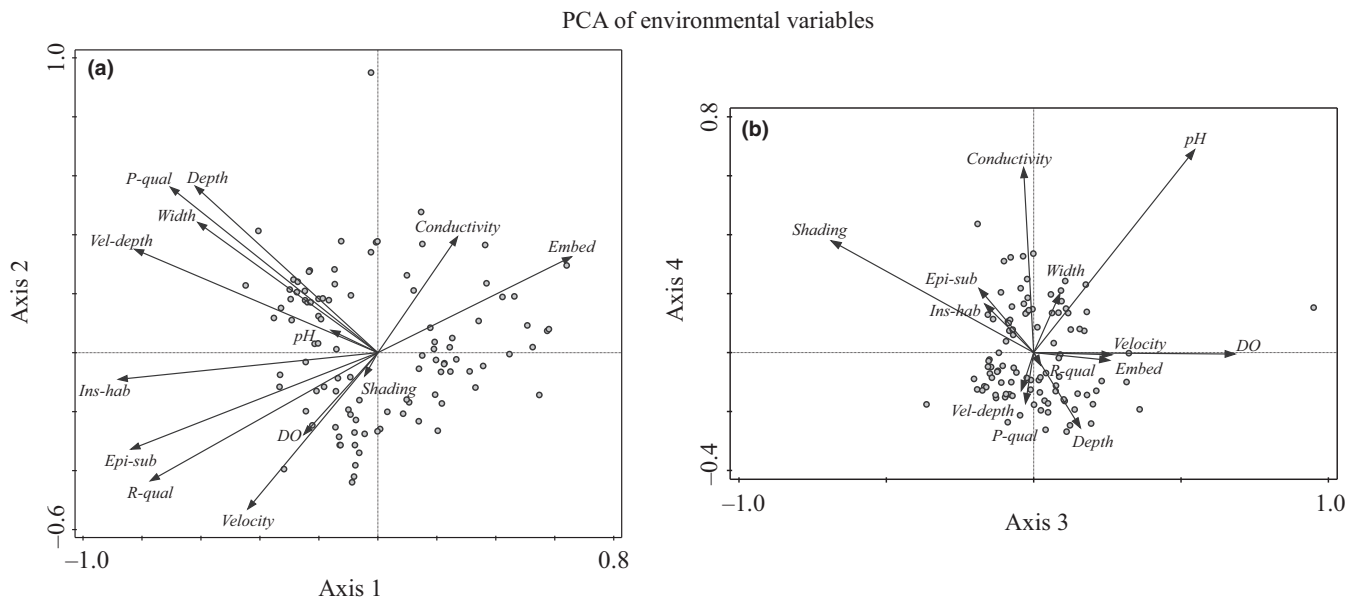


Fig. 3 Biplot of axes 1 and 2 (a) and 3 and 4 (b) for the principal component analysis of environmental variables used to calculate environmental dissimilarity. Biplots were generated with CANOCO v5.0 (Ter Braak & Šmilauer, 2012), site and factor scores were rescaled, and only 100 sites representing the highest percentage of variation explained by the two axes are shown for presentation. Vectors represent environmental variables, and points represent samples (DO = dissolved oxygen, Ins-hab = in-stream habitat, Epi-sub = epifaunal substratum, Vel-depth = velocity depth diversity, P-qual = pool quality, R-qual = riffle quality, Embed = per cent embedded, shading = per cent shading, Width = mean stream width, Depth = mean stream depth, and Velocity = mean velocity).

very low habitat quality scores and high conductivity). Thus, the measure of environmental dissimilarity used in this analysis potentially represented a greater environmental gradient among sample sites within the Patapsco than the other drainage units.

Geographic distances and dispersal pathways

The Pearson correlation coefficient calculated for geographic distances separating sample site locations using overland and corridor pathways (Table S2.1) indicated only moderate correlation between these variables ($r = 0.59$). The first principal component (PC1) for overland pathway land-use/land-cover attributes (Table S2.1) accounted for 69.6% of the variance (eigenvalue = 2.784). Factor loadings for overland PC1 were greatest for the percentage of impervious surfaces in the 100 m buffer (-0.564), road intersections (-0.543), and per cent commercial and high-density residential in the 100 m buffer (-0.531). Principal component 1 for corridor pathway land-use/land-cover attributes (Table S2.1) accounted for 63.4% of the variance (eigenvalue = 2.534). Factor loadings for the corridor PC1 were greatest for the percentage of impervious surfaces in the 100 m buffer (-0.590), per cent commercial and high-density residential in the 100 m buffer (-0.577), and road

intersections (-0.564). All factor loadings indicated that component scores had similar moderately negative relationships with the percentage of impervious surfaces, per cent commercial and high-density residential, and road intersections.

Model selection

Thirteen models were fitted to assemblage dissimilarity consistent with our three research questions (Table 3). All variables were significant predictors in all models, with the single exception of corridor pathway land-use/land-cover attributes (estimate = 0.0012, standard error = 0.00086, t value = 1.44, $P = 0.15$) in the model combining it and environmental dissimilarity (model 6; Table 3). Across all comparisons, the model incorporating overland geographic distance, overland pathway land-use/land-cover attributes, and environmental dissimilarity (model 1; Table 3) was clearly superior to other candidate models ($\Delta\text{AICc} > 50$; Anderson, 2008). This model represents a combined influence of in-stream (habitat filtering) and dispersal processes on stream insect assemblages (Table 3). Standardised coefficients for the best model indicated that environmental dissimilarity had a stronger effect on Jaccard dissimilarity than the other predictors (Table 4), which indicates

Table 3 List of models showing model structure, descriptions of the process supported and the results of the model selection procedure. The dispersal pathway is indicated in the model structure. Models are listed from highest (top) to lowest (bottom) fit.

Model structure*	Processes supported [†]	Model number	AICc score	Δ_i^{\ddagger}	Pseudo-r-squared [§]	Evidence ratio [¶]
$C_J = D_{OVR} + B_{OVR} + E$	In-stream & dispersal	1	-8764.91	0	0.151	1
$C_J = D_{OVR} + E$	In-stream & dispersal	2	-8707.25	57.66	0.138	3.3e + 12
$C_J = B_{OVR} + E$	In-stream & dispersal	3	-8627.67	137.24	0.122	6.3e + 29
$C_J = D_{COR} + B_{COR} + E$	In-stream & dispersal	4	-8624.54	140.37	0.121	3.0e + 30
$C_J = D_{COR} + E$	In-stream & dispersal	5	-8621.13	143.78	0.120	1.7e + 31
$C_J = B_{COR} + E$	In-stream & dispersal	6	-8586.07	178.84	0.113	6.8e + 38
$C_J = E$	In-stream	7	-8586.00	178.91	0.112	7.1e + 38
$C_J = D_{OVR} + B_{OVR}$	Dispersal	8	-8415.40	349.51	0.076	7.9e + 75
$C_J = D_{OVR}$	Dispersal	9	-8263.56	501.35	0.041	7.4e + 108
$C_J = B_{OVR}$	Dispersal	10	-8220.99	543.92	0.031	1.3e + 118
$C_J = D_{COR} + B_{COR}$	Dispersal	11	-8158.54	606.37	0.017	4.7e + 131
$C_J = D_{COR}$	Dispersal	12	-8155.40	609.51	0.015	2.3e + 132
$C_J = B_{COR}$	Dispersal	13	-8102.96	661.95	0.003	5.5e + 143

*The variables in the models are: C_J = Jaccard dissimilarity index, D_{OVR} = overland geographic distance, D_{COR} = corridor geographic distance, E = environmental dissimilarity between sample site pairs, B_{OVR} = land-use/land-cover attributes of overland dispersal pathways, and B_{COR} = land-use/land-cover attributes of corridor pathways.

[†]The process supported is either described as 'in-stream' representing in-stream habitat filtering measured through environmental dissimilarity, 'dispersal' measured through geographic distance or land-use/land-cover attributes of dispersal pathways, or a combination of both.

[‡] Δ_i represents the difference between AICc scores for each model and the best model.

[§]The maximum-likelihood pseudo-r-squared was calculated using R package *pscl* (v1.04.4).

[¶]Evidence ratios calculated as in Johnson & Omland (2004) and are relative to the best model.

Table 4 Summary of standardised model coefficient estimates and significance for the best model ($C_J = D_{OVR} + B_{OVR} + E$)

Coefficients	β	SE	t -value	P
D_{OVR} (overland distance)	0.1721	0.00012	11.9	<0.001
B_{OVR} (overland pathway habitat)	-0.1148	0.00081	-7.7	<0.001
E (environmental dissimilarity)	0.2854	0.00071	19.1	<0.001

that environmental conditions in the stream had greater impact on insect assemblages than aspects of the terrestrial landscape that affect dispersal. The data did not appear to be overdispersed, and the predictor variables representing in-stream and dispersal processes were not highly correlated (Table 3, Appendix S1). The maximum-likelihood pseudo-r-squared values, though, generally indicated poor fit for all models, with the highest value of 0.151 occurring for the best model (Fig. 4).

Discussion

We used a model selection approach to examine the relative importance of in-stream habitat filtering and dispersal for controlling stream insect assemblage composition across an urbanizing landscape. Using the wealth of existing MBSS biomonitoring data, we were

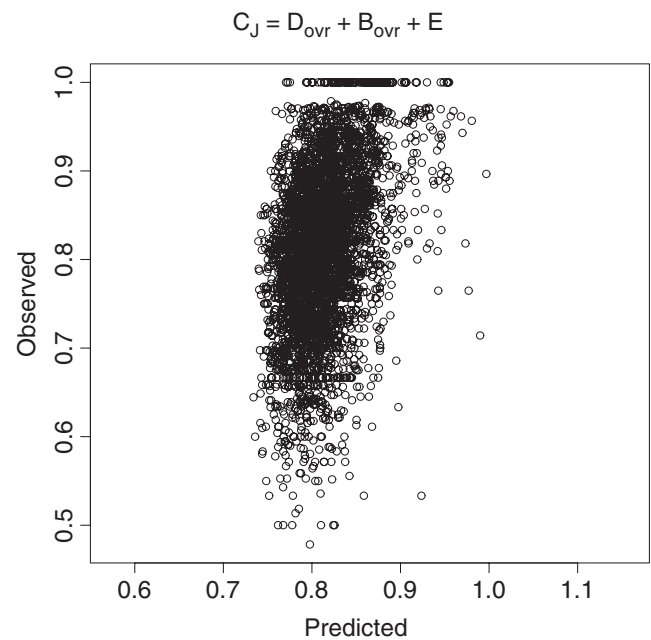


Fig. 4 Plot of predicted versus observed values of assemblage dissimilarity derived from the best model. Variables representing model structure are as follows: C_J = Jaccard dissimilarity index, D_{OVR} = overland geographic distance, B_{OVR} = land-use/land-cover attributes of overland dispersal pathways and E = environmental dissimilarity between sample site pairs.

able to test a number of models comparing assemblage dissimilarity with geographic distance, environmental dissimilarity or both, while incorporating the potential

effects of urban land-use/land-cover along two dispersal pathways. Focussing on non-nested reaches that cannot exchange individuals solely via drift, we tested (i) the relative importance of in-stream habitat filtering and dispersal processes, (ii) the importance of dispersal through overland and corridor pathways, and (iii) the effect of land-use/land-cover attributes along dispersal pathways on connectivity.

What is the relative importance of habitat filtering and dispersal for determining assemblage composition?

Both in-stream habitat filtering and dispersal were apparently important for determining differences in taxonomic composition among the sites, although in-stream habitat filtering predominated. These results supported our prediction and conformed to other studies in similar sized streams (Table S2.2; e.g. Brown & Swan, 2010; Campbell & McIntosh, 2013; Göthe *et al.*, 2013). Conductivity values suggested that our sample sites spanned a broad range of stream quality (Roy *et al.*, 2003), which could have promoted in-stream habitat filtering processes. While urbanizing terrestrial landscapes can fragment stream habitats (Elmore & Kaushal, 2008) and directly decrease adult fitness and survival (Smith *et al.*, 2009), these effects are unlikely to outweigh the direct 'filtering' effect of poor conditions in urban streams.

Even though dispersal may have played a lesser role than in-stream habitat filtering, the strength of the inter-site distance effect suggested that dispersal was an important factor for determining assemblage composition (Cottenie & De Meester, 2005; Driscoll & Lindenmayer, 2009). The structure of communities in first-order streams (similar in size to a portion of the sites included in our study) may be less affected by dispersal processes than communities in higher order streams (Brown & Swan, 2010; Göthe *et al.*, 2013). As expected, we observed an effect of dispersal, in addition to in-stream habitat filtering, by including both first- and second-order streams. Our results, however, differ from the findings of Heino & Mykrä (2008), who found little evidence that dispersal limitation affected insect communities in the streams they classified as 'headwater streams', which included streams with mean widths greater than those used in our study.

The poor fit of the best model requires cautious interpretation of results, but increasing the explanatory power of individual predictor variables would generally not change the main conclusion that habitat filtering and dispersal both affect stream insects. An increase in explanatory power for environmental dissimilarity

would increase overall model fit, but the rank order of models would not change given that top seven models all contained this variable (Table 3), and our assertion that multiple factors control assemblage composition, based on our model selection approach, would still hold true. Increased explanatory power for environmental dissimilarity would also strengthen the interpretation that in-stream conditions were more important than dispersal. Direct measures of distance cannot be altered; thus, their effects would not change. Greater explanatory power for pathway habitat variables could indicate a greater importance of dispersal than habitat filtering and suggest that distance alone is a poor predictor of dispersal and connectivity within the distance-decay framework (Moritz *et al.*, 2013). Thus, future studies could refine the analyses used for characterizing dispersal across the landscape, especially with regard to understanding dispersal pathway habitats.

Species traits may have a substantial effect on the relative importance of habitat filtering and dispersal. Studies focussed on assemblages that included non-flying taxa or poor dispersers, and that found little effect of dispersal processes in headwater streams, suggest that dispersal ability of taxa may influence the relative importance of dispersal processes (Brown & Swan, 2010; Finn & Poff, 2011; see Poff *et al.*, 2006 for the relative flight ability of Chironomidae). Patterns of dissimilarity in our study, however, did not appear to be related to differences in dispersal ability or tolerance to pollution among flying insects. We did find, however, that site pairs with a combined low taxonomic richness were more likely to be more dissimilar than pairs of sites with high combined richness. Taxonomic richness typically declines with increasing human impacts (Roy *et al.*, 2003), and the elimination of pollution-intolerant taxa from the benthos in highly urbanised streams may have driven some of the patterns in taxonomic dissimilarity observed among the site pairs with low taxonomic richness. A detailed analysis of the relationship between species traits (including tolerance to anthropogenic impacts) and beta diversity across our sample sites was beyond the scope of this study. Our results should not be interpreted as empirical evidence that species traits do not affect the role of habitat filtering and dispersal-based processes for determining community composition.

The use of biomonitoring data meant that samples from a number of years were used for the analysis. Inter-annual variability in invertebrate communities often depends more on annual changes in weather than local environmental conditions (Scarsbrook, 2002;

Collier, 2008). Local site characteristics, however, may interact with variation between years in weather (Mazor, Purcell & Resh, 2009), and weather may affect stream communities by altering local environmental conditions, such as stream flow (Scarsbrook, 2002). The environmental data used in this study were collected at the same time as the insects, and any temporal shifts in local conditions driving changes in taxonomic composition would probably be captured by our measure of environmental dissimilarity. Inter-annual variability in assemblage dissimilarity may have obscured the relationships with geographic distance and decreased our ability to detect the effects of dispersal-based processes. Long-term biomonitoring sites (called 'sentinel sites') in Maryland's Piedmont physiographic province showed little annual variation in Benthic Indices of Biotic Integrity (which describe community structure) in response to severe droughts in 2001, 2002 and 2007, and higher than average precipitation in 2003 (Versar Inc., 2011). These results from the MBSS suggest that the insect assemblages in our study did not change drastically in the face of severe weather events (which might have indicated habitat degradation). Additionally, species presence-absence generally varies less among years than species relative abundance (Robinson, Minshall & Royer, 2000; Scarsbrook, 2002). Our use of presence-absence data for measures of dissimilarity is likely to have decreased the effect of annual variability of the assemblage on our results.

Are overland pathways or the stream corridor more important for dispersal of stream insects between non-nested reaches?

The best model included overland geographic distance, which suggested that the dispersal processes controlling assemblage composition in non-nested reaches are based more on movement overland than through the stream corridor. The results of our work support the view that some flight-capable adult stream insects disperse between non-nested stream reaches in neighbouring catchments through upland areas, but do not suggest that movement through the corridor between non-nested reaches is absent for some or even all species. The distance-decay framework used in this study assesses the mechanisms structuring the assemblage, and species differences in dispersal ability and behaviours, habitat specialisation and other traits that control dispersal routes are likely to exist (Hughes, Schmidt & Finn, 2009). The fact that no clear group of insects controlled patterns of dissimilarity across sites limits the inferences we can

make about individual taxa. In addition, the importance of overland dispersal at the assemblage level could indicate that the group of taxa mostly responsible for patterns of dissimilarity is dispersing between non-nested reaches through upland landscapes, but the use of genus-level and presence-absence data further limits the interpretation of taxon-specific differences of dispersal within the assemblage.

Adult stream insect abundance is typically greatest near the stream channel, and this observation is cited as evidence that insects disperse throughout the stream network primarily along the stream corridor (Sode & Wiberg-Larsen, 1993; Petersen *et al.*, 2004, 2006). Dispersal along the stream corridor is important for fully aquatic stages, and dispersal between nested reaches (i.e. reaches that are up- and downstream of each other) is occurring through the stream corridor (Hershey *et al.*, 1993; Chaput-Bardy *et al.*, 2008). Macneale *et al.* (2005) found evidence that movement between adjacent catchments occurred through upland areas to the upper reach of an adjacent headwater stream and through the corridor to the lower reach. Given that our assessment is at the assemblage level, our results only indicate that overland dispersal is more important for determining patterns of dissimilarity across non-nested sites than corridor dispersal at the spatial scale of our analysis. Our interpretation is based on the distance-decay framework (Nekola & White, 1999) and should not be interpreted as proof that corridor dispersal between non-nested reaches is non-existent. For example, Rouquette *et al.* (2013) found that taxonomic turnover of stream insects was more correlated to corridor than overland pathways when examining a mix of nested and non-nested sites at a finer spatial scale in an urbanizing landscape.

Are land-use/land-cover attributes of dispersal pathways important for assessing connectivity?

The significant coefficient for land-use/land-cover attributes of overland pathways in the best model indicated that landscape characteristics mediate dispersal-based processes determining insect assemblage composition (Fahrig, 2007). Barriers to dispersal in urbanizing landscapes can decouple connectivity from geographic distance (Urban *et al.*, 2006). Thus, analyses of distance-decay patterns in urbanizing landscapes should incorporate measures of land-use/land-cover attributes along dispersal pathways, in addition to geographic distance, to adequately characterise connectivity between sites (Urban *et al.*, 2006). Additionally, the low-resolution GIS

data that required our use of geographic proxies may have underestimated the effects of urban landscapes on adult insect dispersal and reduced the strengths of pathway land-use/land-cover effects.

The spatial location of anthropogenic land use in relation to stream channels can alter the type and strength of effects on habitat conditions in the stream (King *et al.*, 2005). The lack of correlation between land-use/land-cover attributes of dispersal pathways and environmental dissimilarity of in-stream conditions indicated that effects of urbanisation captured by these two measures were independent. Similarly, *post hoc* analyses found little correlation between land-use/land-cover attributes of dispersal pathways and geographic distance (Pearson's correlation coefficient for overland pathways ≤ 0.04 and for corridor pathways ≤ 0.25), and no increase in model fit when including an interaction between geographic distance and land-use/land-cover attributes in the best model. Thus, conditions along dispersal pathways acted independently of geographic distance but were a poor predictor on their own. As stated above, however, this interpretation should be made with caution given overall low model fits.

Implications for stream management and restoration

Catchment land use and landscape characteristics that affect dispersal should be considered when examining human impacts on stream ecosystems. Catchment land use can clearly alter conditions in the stream channel (Paul & Meyer, 2001; Walsh *et al.*, 2005; Wenger *et al.*, 2009). Even though dispersal may be secondary to habitat filtering, we suggest that landscape characteristics at small and broad spatial scales that affect dispersal be used as additional explanatory variables in studies examining the effect of urban land use on stream insects. Analyses should examine dispersal routes through the stream corridor (by drift or flight) and through upland areas across catchment boundaries. The relationship between catchment land-use/land-cover and stream assemblages can be highly variable (especially at low levels of development), and we believe that a fruitful avenue of research is to determine whether factors related to dispersal-based processes may be able to explain some of that variability (Wenger *et al.*, 2009).

Additional information on species dispersal abilities and ranges are needed to understand how stream insects interact with urbanizing landscapes (Fahrig, 2007). While general descriptions of dispersal traits, such as in Poff *et al.* (2006), are useful for the coarse-scale analyses performed in this study, quantitative descrip-

tions of species dispersal abilities, combined with observational studies, landscape analyses or genetic analyses, can best determine the mechanisms that effect dispersal in natural and human impacted landscapes (Hughes *et al.*, 2009).

Our results also indicate that the interaction between improved in-stream conditions and the connectivity of stream reaches to surrounding source populations in neighbouring catchments will provide the strongest foundation for prioritizing projects to restore insect biodiversity in urban streams (Palmer, Ambrose & Poff, 1997; Bond & Lake, 2003). While dispersal through the corridor should be considered an important source of immigrants, our study indicates that assessing connectivity between potential restoration sites and surrounding streams in non-nested catchments should incorporate overland dispersal pathways. Our results also support the recommendation by Heino (2013) that the potential effects of dispersal processes should be considered when designing and interpreting stream bioassessments.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Additional Methodological Details and Results

Appendix S2. Summary tables of raw data used to calculate all explanatory variables in the model selection procedure.

Table S2.1 Summary of geographic distances between sites and variables used to create land-use/cover attributes of dispersal pathways.

Table S2.2 Summary of environmental variables used to calculate environmental dissimilarity.

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