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Loss of phylogenetic diversity under landscape change

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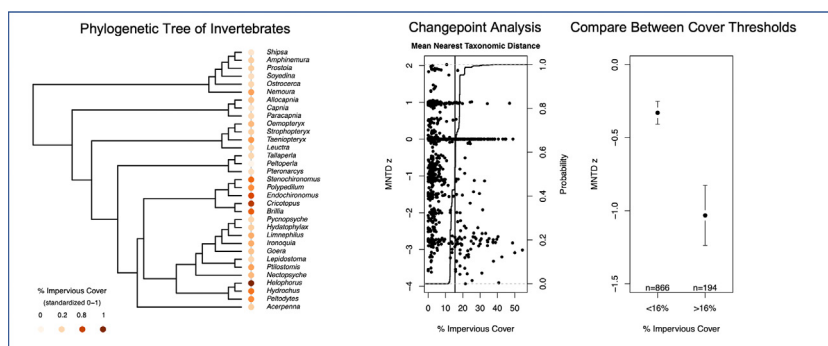
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HIGHLIGHTS

- Loss of biodiversity with land use change is a major concern.
- Surveys from 1060 streams were analyzed to relate biodiversity to urbanization.
- Change point analysis related biodiversity to a gradient in impervious land cover.
- Decreases in species richness and phylogenetic diversity were found.
- Urbanization reduces phylogenetic relationships of remnant stream communities.

GRAPHICAL ABSTRACT



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ABSTRACT

Habitat alteration and destruction are primary drivers of biodiversity loss. However, the evolutionary dimensions of biodiversity loss remain largely unexplored in many systems. For example, little is known about how habitat alteration/loss can lead to phylogenetic deconstruction of ecological assemblages at the local level. That is, while species loss is evident, are some lineages favored over others? Using a long-term dataset of a globally, ecologically important guild of invertebrate consumers, stream leaf “shredders,” we created a phylogenetic tree of the taxa in the regional species pool, calculated mean phylogenetic distinctiveness for >1000 communities spanning >10 year period, and related species richness, phylogenetic diversity, and distinctiveness to watershed-scale impervious cover. Using a combination of change point and compositional analyses, we learned that increasing impervious cover produced marked reductions in all three measures of diversity. These results aid in understanding both phylogenetic diversity and mean assemblage phylogenetic distinctiveness. Our findings indicate that, not only are species lost when there is an increase in watershed urbanization, as other studies have demonstrated, but that those lost are members of more distinct lineages relative to the community as a whole.

1. Introduction

As humans increasingly convert the Earth's surface, the fate of global biodiversity will greatly depend on whether organismal guilds are able to withstand or adapt to habitat changes and whether humans are able to conserve habitats within a range of species' tolerances. This paper contributes

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to research on biodiversity loss and resilience by asking whether novel disturbance regimes in riverine systems alter habitats sufficiently to transform the composition and phylogenetic structure of organismal guilds (Fox, 2007). Riverine systems vary widely in their ability to support biodiversity, with many species extirpated due to disturbance events, shifting habitat in space and time, or loss of suitable habitat altogether (Hobbs et al., 2009; Williams and Jackson, 2007). In addition, characteristics of the species themselves have evolved over millions of years, and may predispose some lineages to suffer or benefit from habitat alteration (McKinney and Lockwood, 1999; Purvis et al., 2000).

One of the primary causes of biodiversity loss is the loss or degradation of habitats (Chase et al., 2019; Reichstein et al., 2014). In built environments, it is well known that the degree of impervious land cover in a contributing area is strongly associated with altered habitat conditions in downstream waterways, specifically the frequency and intensity of disturbance events in rivers and streams (Baker et al., 2019; Utz et al., 2011; Walsh et al., 2005; Paul and Meyer, 2008; Roy et al., 2005). Furthermore, changes to water routing and flow regimes produce complex changes in local habitat conditions (Paul and Meyer, 2008); these can include changes in the relative balance of erosional versus depositional forces, shifts in the size distribution of substrates (Utz et al., 2016), increases in solute concentrations, and altered temperature regimes (Paul and Meyer, 2008). There is substantial research showing a link between watershed urbanization and significant loss of biodiversity in bottom dwelling invertebrates as well as fish species (Paul and Meyer, 2008; Brown et al., 2009). This has been important to recognize as many stream invertebrates are particularly critical trophic links between basal resources and higher trophic levels (Wallace et al., 1997).

Decades of research has led to the conclusion that species loss can substantially alter the magnitude of important ecosystem processes, for several reasons (e.g., Utz et al., 2016; Srivastava et al., 2009). For example, the more species in an assemblage, the more efficiently the assemblage as a whole can contribute to ecosystem processing of carbon and other nutrients. Such niche complementarity has been demonstrated for detritivores

in rivers (Jonsson and Malmqvist, 2003; Jonsson et al., 2001). Detritivorous “shredders” are a functional feeding group known to be important for the processing of externally derived carbon - namely senesced leaf litter from streamside vegetation (Wallace et al., 1997; Cummins and Klug, 1979). Breakdown of litter liberates energy necessary to sustain higher trophic levels (Wallace et al., 1997; Cross et al., 2006). As such, species loss from this functional group can have important consequences for stream food-web dynamics (Jonsson et al., 2002).

Research linking land-use change to stream biota has predominantly focused on taxonomic diversity. With the development of new and more widely accepted techniques for understanding evolutionary relatedness among species, ecologists are turning to the phylogenetic structure of local assemblages to learn not only if habitat degradation results in species loss, but whether remaining species are more or less evolutionarily distinct (Purvis et al., 2000). Phylogenetic diversity represents an ecological community's total evolutionary history, commonly taken as the sum total of branch lengths within its phylogenetic tree (Cadotte et al., 2010), and is considered to have important and relevant conservation value (Faith, 1992). Experiments at fine scales indicate that increasing the phylogenetic diversity of a local community - independent of species diversity - can lead to greater persistence after a disturbance, generate higher productivity in plants, and even sustain more species at higher trophic levels (Cadotte et al., 2008; Cadotte et al., 2012). However, the consequences of broader habitat modification on local phylogenetic structure remain largely unknown. Are those species most at risk of being affected by land-use change more evolutionarily distinct compared to others in an assemblage with high relatedness? This question has yet to be systematically explored in the literature.

Here, we sought to learn how both taxonomic and phylogenetic structure of freshwater detritivore communities shift in response to landscape change, specifically the expansion of impervious cover. We used a large stream-monitoring dataset collected to support assessment of benthic biological integrity (Klauda et al., 1998). After developing a phylogenetic tree for detritivores (Fig. 1), we calculated local phylogenetic diversity

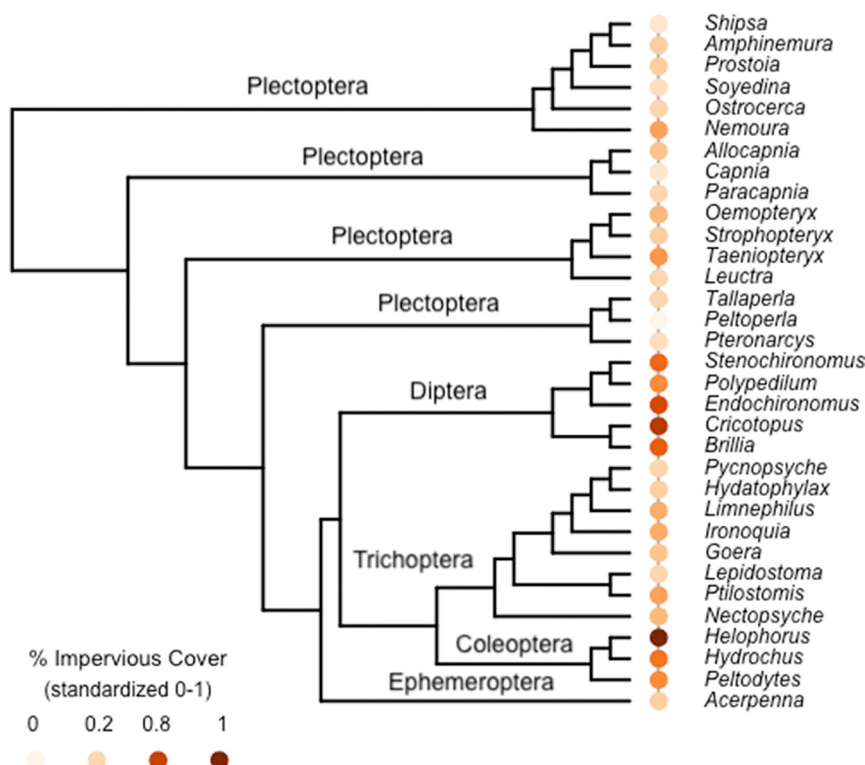


Fig. 1. Phylogenetic tree of stream detritivore genera with affinity to impervious cover. Darker colors indicate that species were found in sites that included higher impervious cover. The outgroup, *Apis*, is omitted for clarity.

(indicated by mean nearest taxonomic distance, MNTD) and the assemblage-level mean phylogenetic distinctiveness. We predicted that (1) consistent with the literature, taxonomic richness would decline with increasing impervious cover draining to the sample location, (2) phylogenetic diversity would also decline in a similar manner, and (3) so too would mean evolutionary distinctiveness. We predicted declines in both phylogenetic diversity and evolutionary distinctiveness in addition to taxonomic richness because we expected habitat shifts from increasing impervious cover would be sufficient to narrow environmental adaptations of detritivores such that only a select few, closely-related species could coexist.

2. Materials and methods

2.1. Data source & collection

We conducted an analysis using abundance data for macroinvertebrate taxa from 1060 stream reaches sampled by the Maryland Biological Stream Survey (MBSS; Klauda et al., 1998). The MBSS is a stream-monitoring program based on probabilistic sampling stratified by major basins and stream order (first to third order on a 1:250000 stream map during 1995–1997 and first to fourth order on a 1:100000 stream map during 2000–2003). Sampling locations were randomly assigned to non-overlapping, 75-m stream segments in the Piedmont physiographic region across the state of Maryland. Within each randomly selected segment, the survey included rapid-assessment metrics of stream physical characteristics, conventional water chemistry, in-stream habitat, discharge, and macroinvertebrate assemblage composition (2-m² sample collected with a 500- μ m D-framed dip net from favorable habitat. All macroinvertebrates were classified using genus-level identification and 100-organism, fixed-count methods (Maryland Department of Natural Resources, 2000). All of the selected sites were sampled once during 1995–2006, a period that overlapped with the 1985–2010 satellite imagery used to quantify impervious cover (see below). Greater details on data collection methods and quality assurance and quality control are provided in Roth et al. (2001).

Macroinvertebrate data were screened for consistency prior to analysis and ambiguous taxa were resolved following the operational-taxonomic-unit approach method of Cuffney et al. (2007). Individuals were identified to the level of genus as is the standard for the larval stage because adult features are required for identification to species level (Maryland Department of Natural Resources, 2000). If more than 100 individuals were enumerated for a stream reach, we used a computer-generated random sampling procedure to select a subsample of 100 individuals (Ostermiller and Hawkins, 2004) to ensure that individual taxa frequencies and abundances were expressed consistently for all sample units because both depend on the number of individuals in the subsample (Larsen and Herlihy, 1998). Samples with fewer than 100 individuals were not altered because they represent stream reaches with low densities of individuals possibly due to anthropogenic stressors, including catchment imperviousness.

2.2. Phylogenetic tree construction

A list of target genera was created by selecting those from the master data set designated as shredders by the MBSS. Only insects were included in the analysis. We used the command-line program phyloGenerator (Pearse and Purvis, 2013) to create a phylogenetic tree. The method for the creation of this tree is based on the BioPython framework (Talevich et al., 2012) and automates the retrieval of sequence information from GenBank, in addition to automating alignment and phylogenetic tree estimation. We constructed our tree based on five commonly sequenced genes, COI, 16S, 18S, 28S, and H3. The trimmed sequences were aligned using MAFFT (Katoh and Standley, 2013) after being visually examined for misalignment using ClustalX (Larkin et al., 2007). We then generated a maximum likelihood tree with RaxML (Stamatakis, 2014), using 1000

accelerated bootstrap replicates (Stamatakis et al., 2008) and constrained the final tree based on a taxonomic tree. Finally, we rate-smoothed the resulting tree to be ultrametric using the PATHd8 algorithm, with the *Apis* genus set as an outgroup (Britton et al., 2007).

2.3. Phylogenetic diversity & taxonomic richness

Phylogenetic diversity was calculated as the total branch length of all genera observed for each assemblage. We calculated the abundance-weighted mean nearest taxon distance (MNTD). MNTD measures the mean distance between each taxon's closest relative in a community, and thus focuses on similarity between co-occurring genera. The number of genera in a community and the structure of the phylogeny of the regional taxa pool can influence both metrics (Kraft et al., 2007; Cadotte et al., 2010). To remove effects of richness and regional phylogenetic structure, we compared observed MNTD against metrics calculated from null communities. We generated null communities by randomly drawing the same number of genera as observed at each site from the regional pool. The probability of drawing a taxon was proportional to the frequency that the taxon occurred within the sampling strata (basin) that defined the regional taxa pool. Next, we calculated MNTD for all 1000 null community sites, and expressed our results as the standardized effect size (*z*). Taxonomic richness was chosen as the measure of diversity for the study. Here, this is taken as the number of taxa at each site.

2.4. Mean phylogenetic distinctiveness

We quantified the evolutionary distinctness of each genera using the fair proportion metric (Cadotte et al., 2010), which is the weighted sum of the edge lengths along the path from the root of an ultra-metric tree to a leaf. The weights are 1/number of genera that share that edge. We then calculated this value for each genera occurring at a site. The mean for the assemblage was taken and then related to impervious cover.

2.5. Analysis of impervious cover

Impervious cover was estimated from a time series of Landsat satellite imagery using the Dynamic Impervious Surface Cover Observation and Retrieval System (DISCORS; Sexton et al., 2013). DISCORS uses high-resolution, municipal planimetric data collected over time to train a nonparametric regression tree, which is then applied to both wintertime reflectance and changes in summertime greenness to estimate impervious cover at annual, 30-m resolution across the study area from 1985 to 2010. Only one year in the series, 2009, was interpolated from 2008 and 2010 due to insufficient cloud-free satellite measurements. Pixels in the raster are zero (no impervious cover) or have an integer value of percent imperviousness ranging from 10% to 100%. DISCORS produced a 25-yr time series of annual impervious cover for the Baltimore-Washington, DC metropolitan area with misclassification error (i.e., ~6% per pixel root mean square error, RMSE) comparable to the impervious cover layer of the National Land Cover Database (NLCD; Fry et al., 2011). We distinguished real interannual change from noise by ignoring annual per-pixel differences <12% (i.e., RMSE*2). Aggregation of pixels to the scale of catchments (typically thousands of pixels) neutralizes omissions due to randomly distributed errors (Hodgson et al., 2003), so catchment-scale impervious estimates became increasingly precise as a function of increasing spatial scale (Baker et al., 2019).

Contributing areas for each stream sampling site were delineated using the 1/3 arc-second DEM resolution, which is approximately the 10 m resolution obtained from the National 3D Elevation Program (3DEP) <https://www.sciencebase.gov/catalog/item/4f70aa9fe4b058caae3f8de5>. DEMs were hydrologically corrected by filling internal drainages, deriving a flow direction field, and accumulating drainage. The contributing area upstream from each sample point was delineated following its manual alignment with the closest flow line and was used to summarize the proportion of impervious cover for each year in the impervious time series.

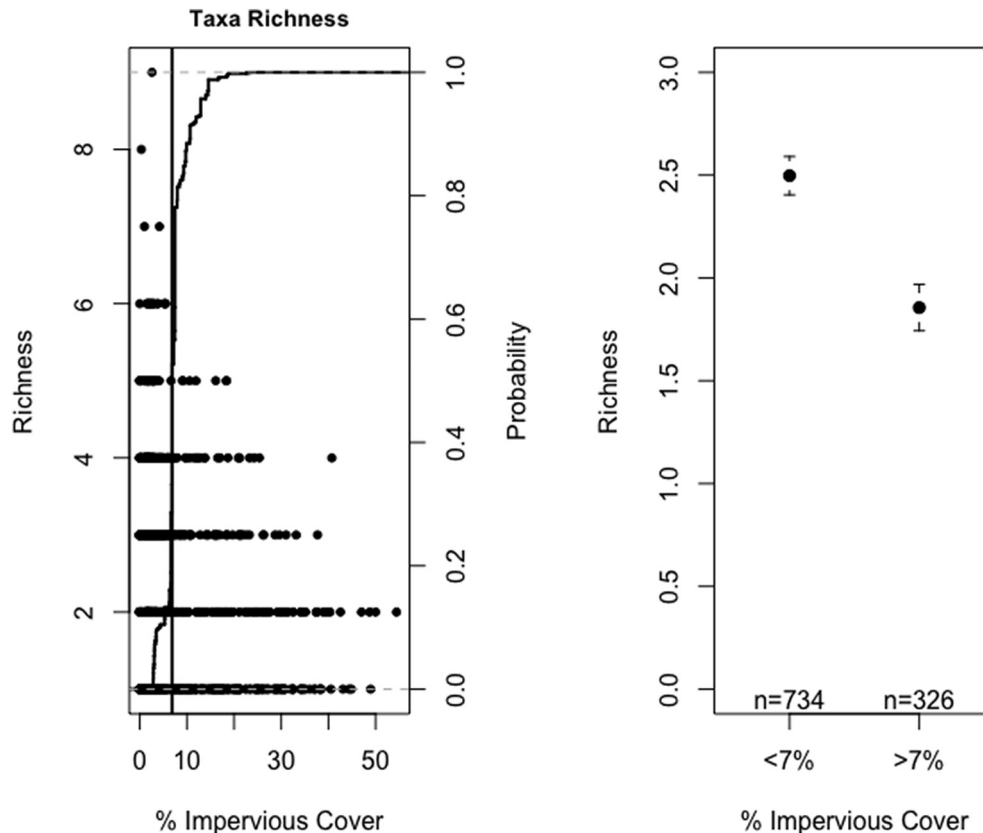


Fig. 2. Assemblage level taxonomic response to upstream impervious cover. Change point analysis identified the observed threshold (solid vertical line, left panel) and the cumulative probability that change has occurred. As stated, the closer the distribution is to the observed value, the more confident we can be in its estimation. Right panel is the mean and 95% confidence interval for taxonomic richness below and above the threshold of 7% impervious cover.

2.6. Data analysis

Our approaches to testing the hypotheses that taxonomic richness, phylogenetic diversity, and mean community-level evolutionary distinctiveness each decline with increasing percent of watershed impervious cover were identical. No linear relationship was found between any diversity metric and percent impervious cover. As such, we used nonparametric change point analysis (nCPA; King and Richardson, 2003) whereby each change point was identified by maximizing deviance reduction and hence the change in diversity across binary partitions. nCPA uses a permutation procedure to assess observed deviance reductions relative to those obtained from random selection of equivalent group sizes. We defined a detectable change in the mean and/or variance invertebrate diversity, coupled with uncertainty estimates, as an indication of an ecological threshold response to impervious cover. Because our data spanned gradients from very low (0%) impervious cover, to very high, we assumed that any such changes detected represented a significant deflection from 0% impervious cover conditions, and consequently, degradation of biological diversity.

Once a change point was detected and impervious cover threshold identified, a simple two-sample *t*-test was performed comparing the mean diversity below the threshold, or those diversities associated with low impervious cover, to the mean above the impervious cover threshold.

Confidence in the observed change point, as outlined by King and Richardson (2003), was assessed by cumulative probability distributions. Cumulative probability functions were used to represent variation in change point estimates obtained from 1000 bootstrap replicates. The percentile of any given location along the resulting curves corresponded to the specific cumulative probability of a change point. Greater alignment between the cumulative probability curve and the observed change point thus indicated the observed change point estimate, or impervious cover threshold, was more robust.

We assessed whether community-level phylogenetic composition shifted between below and above the threshold identified for phylogenetic diversity. We used permutational multivariate analysis of variance (PERMANOVA) with the ‘adonis’ function in the ‘vegan’ package (Oksanen et al., 2020) in R (R Core Team, 2020). Analysis was done by calculating MPD (mean pairwise distance) separating taxa into two communities, which is a measure of phylogenetic beta diversity, according to Webb et al. (2008). To test for differences in composition turnover in phylogenetic structure, which is an indication of phylogenetic homogenization, we used the ‘betadisper’ function as part of the “vegan” package in R (Team, 2014). All taxonomic and phylogenetic analyses were conducted in R v 3.3.3. (R Core Team, 2020). Statistical significance was assumed when $p < 0.05$.

3. Results

Our dataset comprised $n = 1060$ assemblages representing a sampling effort from 1995 to 2010 in Maryland, USA. Percent impervious cover was estimated for each drainage using a corresponding spatial timeseries (44). Regionally, we identified 33 taxa, with local communities ranging from 1 to 9 genera and a mean of 2.3 genera per site (standard deviation, $SD = 1.25$). Our phylogenetic tree was comprised of only insects, with representatives from the Plecoptera, Trichoptera, Ephemeroptera, Coleoptera and Diptera.

We learned from threshold analysis that both taxonomic and phylogenetic diversities declined with an increase in impervious cover. We identified points along impervious cover gradients at which both the magnitude and variance of diversity metrics were significantly reduced (King and Richardson, 2003). For taxonomic diversity, the observed threshold was estimated as 6.8% impervious cover (90% confidence interval, CI 3.0–12.9%) with a mean decline from 2.5 to 1.8 taxa ($p < 0.001$). Cumulative probability distributions generated from change point analysis

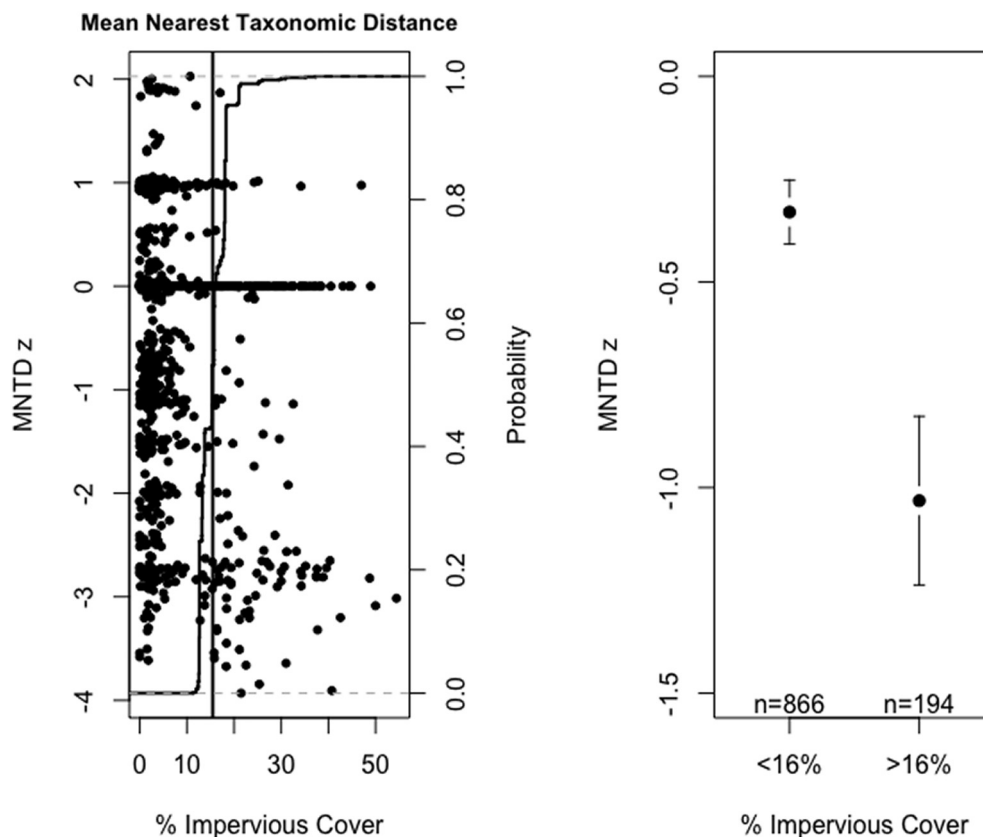


Fig. 3. Assemblage level phylogenetic diversity response as measured by mean nearest taxonomic distance z-score to upstream impervious cover. Change-point analysis identified the threshold (solid vertical line, left panel) and the cumulative probability that change has occurred. Right panel is the mean and 95% confidence interval for mean nearest taxonomic distance below and above the threshold of 16% impervious cover.

indicated that a threshold was also >50% probable at 6.8% impervious cover (Fig. 2). Phylogenetic diversity shifted downward at 12.7% impervious cover, becoming >50% probable at 15.4% of the watershed cover ($p < 0.001$; 90% CI 12.6–18.3%; Fig. 3). Furthermore, mean assemblage level phylogenetic distinctiveness was also reduced with increasing impervious cover, with an observed threshold of 7.4% becoming >50% probable at 7.8% ($p < 0.001$, 95% CI 6.8–12.9%; Fig. 4). Thus, although phylogenetic distinctiveness closely tracked patterns of taxonomic richness, phylogenetic diversity declined at somewhat higher levels of watershed impervious cover, with similar ranges of uncertainty (~6%).

Taxa loss alone did not account for loss of phylogenetic diversity under high impervious cover conditions (e.g., > 13–15%). Importantly, taxa occurring under low impervious cover, as ascertained via change-point analysis, were *less* closely related and more representative of the regional taxa pool than under high impervious cover. Taxa loss due to habitat degradation associated with watershed imperviousness can be compounded by not only losing taxa, but losing distantly related taxa in particular. Taxa with certain traits were lost. Consistent with strong environmental filtering, traits associated with sensitivity to certain habitat requirements are phylogenetically conserved, resulting in decreased success for taxa possessing these traits in degraded habitats imposed by increased impervious cover (Dinnage, 2009; Roy et al., 2005). Such traits with hypothesized implications include loss of taxa with gills, loss of taxa that prefer riffle habitats, and loss of eurythermal taxa, among others (Barnum et al., 2017). The result is a narrowing of not only the number of taxa that occur, but also the similarity of ecological traits that allow persistence under degraded habitat conditions.

Subsequent and complementary compositional analysis of phylogenetic turnover revealed (1) significantly different phylogenetic structures above and below the threshold of MNTD owing to a difference in centroid position

(Fig. 5), and (2) significantly reduced phylogenetic turnover taken as distance to centroid of each community, or gain and/or loss of evolutionarily related species compared between above and below the threshold of MNTD (Fig. 5). These findings are evidence of biotic homogenization (i.e., the simplification of species composition resulting from decreases in beta-diversity across sites), as predicted in other systems when habitat is degraded (McKinney and Lockwood, 1999).

4. Discussion

Our goal was learn how taxonomic and phylogenetic diversities of a freshwater guild of detritivorous invertebrates changes in response to the expansion of impervious land cover. We generated a phylogenetic tree for the regional taxa pool, then calculated taxonomic richness, phylogenetic diversity, and community-level phylogenetic distinctiveness for >1,000 stream communities. We learned that all three dimensions of biodiversity significantly declined with increasing impervious cover. Furthermore, multivariate analysis of phylogenetic structure revealed an overall shift in composition between low (<16% cover) and higher (>16%) impervious cover. Overall, increasing impervious cover on the landscape is associated with declines in the phylogenetic structure of this important guild of stream invertebrate consumers.

Because not enough time has passed for the evolution of traits suitable to habitat alterations following shifts to impervious cover, we suggest the following two explanations. The first is that species inhabiting streams with higher upstream impervious cover may have evolved traits similar to the habitat conditions that develop under increasing impervious drainage. That is, taxa that inhabit streams draining high levels of impervious cover may have evolved primarily in habitats that can reflect conditions generated by impervious cover. We view this explanation as unlikely as

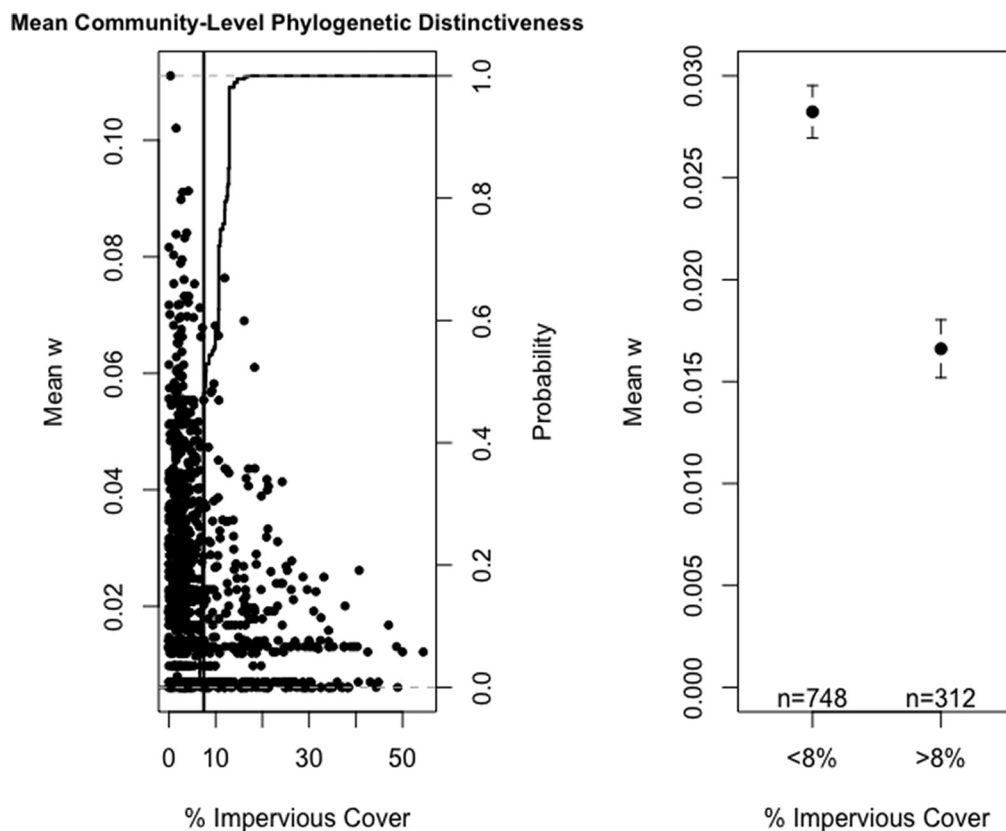


Fig. 4. Mean assemblage level phylogenetic distinctiveness in response to upstream impervious cover. Change point analysis identified the change point (solid vertical line, left panel) and the cumulative probability that change has occurred. Right panel is the mean and 95% confidence interval for mean assemblage level phylogenetic distinctiveness below and above the threshold of 8% impervious cover.

most genera in these taxonomic Orders do not tolerate the instream implications of upstream impervious cover. Such conditions include flashier flow regimes, simplification of habitat elements, increases in dissolved ions, sedimentation, shifts to warmer temperatures during summer months, or some combination of the above (Paul and Meyer, 2008). A few taxa (mostly restricted to Dipterans and one Coleopteran; Fig. 1) were found to have a high tolerance/affinity to streams with elevated upstream impervious cover, as a similar subset of the tolerant taxa identified by King et al. (2011) in a study of individual taxa responses to impervious cover in the same region studied here.

Second, in comparison to streams with low upstream impervious cover, habitats with high levels of upstream impervious cover are often less stable and more regularly disturbed (e.g., flooding, sedimentation, elevated pH, conductivity, and altered temperature; Moore et al., 2020; Griffith, 2017). Such habitat profiles could preclude sustained competition and favor related species with traits that allow them to persist in novel and highly variable environments (Paul and Meyer, 2008; Allan, 2004). Such traits include loss of taxa with gills, loss of eurythermal taxa, decreased drifting taxa, and increased multivoltine taxa (Barnum et al., 2017). This would indicate that assemblage-level functional diversity is expected to be lower in disturbed streams than in less impacted environments and, subsequently, that increasing impervious cover alters instream habitat conditions sufficiently to act as an ecological filter (King and Baker, 2010).

Our results indicate that increasing impervious cover associated with urbanization threatens evolutionarily distinct taxa (Fig. 4), aligning with many findings of the heightened threat landscape development has on instream biota at the taxonomic level (King et al., 2011; Paul and Meyer, 2008; Roy et al., 2005; Hansen et al., 2005). In contrast, taxa from more recently diversifying clades (e.g., the Diptera, Fig. 1) appear best able to persist in streams with higher upstream impervious cover and may actually benefit from landscape development. This may be due to the opening of

niche space (e.g., flow regimes), release from competition and/or predation owing to species loss, or other metabolic factors such as an increase in temperature associated with impervious cover. Nevertheless, persistence of some taxa from more recently diversifying lineages cannot mitigate overall taxonomic losses and the concomitant declines in phylogenetic diversity that accompany landscape development.

Areas minimally impacted by extensive land degradation brought on by increases in impervious surface cover and other land use alterations detrimental to taxonomic persistence are essential for preserving biodiversity and, as demonstrated here and elsewhere, phylogenetic diversity. In this study, we found that maintaining percent impervious cover below 16% can conserve phylogenetic diversity of stream detritivores in this region. However, ensuring sustainable levels of taxonomically distinct and phylogenetically diverse assemblages may require much lower levels (i.e., <7%) of development given the uncertainty depicted in change point probabilities and imprecision of richness as a measure of community change (King and Baker 2010). Until the process of urbanization and the causes of species loss are better understood, maintaining low levels of impervious cover in some watersheds may be crucial for allowing shredders to more efficiently process carbon in stream ecosystems (Utz et al., 2011; Srivastava et al., 2009).

Given that streams and rivers transport nearly 1.9 Pg C per year globally (Cole et al., 2007), understanding the primary drivers of carbon processing and factors that mediate carbon cycling is important. The freshwater consumer guild under study here, leaf shredding insects, is known to be instrumental to the carbon decay process and to exhibit substantial interspecific variation in feeding rates (Cummins and Klug, 1979). As such, the loss of just one species from this guild has potential to substantively influence carbon processing. Our analysis opens up the question as to whether the importance of functional diversity – here the variation in feeding rates among detritivore taxa – extends to the phylogenetic level. If so, it would

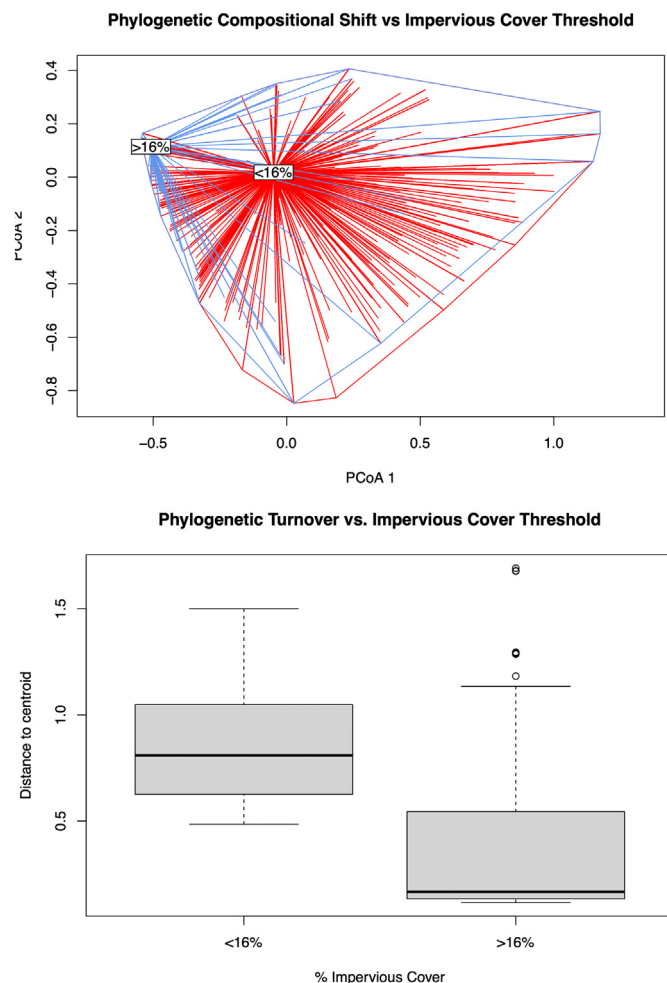


Fig. 5. To visualize phylogenetic homogenization, a principal coordinates analysis was performed and results plotted by group – above or below the observed threshold of 16% for phylogenetic diversity. Centroids are identified with red for those communities below the changepoint (i.e., associated with low impervious cover), and blue for those above. Labels cover the centroids. The bottom panel is a boxplot (median distance to centroid with interquartile range; range as whiskers) of phylogenetic turnover above and below the observed changepoint with 95% confidence interval clearly indicating lower turnover – or higher homogenization – in streams draining higher levels of impervious cover.

be important to understand how multiple dimensions of biodiversity contribute to important ecosystem processes.

CRediT authorship contribution statement

Christopher M. Swan: Conceptualization, Methodology, Investigation, Data curation, Writing- Original draft preparation, Writing- Reviewing and Editing. **Matthew Baker:** Methodology, Writing- Reviewing and Editing. **Dorothy Borowy:** Methodology, Investigation. **Anna Johnson:** Methodology, Investigation. **Mariya Shcheglovitova:** Methodology, Investigation. **April Sparkman:** Methodology, Investigation. **Francisco Valente Neto:** Methodology, Investigation. **Molly Van Appledorn:** Methodology, Investigation, Writing- Reviewing and Editing. **Nicole Voelker:** Methodology, Investigation.

Declaration of competing interest

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

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References

- Allan, J.D., 2004. Landscapes and riverscapes: the influence of land use on stream ecosystems. *Annu. Rev. Ecol. Evol. Syst.* 35, 257–284.
- Baker, M.E., Schley, M.L., Sexton, J.O., 2019. Impacts of expanding impervious surface on specific conductance in urbanizing streams. *Water Resour. Res.* 55, 6482–6498.
- Barnum, T.R., Weller, D.E., Williams, M., 2017. Urbanization reduces and homogenizes trait diversity in stream macroinvertebrate communities. *Ecol. Appl.* 27, 2428–2442.
- Britton, T., Anderson, C.L., Jacquet, D., Lundqvist, S., Bremer, K., 2007. Estimating divergence times in large phylogenetic trees. *Syst. Biol.* 56, 741–752.
- Brown, L.R., Gregory, M.B., May, J.T., 2009. Relation of urbanization to stream fish assemblages and species traits in nine metropolitan areas of the United States. *Urban Ecosyst.* 12, 391–416.
- Cadotte, M.W., Cardinale, B.J., Oakley, T.H., 2008. Evolutionary history and the effect of biodiversity on plant productivity. *Proc. Natl. Acad. Sci. U. S. A.* 105, 17012–17017.
- Cadotte, M.W., Jonathan Davies, T., Regetz, J., Kembel, S.W., Cleland, E., Oakley, T.H., 2010. Phylogenetic diversity metrics for ecological communities: integrating species richness, abundance and evolutionary history. *Ecol. Lett.* 13, 96–105.
- Cadotte, M.W., Dinnage, R., Tilman, D., 2012. Phylogenetic diversity promotes ecosystem stability. *Ecology* 93, S223–S233.
- Chase, J.M., McGill, B.J., Thompson, P.L., Antão, L.H., Bates, A.E., Blowes, S.A., Dornelas, M., Gonzalez, A., Magurran, A.E., Supp, S.R., Winter, M., Bjorkman, A.D., Bruehlheide, H., Byrnes, J.E.K., Cabral, J.S., Elahi, R., Gomez, C., Guzman, H.M., Isbell, F., Myers-Smith, I.H., Jones, H.P., Hines, J., Vellend, M., Walck, C., O'Connor, M., 2019. Species richness change across spatial scales. *Oikos* 128, 1079–1091.
- Cole, J.J., Prairie, Y.T., Caraco, N.F., McDowell, W.H., Tranvik, L.J., Striegl, R.G., Duarte, C.M., Kortelainen, P., Downing, J.A., Middelburg, J.J., Melack, J., 2007. Plumbing the global carbon cycle: integrating inland waters into the terrestrial carbon budget. *Ecosystems* 10, 172–185.
- Cross, W.F., Wallace, J.B., Rosemond, A.D., Eggert, S.L., 2006. Whole-system nutrient enrichment increases secondary production in a detritus-based ecosystem. *Ecology* 87, 1556–1565.
- Cuffney, T.F., Bilger, M.D., Haigler, A.M., 2007. Ambiguous taxa: effects on the characterization and interpretation of invertebrate assemblages. *J. North Am. Benthol. Soc.* 26, 286–307.
- Cummins, K.W., Klug, M.J., 1979. Feeding ecology of stream invertebrates. *Annu. Rev. Ecol. Syst.* 10, 147–172.
- Dinnage, R., 2009. Disturbance alters the phylogenetic composition and structure of plant communities in an old field system. *PLoS One* 4, e7071.
- Faith, D.P., 1992. Conservation evaluation and phylogenetic diversity. *Biol. Conserv.* 61, 1–10.
- Fox, D., 2007. Back to the no-analog future? *Science* 316, 823–825.
- Fry, J.A., Xian, G., Jin, S.M., Dewitz, J.A., Homer, C.G., Yang, L.M., Barnes, C.A., Herold, N.D., Wickham, J.D., Others, 2011. Completion of the 2006 national land cover database for the conterminous United States. *Photogramm. Eng. Remote. Sens.* 77, 858–864.
- Griffith, M.B., 2017. Toxicological perspective on the osmoregulation and ionoregulation physiology of major ions by freshwater animals: teleost fish, crustacea, aquatic insects, and mollusca. *Environ. Toxicol. Chem.* 36, 576–600.
- Hansen, A.J., Knight, R.L., Marzluff, J.M., Powell, S., Brown, K., Gude, P.H., Jones, K., 2005. Effects of exurban development on biodiversity: patterns, mechanisms, and research needs. *Ecol. Appl.* 15, 1893–1905.
- Hobbs, R.J., Higgs, E., Harris, J.A., 2009. Novel ecosystems: implications for conservation and restoration. *Trends Ecol. Evol.* 24, 599–605.
- Hodgson, M.E., Jensen, J.R., Tullis, J.A., Riordan, K.D., Archer, C.M., 2003. Synergistic use of LiDAR and color aerial photography for mapping urban parcel imperviousness. *Photogramm. Eng. Remote Sens.* 69, 973–980.
- Jonsson, M., Malmqvist, B., 2003. Mechanisms behind positive diversity effects on ecosystem functioning: testing the facilitation and interference hypotheses. *Oecologia* 134, 554–559.
- Jonsson, M., Malmqvist, B., Hoffsten, P.-O., 2001. Leaf litter breakdown rates in boreal streams: does shredder species richness matter? *Freshw. Biol.* 46, 161–171.
- Jonsson, M., Dangles, O., Malmqvist, B., Guérol, F., 2002. Simulating species loss following perturbation: assessing the effects on process rates. *Proc. Biol. Sci.* 269, 1047–1052.
- Katoh, K., Standley, D.M., 2013. MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Mol. Biol. Evol.* 30, 772–780.
- King, R.S., Richardson, C.J., 2003. Integrating bioassessment and ecological risk assessment: an approach to developing numerical water-quality criteria. *Environ. Manag.* 31, 795–809.
- King, R.S., Baker, M.E., 2010. Considerations for analyzing ecological community thresholds in response to anthropogenic environmental gradients. *J. North Am. Benthol. Soc.* 29, 998–1008.

- King, R.S., Baker, M.E., Kazyak, P.F., Weller, D.E., 2011. How novel is too novel? Stream community thresholds at exceptionally low levels of catchment urbanization. *Ecol. Appl.* 21, 1659–1678.
- Klauda, R., Kazyak, P., Stranko, S., Southerland, M., Roth, N., Chaillou, J., 1998. Maryland biological stream survey: a state agency program to assess the impact of anthropogenic stresses on stream habitat quality and biota. *Environ. Monit. Assess.* 51, 299–316.
- Kraft, N.J.B., et al., 2007. Trait evolution, community assembly, and the phylogenetic structure of ecological communities. *Am. Nat.* 170, 271–283.
- Larkin, M.A., Blackshields, G., Brown, N.P., Chenna, R., McGettigan, P.A., McWilliam, H., Valentin, F., Wallace, I.M., Wilm, A., Lopez, R., Thompson, J.D., Gibson, T.J., Higgins, D.G., 2007. Clustal W and clustal X version 2.0. *Bioinformatics* 23, 2947–2948.
- Larsen, D.P., Herlihy, A.T., 1998. The dilemma of sampling streams for macroinvertebrate richness. *J. North Am. Benthol. Soc.* 17, 359–366.
- Maryland Department of Natural Resources, 2000. Laboratory methods for benthic macroinvertebrate processing and taxonomy title. CBWP-MANTA-EA-00-6. Monitoring and Nontidal Assessment Division. Monitoring and Non-tidal Assessment Division, Ecological Assessment Program, Annapolis, Maryland, USA.
- McKinney, M.L., Lockwood, J.L., 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends Ecol. Evol.* 14, 450–453.
- Moore, J., Fanelli, R.M., Sekellick, A.J., 2020. High-frequency data reveal deicing salts drive elevated specific conductance and chloride along with pervasive and frequent exceedances of the U.S. Environmental Protection Agency aquatic life criteria for chloride in urban streams. *Environ. Sci. Technol.* 54, 778–789.
- Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., 2020. *vegan: Community Ecology Package*.
- Ostermiller, J.D., Hawkins, C.P., 2004. Effects of sampling error on bioassessments of stream ecosystems: application to RIVPACS-type models. *J. North Am. Benthol. Soc.* 23, 363–382.
- Paul, M.J., Meyer, J.L., 2008. Streams in the urban landscape. In: Marzluff, J.M., Shulenberger, E., Endlicher, W., Alberti, M., Bradley, G., Ryan, C., Simon, U., ZumBrunnen, C. (Eds.), *Urban Ecology: An International Perspective on the Interaction between Humans and Nature*. Springer, US, Boston, MA, pp. 207–231.
- Pearse, W.D., Purvis, A., 2013. phyloGenerator: an automated phylogeny generation tool for ecologists. *Methods Ecol. Evol.* 4, 692–698.
- Purvis, A., Agapow, P.M., Gittleman, J.L., Mace, G.M., 2000. Nonrandom extinction and the loss of evolutionary history. *Science* 288, 328–330.
- R Core Team, 2020. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Reichstein, M., et al., 2014. Linking plant and ecosystem functional biogeography. *Proc. Natl. Acad. Sci. U. S. A.* 111, 13697–13702.
- Roth, N.E., Southerland, M.T., Mercurio, G., Volstad, J.H., 2001. *Maryland biological stream survey 2000–2004. Volume 6: Laboratory, Field and Analytical Methods*. DNR-12-0305-0108. Maryland Department of Natural Resources, Monitoring and Non-tidal Assessment Division, Annapolis, Maryland, USA.
- Roy, A.H., Freeman, M.C., Freeman, B.J., Wenger, S.J., Ensign, W.E., Meyer, J.L., 2005. Investigating hydrologic alteration as a mechanism of fish assemblage shifts in urbanizing streams. *J. North Am. Benthol. Soc.* 24, 656–678.
- Sexton, J.O., Song, X.-P., Huang, C., Channan, S., Baker, M.E., Townshend, J.R., 2013. Urban growth of the Washington, D.C.–Baltimore, MD metropolitan region from 1984 to 2010 by annual, landsat-based estimates of impervious cover. *Remote Sens. Environ.* 129, 42–53.
- Srivastava, D.S., Cardinale, B.J., Downing, A.L., Duffy, J.E., Jouseau, C., Sankaran, M., Wright, J.P., 2009. Diversity has stronger top-down than bottom-up effects on decomposition. *Ecology* 90, 1073–1083.
- Stamatakis, A., 2014. RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* 30, 1312–1313.
- Stamatakis, A., Hoover, P., Rougemont, J., 2008. A rapid bootstrap algorithm for the RAxML web servers. *Syst. Biol.* 57, 758–771.
- Talevich, E., Invergo, B.M., Cock, P.J.A., Chapman, B.A., 2012. Bio. Phylo: a unified toolkit for processing, analyzing and visualizing phylogenetic trees in biopython. *BMC Bioinformatics* 13, 209.
- Utz, R.M., Eshleman, K.N., Hilderbrand, R.H., 2011. Variation in physicochemical responses to urbanization in streams between two mid-Atlantic physiographic regions. *Ecol. Appl.* 21, 402–415.
- Utz, R.M., Hopkins, K.G., Beesley, L., Booth, D.B., Hawley, R.J., Baker, M.E., Freeman, M.C., Jones, K.L., 2016. Ecological resistance in urban streams: the role of natural and legacy attributes. *Freshwater Sci.* 35 (1), 380–397.
- Wallace, J.B., Eggert, S.L., Meyer, J.L., Webster, J.R., 1997. Multiple trophic levels of a forest stream linked to terrestrial litter inputs. *Science* 277, 102–104.
- Walsh, C.J., Roy, A.H., Feminella, J.W., Cottingham, P.D., Groffman, P.M., Morgan, R.P., 2005. The urban stream syndrome: current knowledge and the search for a cure. *J. North Am. Benthol. Soc.* 24, 706–723.
- Webb, C.O., Ackerly, D.D., Kembel, S.W., 2008. Phylocom: software for the analysis of phylogenetic community structure and trait evolution. *Bioinformatics* 18, 2098–2100.
- Williams, J.W., Jackson, S.T., 2007. Novel climates, no-analog communities, and ecological surprises. *Front. Ecol. Environ.* 5, 475–482.