

1 **Loss of Phylogenetic Diversity under Landscape Change**

2 Christopher M. Swan^{1*}, Matthew Baker¹, Dorothy Borowy², Anna Johnson³, Mariya Shcheglovitova⁴, April
3 Sparkman¹, Francisco Valente Neto⁵, Molly Van Appledorn⁶, Nicole Voelker¹

4
5 ¹Department of Geography & Environmental Systems
6 University of Maryland, Baltimore County
7 Baltimore, Maryland 21250 USA

8
9 ²Natural Resources & Science,
10 National Capital Area-Region 1,
11 National Park Service
12 4598 MacArthur Blvd., NW
13 Washington D.C. 20007 USA

14
15 ³Pennsylvania Natural Heritage Program
16 Western Pennsylvania Conservancy
17 Pittsburgh, PA 15222 USA

18
19 ⁴Department of Environment and Society
20 5215 Old Main Hill
21 Utah State University
22 Logan, UT 84322-5215 USA

23
24 ⁵Laboratório de Ecologia, Instituto de Biociências,
25 Universidade Federal de Mato Grosso do Sul,
26 Caixa Postal 549, Campo Grande, Mato Grosso do Sul CEP
27 79070-900, Brazil

28
29 ⁶U.S. Geological Survey
30 Upper Midwest Environmental Sciences Center
31 2630 Fanta Reed Road
32 La Crosse WI 54603

33
34 *Christopher M. Swan
35 Department of Geography & Environmental Systems
36 211 Sondheim Hall
37 1000 Hilltop Circle
38 University of Maryland, Baltimore County
39 Baltimore, Maryland 21250 USA

40
41 **Email:** Chris.Swan@umbc.edu

42
43
44
45
46
47
48
49
50
51
52
53
54
55
56

57 **Abstract**

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

71

72 **Keywords:** biodiversity, detritivores, impervious cover, species loss, streams

73

74 **1. Introduction**

75 As humans increasingly convert the Earth’s surface, the fate of global biodiversity will greatly depend on
76 whether organismal guilds are able to withstand or adapt to habitat changes and whether humans are
77 able to conserve habitats within a range of species’ tolerances. This paper contributes to research on
78 biodiversity loss and resilience by asking whether novel disturbance regimes in riverine systems alter
79 habitats sufficiently to transform the composition and phylogenetic structure of organismal guilds (Fox,
80 2007). Riverine systems vary widely in their ability to support biodiversity, with many species extirpated
81 due to disturbance events, shifting habitat in space and time, or loss of suitable habitat altogether (Hobbs
82 et al., 2009; Williams and Jackson, 2007). In addition, characteristics of the species themselves have

83 evolved over millions of years and may predispose some lineages to suffer or benefit from habitat
84 alteration (McKinney and Lockwood, 1999; Purvis et al., 2000).

85
86 One of the primary causes of biodiversity loss is the loss or degradation of habitats (Chase et al., 2019;
87 Reichstein et al., 2014). In built environments, the degree of impervious land cover in a contributing area
88 is strongly associated with altered habitat conditions in downstream waterways, specifically the frequency
89 and intensity of disturbance events in rivers and streams (Baker et al., 2019; Utz et al., 2011; Walsh et al.,
90 2005; Paul and Meyer, 2008; Roy et al., 2005). Furthermore, changes to water routing and flow regimes
91 produce complex changes in local habitat conditions (Paul and Meyer, 2008); these can include changes
92 in the relative balance of erosional versus depositional forces, shifts in the size distribution of substrates
93 (Utz et al., 2016), increases in solute concentrations, and altered temperature regimes (Paul and Meyer,
94 2008). Research has shown a link between watershed urbanization and significant loss of biodiversity in
95 bottom-dwelling invertebrates as well as fish species (Paul and Meyer, 2008; Brown et al., 2009). This
96 has been important to recognize as many stream invertebrates are particularly critical trophic links
97 between basal resources and higher trophic levels (Wallace et al., 1997).

98
99 Decades of research have led to the conclusion that species loss can substantially alter the magnitude of
100 important ecosystem processes for several reasons (e.g., Utz et al., 2016; Srivastava et al., 2009). For
101 example, the more species in an assemblage, the more efficiently the assemblage as a whole can
102 contribute to ecosystem processing of carbon and other nutrients. Such niche complementarity has been
103 demonstrated for detritivores in rivers (Jonsson and Malmqvist, 2003; Jonsson et al., 2001). Detritivorous
104 “shredders” are a functional feeding group known to be important for the processing of externally derived
105 carbon - namely senesced leaf litter from streamside vegetation (Wallace et al., 1997; Cummins and Klug,
106 1979). Breakdown of litter liberates energy necessary to sustain higher trophic levels (Wallace et al.,

107 1997; Cross et al., 2006). As such, species loss from this functional group can have important
108 consequences for stream food- web dynamics (Jonsson et al., 2002).

109
110 Research linking land-use change to stream biota has predominantly focused on taxonomic diversity.
111 With the development of new and more widely accepted techniques for understanding evolutionary
112 relatedness among species, ecologists are turning to the phylogenetic structure of local assemblages to
113 learn not only if habitat degradation results in species loss, but whether remaining species are more or
114 less evolutionarily distinct (Purvis et al., 2000). Phylogenetic diversity represents an ecological
115 community's total evolutionary history, commonly taken as the sum total of branch lengths within its
116 phylogenetic tree (Cadotte et al., 2010), and is now considered to have important and relevant
117 conservation value (Faith, 1992). Experiments at fine scales indicate that increasing the phylogenetic
118 diversity of a local community - independent of species diversity - can lead to greater persistence after a
119 disturbance, generate higher productivity in plants, and even sustain more species at higher trophic levels
120 (Cadotte et al., 2008; Cadotte et al., 2012). However, the consequences of broader habitat modification
121 on local phylogenetic structure remain largely unknown. Are those species most at risk of being affected
122 by land-use change more evolutionarily distinct compared to others in an assemblage with high
123 relatedness? This question has yet to be systematically explored in the literature.

124
125 Here, we sought to learn how taxonomic and phylogenetic structure of freshwater detritivore communities
126 shift in response to landscape change, specifically the expansion of impervious cover. We used a large
127 stream-monitoring dataset collected to support assessment of benthic biological integrity (Klauda et al.,
128 1998). After developing a phylogenetic tree for detritivores (Fig. 1), we calculated local phylogenetic
129 diversity (indicated by mean nearest taxonomic distance, MNTD) and the assemblage-level mean
130 phylogenetic distinctiveness. We predicted that (1) consistent with the literature, taxonomic richness
131 would decline with increasing impervious cover draining to the sample location, (2) phylogenetic diversity
132 would also decline in a similar manner, and (3) so too would mean evolutionary distinctiveness. We
133 predicted declines in both phylogenetic diversity and evolutionary distinctiveness in addition to taxonomic
134 richness because we expected habitat shifts from increasing impervious cover would be sufficient to

135 narrow environmental adaptations of detritivores such that only a select few, closely related species could
136 coexist.

137

138 **2. Materials and Methods**

139 **2.1 Data Source & Collection**

140 We conducted an analysis using abundance data for macroinvertebrate taxa from 1,060 stream reaches
141 sampled by the Maryland Biological Stream Survey (MBSS; Klauda et al., 1998). The MBSS is a stream-
142 monitoring program based on probabilistic sampling stratified by major basins and stream order (first to
143 third order on a 1:250,000 stream map during 1995–1997 and first to fourth order on a 1:100,000 stream
144 map during 2000–2003). Sampling locations were randomly assigned to non-overlapping, 75-m stream
145 segments in the Piedmont physiographic region across the state of Maryland. Within each randomly
146 selected segment, the survey included rapid-assessment metrics of stream physical characteristics,
147 conventional water chemistry, in-stream habitat, discharge, and macroinvertebrate assemblage
148 composition (2-m² sample collected with a 500- μ m D-framed dip net from favorable habitat. All
149 macroinvertebrates were classified using genus-level identification and 100-organism, fixed-count
150 methods (Maryland Department of Natural Resources, 2000). All of the selected sites were sampled once
151 during 1995–2006, a period that overlapped with the 1985–2010 satellite imagery used to quantify
152 impervious cover (see below). Greater details on data collection methods and quality assurance and
153 quality control are provided in Roth et al. (2001).

154

155 Macroinvertebrate data were screened for consistency prior to analysis and ambiguous taxa were
156 resolved following the operational-taxonomic-unit approach method of Cuffney et al. (2007). Individuals
157 were identified to the level of genus as is the standard for the larval stage because adult features are
158 required for identification to species level (Maryland Department of Natural Resources, 2000). If more
159 than 100 individuals were enumerated for a stream reach, we used a computer-generated random
160 sampling procedure to select of subsample of 100 individuals (Ostermiller and Hawkins, 2004) to ensure
161 that individual taxa frequencies and abundances were expressed consistently for all sample units
162 because both depend on the number of individuals in the subsample (Larsen and Herlihy, 1998).

163 Samples with fewer than 100 individuals were not altered because they represent stream reaches with
164 low densities of individuals possibly due to anthropogenic stressors, including catchment imperviousness.
165

166 **2.2 Phylogenetic Tree Construction**

167 A list of target genera was created by selecting those from the master dataset designated as shredders
168 by the MBSS. Only insects were included in the analysis. We used the command-line program
169 phyloGenerator (Pearse and Purvis, 2013) to create a phylogenetic tree. The method for the creation of
170 this tree is based on the BioPython framework (Talevich et al., 2012) and automates the retrieval of
171 sequence information from GenBank, in addition to automating alignment and phylogenetic tree
172 estimation. We constructed our tree based on five commonly sequenced genes, COI, 16S, 18S, 28S, and
173 H3. The trimmed sequences were aligned using MAFFT (Kato and Standley, 2013) after being visually
174 examined for misalignment using ClustalX (Larkin et al., 2007). We then generated a maximum likelihood
175 tree with RaxML (Stamatakis, 2014) using 1,000 accelerated bootstrap replicates (Stamatakis et al.,
176 2008) and constrained the final tree based on a taxonomic tree. Finally, we rate-smoothed the resulting
177 tree to be ultrametric using the PATHd8 algorithm, with the *Apis* genus set as an outgroup (Britton et al.,
178 2007).

179

180 **2.3 Phylogenetic Diversity & Taxonomic Richness**

181 Phylogenetic diversity was calculated as the total branch length of all genera observed for each
182 assemblage. We calculated the abundance-weighted mean nearest taxon distance (MNTD). MNTD
183 measures the mean distance between each taxon's closest relative in a community, and thus focuses on
184 similarity between co-occurring genera. The number of genera in a community and the structure of the
185 phylogeny of the regional taxa pool can influence both metrics (Kraft et al., 2007; Cadotte et al., 2010). To
186 remove effects of richness and regional phylogenetic structure, we compared observed MNTD against
187 metrics calculated from null communities. We generated null communities by randomly drawing the same
188 number of genera as observed at each site from the regional pool. The probability of drawing a taxon was
189 proportional to the frequency that the taxon occurred within sampling strata (basin) that defined the
190 regional taxa pool. Next, we calculated MNTD for all 1,000 null community sites and expressed our

191 results as the standardized effect size (z). Taxonomic richness was chosen as the measure of diversity
192 for the study. Here, this is taken as the number of taxa at each site.

193

194 **2.4 Mean Phylogenetic Distinctiveness**

195 We quantified the evolutionary distinctness of each genera using the fair proportion metric (Cadotte et al.,
196 2010), which is the weighted sum of the edge lengths along the path from the root of an ultra-metric tree
197 to a leaf. The weights are $1/\text{number of genera that share that edge}$. We then calculated this value for
198 each genera occurring at a site. The mean for the assemblage was taken and then related to impervious
199 cover.

200

201 **2.5 Analysis of Impervious Cover**

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

217

218 Contributing areas for each stream sampling site were delineated using the 1/3-arc-second DEM
219 resolution, which is approximately the 10-m resolution obtained from the National 3D Elevation Program
220 (3DEP; <https://www.sciencebase.gov/catalog/item/4f70aa9fe4b058caae3f8de5>). DEMs were
221 hydrologically corrected by filling internal drainages, deriving a flow direction field, and accumulating
222 drainage. The contributing area upstream from each sample point was delineated following its manual
223 alignment with the closest flow line and was used to summarize the proportion of impervious cover for
224 each year in the impervious time series.

225

226 **2.6 Data Analysis**

227 Our approaches to testing the hypothesis that taxonomic richness, phylogenetic diversity, and mean
228 community-level distinctiveness declines with increasing percent of watershed impervious cover were
229 identical. No linear relationship was found between any diversity metric and percent impervious cover. As
230 such, we used nonparametric changepoint analysis (nCPA; King and Richardson, 2003) whereby each
231 changepoint was identified by maximizing deviance reduction and hence the change in diversity across
232 binary partitions. nCPA uses a permutation procedure to assess observed deviance reduction relative to
233 those obtained from random selection of equivalent group sizes. We defined a detectable change in the
234 mean and/or variance invertebrate diversity, coupled with uncertainty estimates, as an indication of an
235 ecological threshold response to impervious cover. Because our data spanned gradients from very low,
236 0% impervious cover to very high, we assumed that any such changes detected represented a significant
237 deflection from 0% impervious cover conditions, and consequently, degradation of biological diversity.

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

241

242 Confidence in the observed changepoint, as outlined by King and Richardson (2003), was assessed by
243 cumulative probability distributions. Cumulative probability functions were used to represent variation in
244 changepoint estimates obtained from 1,000 bootstrap replicates. The percentile of any given location
245 along the resulting curves corresponded to the specific cumulative probability of a changepoint. Greater

246 alignment between the cumulative probability curve and the observed changepoint thus indicated the
247 observed changepoint estimate, or impervious cover threshold was more robust.

248

249 We assessed whether community-level phylogenetic composition shifted between below and above the
250 threshold identified for phylogenetic diversity. We used permutational multivariate analysis of variance
251 (PERMANOVA) with the 'adonis' function in the 'vegan' package (Oksanen et al 2020) in R (R Core
252 Team, 2020). Analysis was done on the phylogenetic cophenetic distance matrix. To test for differences
253 in composition turnover in phylogenetic structure, which is an indication of phylogenetic homogenization,
254 we used the 'betadisper' function as part of the "vegan" package in R (R Core Team, 2014). All
255 taxonomic and phylogenetic analyses were conducted in R v 3.3.3. (R Core Team, 2020). Statistical
256 significance was assumed when $p < 0.05$.

257

258 **3. Results**

259 Our dataset comprised $n=1,060$ assemblages representing a sampling effort from 1995 to 2010 in
260 Maryland, USA. Percent impervious cover was estimated for each drainage using a corresponding spatial
261 timeseries (44). Regionally, we identified 33 taxa, with local communities ranging from 1-9 genera and a
262 mean of 2.3 genera per site (standard deviation, $SD=1.25$). Our phylogenetic tree was composed of only
263 insects, with representatives from the Plecoptera, Trichoptera, Ephemeroptera, Coleoptera, and Diptera.

264

265 We learned from threshold analysis that both taxonomic and phylogenetic diversities declined with an
266 increase in impervious cover. We identified points along impervious cover gradients at which both the
267 magnitude and variance of diversity metrics were significantly reduced (King and Richardson, 2003). For
268 taxonomic diversity, the observed threshold was estimated as 6.8% impervious cover (90% confidence
269 interval, CI 3.0-12.9%) with a mean decline from 2.5 to 1.8 taxa ($p < 0.001$). Cumulative probability
270 distributions generated from changepoint analysis indicated that a threshold was also >50% probable at
271 6.8% impervious cover (Fig. 2). Phylogenetic diversity shifted downward at 12.7% impervious cover,
272 becoming >50% probable at 15.4% of the watershed cover ($p < 0.001$; 90% CI 12.6-18.3%; Fig. 3).

273 Furthermore, mean assemblage level phylogenetic distinctiveness was also reduced with increasing

274 impervious cover, with an observed threshold of 7.4% becoming >50% probable at 7.8% ($p < 0.001$, 95%
275 CI 6.8-12.9%; Fig. 4). Thus, although phylogenetic distinctiveness closely tracked patterns of taxonomic
276 richness, phylogenetic diversity declined at somewhat higher levels of watershed impervious cover, with
277 similar ranges of uncertainty (~6%).

278

279 Taxa loss alone did not account for loss of phylogenetic diversity under high impervious cover conditions
280 (e.g., > 13-15%). Importantly, taxa occurring under low impervious cover, as ascertained via changepoint
281 analysis, were *less* closely related and more representative of the regional taxa pool than under high
282 impervious cover. Our finding indicates that taxa loss due to habitat degradation associated with
283 watershed imperviousness can be compounded by not only losing taxa, but losing distantly related taxa in
284 particular. This observation is consistent with strong environmental filtering, whereby traits associated
285 with sensitivity to certain habitat requirements are phylogenetically conserved, resulting in decreased
286 success for taxa possessing these traits in degraded habitats imposed by increased impervious cover
287 (Dinnage, 2009; Roy et al., 2005). Such traits with hypothesized implications include loss of taxa with
288 gills, loss of taxa that prefer riffle habitats, and loss of eurythermal taxa, among others (Barnum et al.,
289 2018) The result is a narrowing of not only the number of taxa that occur, but also the similarity of
290 ecological traits that allow persistence under degraded habitat conditions.

291

292 Subsequent and complementary compositional analysis of phylogenetic turnover revealed (1) significantly
293 different phylogenetic structures above and below the threshold of MNTD, and (2) significantly reduced
294 phylogenetic turnover, or gain and/or loss of evolutionarily related species from one assemblage to the
295 next (Fig. 5). These findings are evidence of biotic homogenization (i.e., the simplification of species
296 composition resulting from decreases in beta-diversity across sites) as predicted in other systems when
297 habitat is degraded (McKinney and Lockwood, 1999).

298

299 **4. Discussion**

300 Our goal was to learn how taxonomic and phylogenetic diversities of a freshwater guild of detritivorous
301 invertebrates changes in response to the expansion of impervious land cover. We generated a

302 phylogenetic tree for the regional taxa pool, then calculated taxonomic richness, phylogenetic diversity,
303 and community-level phylogenetic distinctiveness for >1,000 stream communities. We learned that all
304 three dimensions of biodiversity significantly declined with increasing impervious cover. Furthermore,
305 multivariate analysis of phylogenetic structure revealed an overall shift in composition between low (<16%
306 cover) and higher (>16%) impervious cover. Overall, increasing impervious cover on the landscape is
307 associated with declines in the phylogenetic structure of this important guild of stream invertebrate
308 consumers.

309
310 We offer two possible explanations for why evolutionarily distinct species and phylogenetic diversity are
311 expected to decline under landscape change. The first is that species inhabiting streams with higher
312 upstream impervious cover may have evolved traits suitable to the habitat conditions that develop under
313 increasing impervious drainage. That is, taxa that inhabit streams draining high levels of impervious cover
314 may have evolved primarily in habitats that can reflect conditions generated by impervious cover. We
315 view this explanation as unlikely as most genera in these taxonomic Orders do not tolerate the instream
316 implications of upstream impervious cover. Such conditions include flashier flow regimes, simplification of
317 habitat elements, increases in dissolved ions, sedimentation, shifts to warmer temperatures during
318 summer months, or some combination of the above (Paul and Meyer, 2008). A few taxa (mostly restricted
319 to Dipterans and one Coleopteran; Fig. 1) were found to have a high tolerance/affinity to streams with
320 elevated upstream impervious cover, as a similar subset of the tolerant taxa identified by King et al.
321 (2011) in a study of individual taxa responses to impervious cover in the same region studied here.

322
323 Second, in comparison to streams with low upstream impervious cover, habitats with high levels of
324 upstream impervious cover are often less stable and more regularly disturbed (e.g., flooding,
325 sedimentation, elevated pH, conductivity, and altered temperature; Moore et al., 2020; Griffith, 2017).
326 Such habitat profiles could preclude sustained competition and favor related species with traits that allow
327 them to persist in novel and highly variable environments (Paul and Meyer, 2008; Allan, 2004). Such traits
328 include loss of taxa with gills, loss of eurythermal taxa, decreased drifting taxa, and increased multivoltine
329 taxa (Barnum et al. 2017). This would indicate that assemblage-level functional diversity is expected to be

330 lower in disturbed streams than in less impacted environments and, subsequently, that increasing
331 impervious cover alters instream habitat conditions sufficiently to act as an ecological filter (King and
332 Baker, 2010).

333
334 Our results indicate that increasing impervious cover associated with urbanization threatens evolutionarily
335 distinct taxa (Fig. 4), aligning with many findings of the heightened threat landscape development has on
336 instream biota at the taxonomic level (King et al., 2011; Paul and Meyer, 2008; Roy et al., 2005; Hansen
337 et al., 2005). In contrast, taxa from recently diversifying clades (e.g., the Diptera) appear best able to
338 persist in streams with higher upstream impervious cover and may benefit from landscape development.
339 This may be due to the opening of niche space (e.g., flow regimes), release from competition and/or
340 predation owing to species loss, or other metabolic factors such as an increase in temperature associated
341 with impervious cover. Nevertheless, persistence of some taxa from younger lineages cannot mitigate
342 overall taxonomic losses and the concomitant declines in phylogenetic diversity that accompany
343 landscape development.

344
345 Areas minimally impacted by extensive land degradation brought on by increases in impervious surface
346 cover and other land use alterations detrimental to taxonomic persistence are essential for preserving
347 biodiversity and, as demonstrated here and elsewhere, phylogenetic diversity. In this study, we found that
348 maintaining percent impervious cover below 16% can conserve phylogenetic diversity of stream
349 detritivores in this region. However, ensuring sustainable levels of taxonomically distinct and
350 phylogenetically diverse assemblages may require much lower levels (i.e., <7%) of development given
351 the uncertainty depicted in changepoint probabilities and imprecision of richness as a measure of
352 community change (King and Baker 2010). Until the process of urbanization and the causes of species
353 loss are better understood, maintaining low levels of impervious cover in some watersheds may be crucial
354 for allowing shredders to more efficiently process carbon in stream ecosystems (Utz et al., 2011;
355 Srivastava et al., 2009).

356

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

366

367 **5. Acknowledgments**

368 Funding for this project was provided through NSF LTER grant no. DEB-1027188. The opinions and
369 findings expressed in this paper are those of the authors and not of the National Science Foundation but
370 do represent the views of the U.S. Geological Survey. Any use of trade, firm, or product names is for
371 descriptive purposes only and does not imply endorsement by the U.S. Government.

372

373

374 **6. References**

375

376 Allan, J.D., 2004. Landscapes and riverscapes: The influence of land use on stream ecosystems. *Annu.*
377 *Rev. Ecol. Evol. Syst.* 35, 257–284.

378

379 Baker, M.E., Schley, M.L., Sexton, J.O., 2019. Impacts of expanding impervious surface on specific
380 conductance in urbanizing streams. *Water Resour. Res.* 55, 6482–6498.

381

382 Barnum, T.R., Weller, D.E., Williams, M., 2017. Urbanization reduces and homogenizes trait diversity in
383 stream macroinvertebrate communities. *Ecol. Appl.* 27, 2428–2442.

384

385 Britton, T., Anderson, C.L., Jacquet, D., Lundqvist, S., Bremer, K., 2007. Estimating divergence times in
386 large phylogenetic trees. *Syst. Biol.* 56, 741–752.
387

388 Brown, L.R., Gregory, M.B., May, J.T., 2009. Relation of urbanization to stream fish assemblages and
389 species traits in nine metropolitan areas of the United States. *Urban Ecosyst.* 12, 391–416.
390

391 Cadotte, M.W., Cardinale, B.J., Oakley, T.H., 2008. Evolutionary history and the effect of biodiversity on
392 plant productivity. *Proc. Natl. Acad. Sci. U. S. A.* 105, 17012–17017.
393

394 Cadotte, M.W., Dinnage, R., Tilman, D., 2012. Phylogenetic diversity promotes ecosystem stability.
395 *Ecology* 93, S223–S233.
396

397 Cadotte, M.W., Jonathan Davies, T., Regetz, J., Kembel, S.W., Cleland, E., Oakley, T.H., 2010.
398 Phylogenetic diversity metrics for ecological communities: integrating species richness, abundance and
399 evolutionary history. *Ecol. Lett.* 13, 96–105.
400

401 Chase, J.M., McGill, B.J., Thompson, P.L., Antão, L.H., Bates, A.E., Blowes, S.A., Dornelas, M.,
402 Gonzalez, A., Magurran, A.E., Supp, S.R., Winter, M., Bjorkman, A.D., Bruelheide, H., Byrnes, J.E.K.,
403 Cabral, J.S., Elahi, R., Gomez, C., Guzman, H.M., Isbell, F., Myers-Smith, I.H., Jones, H.P., Hines, J.,
404 Vellend, M., Waldock, C., O'Connor, M., 2019. Species richness change across spatial scales. *Oikos* 128,
405 1079–1091.
406

407 Cole, J.J., Prairie, Y.T., Caraco, N.F., McDowell, W.H., Tranvik, L.J., Striegl, R.G., Duarte, C.M.,
408 Kortelainen, P., Downing, J.A., Middelburg, J.J., Melack, J., 2007. Plumbing the global carbon cycle:
409 Integrating inland waters into the terrestrial carbon budget. *Ecosystems* 10, 172–185.
410

411 Cross, W.F., Wallace, J.B., Rosemond, A.D., Eggert, S.L., 2006. Whole-system nutrient enrichment
412 increases secondary production in a detritus-based ecosystem. *Ecology* 87, 1556–1565.

413
414 Cuffney, T.F., Bilger, M.D., Haigler, A.M., 2007. Ambiguous taxa: effects on the characterization and
415 interpretation of invertebrate assemblages. *J. North Am. Benthol. Soc.* 26, 286–307.
416
417 Cummins, K.W., Klug, M.J., 1979. Feeding ecology of stream invertebrates. *Annu. Rev. Ecol. Syst.* 10,
418 147–172.
419
420 Dinnage, R., 2009. Disturbance alters the phylogenetic composition and structure of plant communities in
421 an old field system. *PLoS One* 4, e7071.
422
423 Faith, D.P., 1992. Conservation evaluation and phylogenetic diversity. *Biol. Conserv.* 61, 1–10.
424
425 Fox, D., 2007. Back to the no-analog future? *Science* 316, 823–825.
426
427 Fry, J.A., Xian, G., Jin, S.M., Dewitz, J.A., Homer, C.G., Yang, L.M., Barnes, C.A., Herold, N.D.,
428 Wickham, J.D., Others, 2011. Completion of the 2006 National Land Cover Database for the
429 conterminous United States. *Photogrammetric Engineering & Remote Sensing* 77, 858–864.
430
431 Griffith, M.B., 2017. Toxicological perspective on the osmoregulation and osmoregulation physiology of
432 major ions by freshwater animals: Teleost fish, crustacea, aquatic insects, and Mollusca. *Environ. Toxicol.*
433 *Chem.* 36, 576–600.
434
435 Hansen, A.J., Knight, R.L., Marzluff, J.M., Powell, S., Brown, K., Gude, P.H., Jones, K., 2005. Effects of
436 exurban development on biodiversity: Patterns, mechanisms, and research needs. *Ecol. Appl.* 15, 1893–
437 1905.
438
439 Hobbs, R.J., Higgs, E., Harris, J.A., 2009. Novel ecosystems: implications for conservation and
440 restoration. *Trends Ecol. Evol.* 24, 599–605.

441
442 Hodgson, M.E., Jensen, J.R., Tullis, J.A., Riordan, K.D., Archer, C.M., 2003. Synergistic use of lidar and
443 color aerial photography for mapping urban parcel imperviousness. *Photogrammetric Engineering &*
444 *Remote Sensing* 69, 973–980.
445
446 Jonsson, M., Dangles, O., Malmqvist, B., Guérol, F., 2002. Simulating species loss following
447 perturbation: assessing the effects on process rates. *Proc. Biol. Sci.* 269, 1047–1052.
448
449 Jonsson, M., Malmqvist, B., 2003. Mechanisms behind positive diversity effects on ecosystem
450 functioning: Testing the facilitation and interference hypotheses. *Oecologia* 134, 554–559.
451
452 Jonsson, M., Malmqvist, B., Hoffsten, P.-O., 2001. Leaf litter breakdown rates in boreal streams: Does
453 shredder species richness matter? *Freshw. Biol.* 46, 161–171.
454
455 Kato, K., Standley, D.M., 2013. MAFFT multiple sequence alignment software version 7: Improvements
456 in performance and usability. *Mol. Biol. Evol.* 30, 772–780.
457
458 King, R.S., Baker, M.E., 2010. Considerations for analyzing ecological community thresholds in response
459 to anthropogenic environmental gradients. *J. North Am. Benthol. Soc.* 29, 998–1008.
460
461 King, R.S., Baker, M.E., Kazyak, P.F., Weller, D.E., 2011. How novel is too novel? Stream community
462 thresholds at exceptionally low levels of catchment urbanization. *Ecol. Appl.* 21, 1659–1678.
463
464 King, R.S., Richardson, C.J., 2003. Integrating bioassessment and ecological risk assessment: An
465 approach to developing numerical water-quality criteria. *Environ. Manage.* 31, 795–809.
466
467 Klauda, R., Kazyak, P., Stranko, S., Southerland, M., Roth, N., Chaillou, J., 1998. Maryland Biological
468 Stream Survey: A State Agency Program to assess the impact of anthropogenic stresses on stream

469 habitat quality and biota. *Environ. Monit. Assess.* 51, 299–316.

470

471 Kraft, N.J.B., Cornwell, W.K., Webb, C.O., Ackerly, D.D., 2007. Trait evolution, community assembly, and
472 the phylogenetic structure of ecological communities. *Am. Nat.* 170, 271–283.

473

474 Larkin, M.A., Blackshields, G., Brown, N.P., Chenna, R., McGettigan, P.A., McWilliam, H., Valentin, F.,
475 Wallace, I.M., Wilm, A., Lopez, R., Thompson, J.D., Gibson, T.J., Higgins, D.G., 2007. Clustal W and
476 Clustal X version 2.0. *Bioinformatics* 23, 2947–2948.

477

478 Larsen, D.P., Herlihy, A.T., 1998. The dilemma of sampling streams for macroinvertebrate richness. *J.*
479 *North Am. Benthol. Soc.* 17, 359–366.

480

481 Maryland Department of Natural Resources, 2000. Laboratory methods for benthic macroinvertebrate
482 processing and taxonomy. Title, in: CBWP-MANTA-EA-00-6. Monitoring and Nontidal Assessment
483 Division. Monitoring and Non-tidal Assessment Division, Ecological Assessment Program, Annapolis,
484 Maryland, USA.

485

486 McKinney, M.L., Lockwood, J.L., 1999. Biotic homogenization: A few winners replacing many losers in the
487 next mass extinction. *Trends Ecol. Evol.* 14, 450–453.

488

489 Moore, J., Fanelli, R.M., Sekellick, A.J., 2020. High-frequency data reveal deicing salts drive elevated
490 specific conductance and chloride along with pervasive and frequent exceedances of the U.S.
491 Environmental Protection Agency aquatic life criteria for chloride in urban streams. *Environ. Sci. Technol.*
492 54, 778–789.

493

494 Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlenn, D., Minchin, P.R., O'Hara,
495 R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., 2020. *vegan: Community
496 Ecology Package.*

497

498 Ostermiller, J.D., Hawkins, C.P., 2004. Effects of sampling error on bioassessments of stream
499 ecosystems: Application to RIVPACS-type models. *J. North Am. Benthol. Soc.* 23, 363–382.

500

501 Paul, M.J., Meyer, J.L., 2008. Streams in the Urban Landscape, in: Marzluff, J.M., Shulenberger, E.,
502 Endlicher, W., Alberti, M., Bradley, G., Ryan, C., Simon, U., ZumBrunnen, C. (Eds.), *Urban ecology: an*
503 *international perspective on the interaction between humans and nature.* Springer US, Boston, MA, pp.
504 207–231.

505

506 Pearse, W.D., Purvis, A., 2013. phyloGenerator: An automated phylogeny generation tool for ecologists.
507 *Methods Ecol. Evol.* 4, 692–698.

508

509 Purvis, A., Agapow, P.M., Gittleman, J.L., Mace, G.M., 2000. Nonrandom extinction and the loss of
510 evolutionary history. *Science* 288, 328–330.

511

512 R Core Team, 2020. R: A language and environment for statistical computing. R Foundation for Statistical
513 Computing, Vienna, Austria.

514

515 Reichstein, M., Bahn, M., Mahecha, M.D., Kattge, J., Baldocchi, D.D., 2014. Linking plant and ecosystem
516 functional biogeography. *Proc. Natl. Acad. Sci. U. S. A.* 111, 13697–13702.

517

518 Roth, N.E., Southerland, M.T., Mercurio, G., Volstad, J.H., 2001. Maryland Biological Stream Survey
519 2000-2004, in: *Volume 6: Laboratory, Field and Analytical Methods.* DNR-12-0305-0108. Maryland
520 Department of Natural Resources, Monitoring and Non-tidal Assessment Division, Annapolis, Maryland,
521 USA.

522

523 Roy, A.H., Freeman, M.C., Freeman, B.J., Wenger, S.J., Ensign, W.E., Meyer, J.L., 2005. Investigating
524 hydrologic alteration as a mechanism of fish assemblage shifts in urbanizing streams. *J. North Am.*

525 Benthol. Soc. 24, 656–678.

526

527 Sexton, J.O., Song, X.-P., Huang, C., Channan, S., Baker, M.E., Townshend, J.R., 2013. Urban growth of
528 the Washington, D.C.–Baltimore, MD metropolitan region from 1984 to 2010 by annual, Landsat-based
529 estimates of impervious cover. *Remote Sens. Environ.* 129, 42–53.

530

531 Srivastava, D.S., Cardinale, B.J., Downing, A.L., Duffy, J.E., Jouseau, C., Sankaran, M., Wright, J.P.,
532 2009. Diversity has stronger top-down than bottom-up effects on decomposition. *Ecology* 90, 1073–1083.

533

534 Stamatakis, A., 2014. RAxML version 8: a tool for phylogenetic analysis and post-analysis of large
535 phylogenies. *Bioinformatics* 30, 1312–1313.

536

537 Stamatakis, A., Hoover, P., Rougemont, J., 2008. A rapid bootstrap algorithm for the RAxML Web
538 servers. *Syst. Biol.* 57, 758–771.

539

540 Talevich, E., Invergo, B.M., Cock, P.J.A., Chapman, B.A., 2012. Bio.Phylo: A unified toolkit for
541 processing, analyzing and visualizing phylogenetic trees in Biopython. *BMC Bioinformatics* 13, 209.

542

543 Utz, R.M., Eshleman, K.N., Hilderbrand, R.H., 2011. Variation in physicochemical responses to
544 urbanization in streams between two Mid-Atlantic physiographic regions. *Ecol. Appl.* 21, 402–415.

545

546 Utz, R.M., Hopkins, K.G., Beesley, L., Booth, D.B., Hawley, R.J., Baker, M.E., Freeman, M.C., Jones,
547 K.L., 2016. Ecological resistance in urban streams: The role of natural and legacy attributes.

548

549 Wallace, J.B., Eggert, S.L., Meyer, J.L., Webster, J.R., 1997. Multiple trophic levels of a forest stream
550 linked to terrestrial litter inputs. *Science* 277, 102–104.

551

552 Walsh, C.J., Roy, A.H., Feminella, J.W., Cottingham, P.D., Groffman, P.M., Morgan, R.P., 2005. The

553 urban stream syndrome: current knowledge and the search for a cure. J. North Am. Benthol. Soc. 24,
554 706–723.

555

556 Williams, J.W., Jackson, S.T., 2007. Novel climates, no-analog communities, and ecological surprises.
557 Front. Ecol. Environ. 5, 475–482.

558

559

560

561

562

563

564

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

568

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

574

575 **Figure 3.** Assemblage level phylogenetic diversity response as measured by mean nearest taxonomic
576 distance (MNTD) z-score to upstream impervious cover. Change point analysis identified the threshold
577 (solid vertical line, left panel) and the cumulative probability that change has occurred. Right panel is the

578 mean and 95% confidence interval for mean nearest taxonomic distance below and above the threshold
579 of 16% impervious cover.

580

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

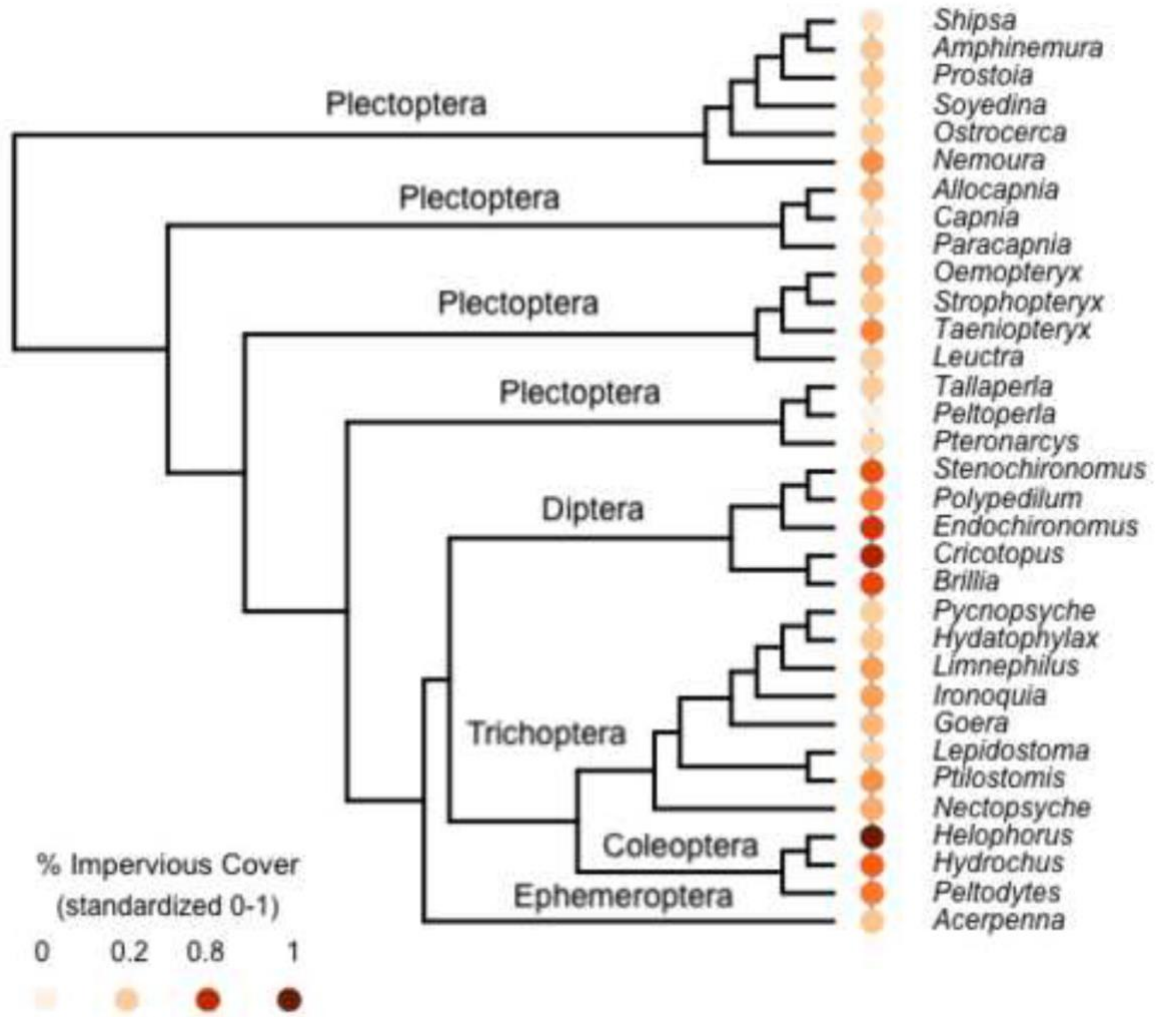
585

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

593

594

595 Figure 1.



596

597

598

599

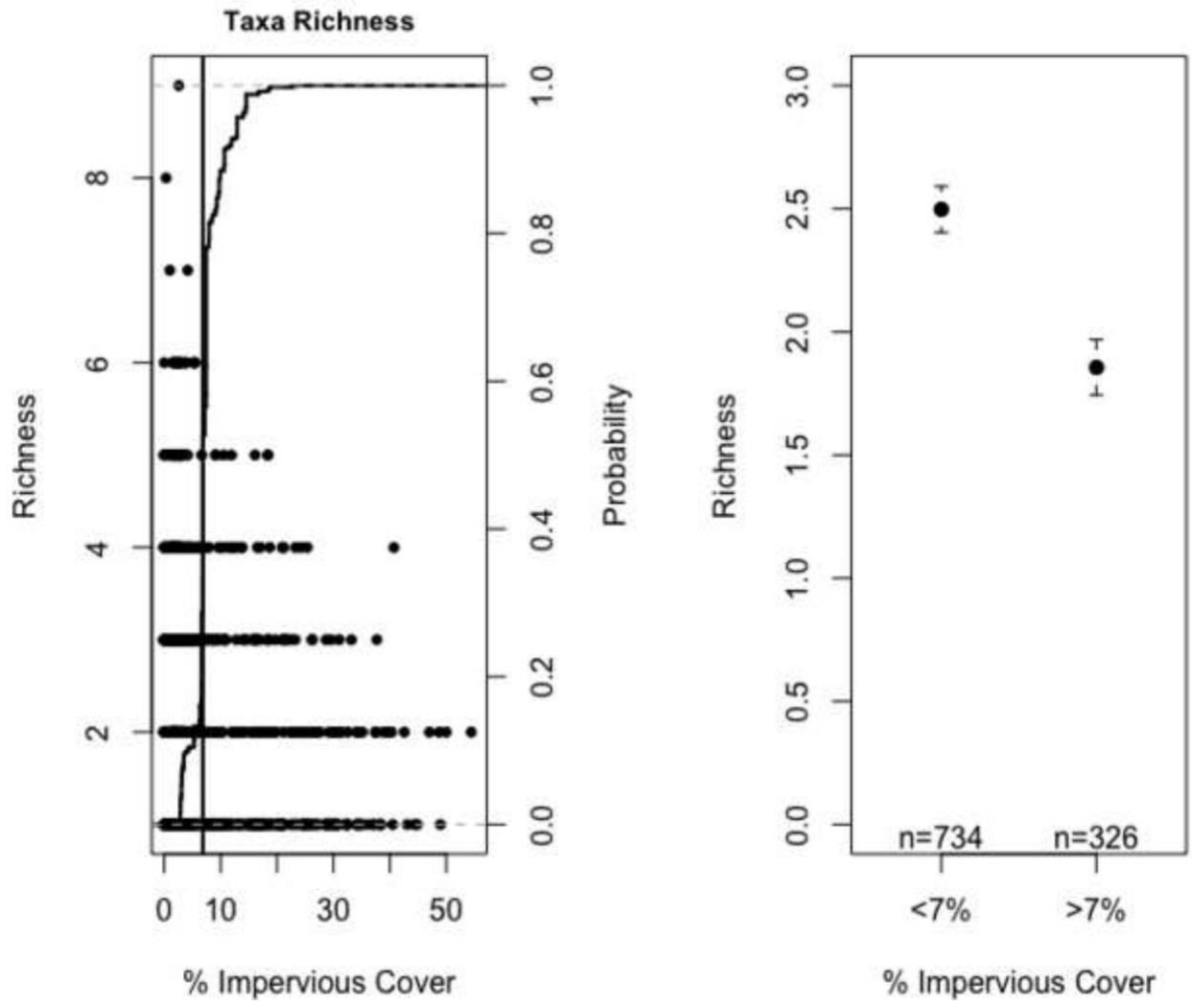
600

601

602

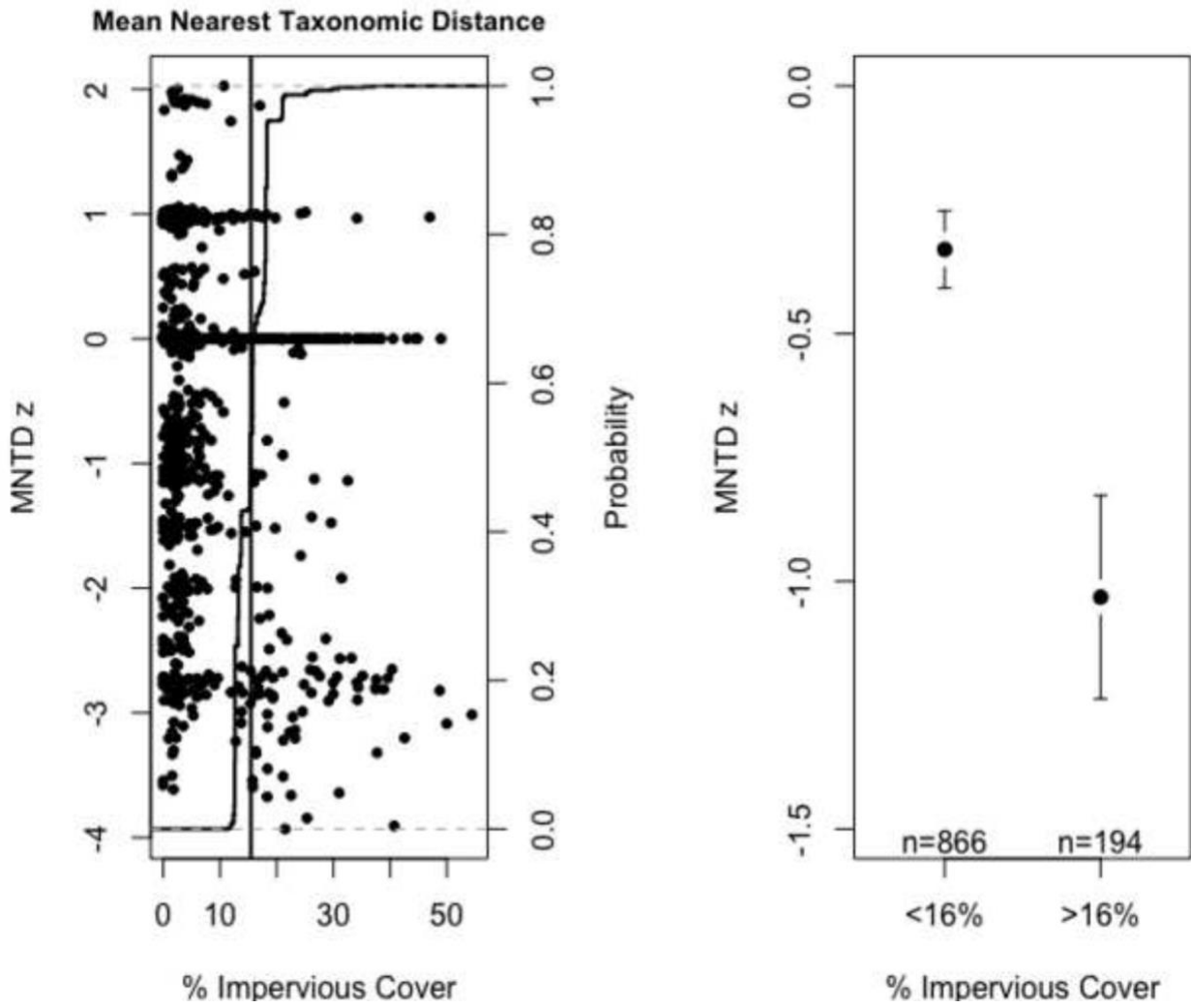
603

604 Figure 2.



605
606
607
608
609
610
611
612
613

614 Figure 3.



615

616

617

618

619

620

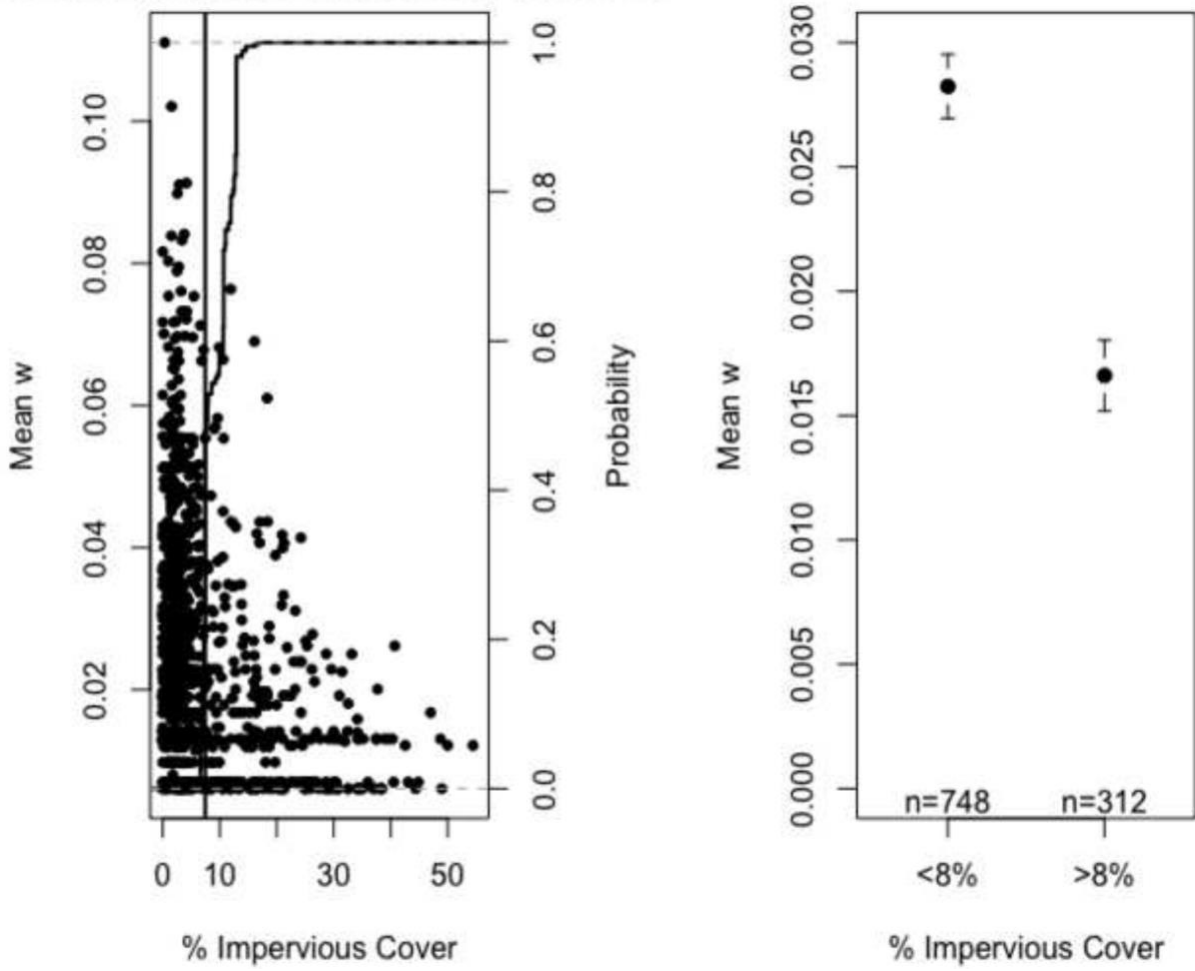
621

622

623

624 Figure 4.

Mean Community-Level Phylogenetic Distinctiveness



625

626

627

628

629

630

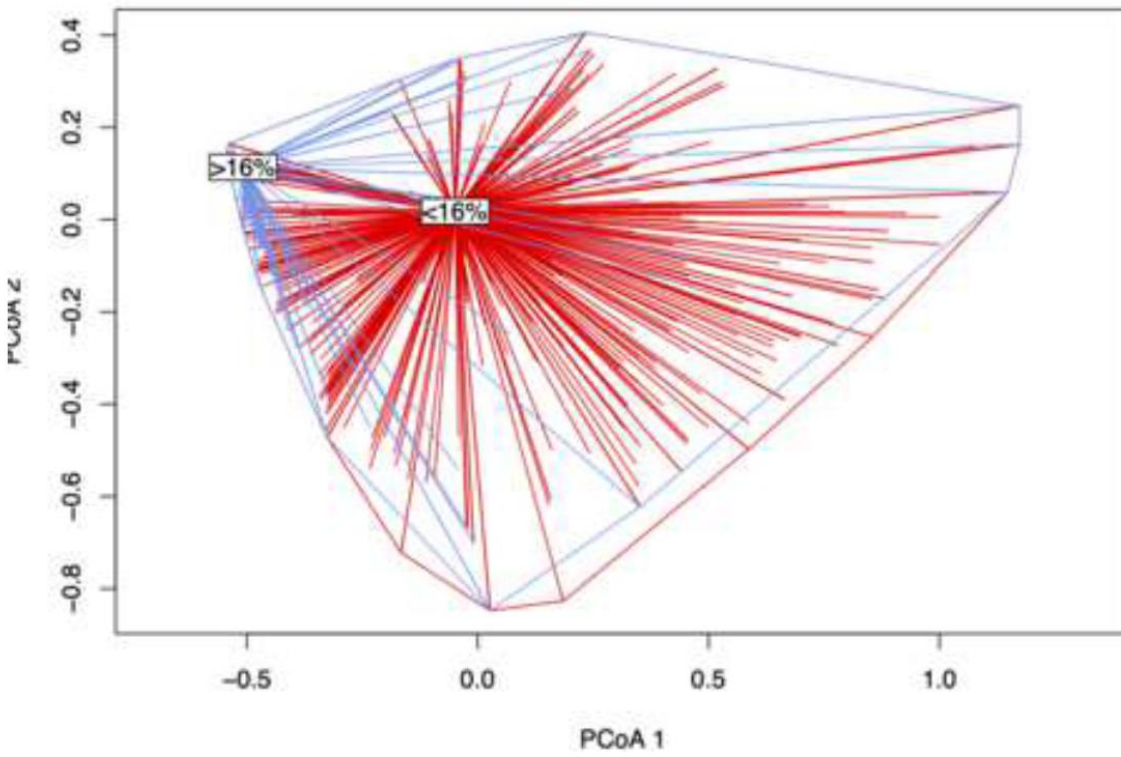
631

632

633

634 Figure 5.

Phylogenetic Compositional Shift vs Impervious Cover Threshold



Phylogenetic Turnover vs. Impervious Cover Threshold

