Differential patterns of taxonomic and functional diversity for two groups of canopy arthropods across spatial scales

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Biosketch: This research team aims to better understand and quantify arthropod community structure and diversity at landscape scales through local experiments and broad scale observational approaches. They are interested in refining our understanding of the structuring of biodiversity to improve conservation efforts.

1 **Differential patterns of taxonomic and functional diversity for two groups of canopy**

2 **arthropods across spatial scales**

3 **Running Title:** Scale impacts canopy arthropod diversity

4 **Key Words:** beta diversity, functional diversity, diversity partitioning, forest canopy,

5 Formicidae, Araneae

6 **Abstract**

7 *Aim*

8 Arthropod diversity is often linked to variation in resource use, dispersal ability, habitat

9 connectivity, and climate factors that differ across spatial scales. The aim of this research was to

10 examine how species richness, functional diversity, and community composition of two taxa

11 differing in functional roles and dispersal ability are structured across spatial scales and to

12 identify the importance of vegetation, climate, and landscape in explaining these patterns at

13 different scales.

14 *Location*

15 96 trees in 24 stands of 6 deciduous forest sites in 2 ecoregions of the eastern USA (North-

16 Central Till Plain and Western Allegheny Plateau)

17 *Time period*

18 2000

19 *Major taxa studied*

20 Canopy dwelling ants (Hymenoptera: Formicidae) and spiders (Araneae)

21 *Methods*

22 Organisms were collected from tree canopies using insecticidal fogging. Ant and spider

23 taxonomic and functional beta diversity were partitioned across four hierarchical spatial scales

1

24   (individual tree, forest stand, site, and ecoregion). The contribution of climactic, landscape, and

25   vegetation variables was determined using model selection.

26   *Results*

27   Ant and spider species richness, functional diversity, and community composition differed

28   between taxa and across spatial scales. Alpha diversity (within trees) was lower than expected for

29   both taxa and types of diversity, with host tree species supporting different species of ants and

30   spiders. While beta components of species diversity among trees and forest stands was greater

31   than expected for both taxa, spiders also showed significant levels of beta diversity among sites.

32   Functional beta diversity was less scale-dependent than taxonomic beta diversity. Stand-level

33   patterns of beta diversity were significantly predicted by variation in climate and landscape

34   connectivity.

35   *Main conclusions*

36   Effects of climate and landscape fragmentation on the diversity and community structure of both

37   taxa indicate that anthropogenic climate change and land use change will alter canopy arthropod

38   communities. Results also suggest that patterns of diversity among fragmentation metrics is

39   influenced by differences in dispersal ability.

1 INTRODUCTION

Understanding drivers of species diversity and distributions are primary goals of ecology and can be used to inform conservation efforts. Measures of biodiversity span local (alpha diversity, α) and regional (gamma diversity, γ) scales. Studies of the variation, or turnover, in biodiversity among sites or communities (beta diversity, β), first proposed by Whittaker (1960), have exploded over the last few decades (Anderson *et al.*, 2011; Socolar *et al.*, 2016; Mammola *et al.*, 2021). Beta diversity has been applied to the spatial scaling of biodiversity, temporal change in communities for conservation monitoring, changes across latitudinal and elevational gradients, and environmental filtering of functional traits and subsequent assembly processes (Crist *et al.*, 2003; Kraft *et al.*, 2011; Barton *et al.*, 2013; Siefert *et al.*, 2013; Jarzyna & Jetz, 2018).

Beta diversity has been primarily focused on measures of taxonomic diversity but not functional diversity (i.e. based on the ecological roles and traits of species). To a certain extent, species diversity and functional diversity are correlated, but not reliably so, as not all species are equivalent in a given system and their relative roles may change depending on the presence of and interactions with other species. Species and functional diversity are, therefore, not interchangeable. Indeed, one could imagine two communities comprised of entirely different species (high species beta diversity) that carry out the same functions (low functional beta diversity; Swenson, 2011; Swenson *et al.*, 2012; Siefert *et al.*, 2013). Because functional diversity quantifies ecological impacts and species interactions, studies including the functional diversity of organisms provide more robust data for conservation and restoration than studies on species presence and abundance alone (Cadotte *et al.*, 2009).

62   Conservation and restoration efforts are landscape-level problems requiring an

63 understanding of how both species and functional diversity scales from local to regional

64 perspectives. Using taxa, such as arthropods, that are widespread, abundant, speciose, and

65 functionally diverse can help researchers test diversity hypotheses across multiple scales (Kemp

66 *et al.*, 2017; McCreadie & Adler, 2018). Ants and spiders play several important roles in

67 ecosystem functioning through direct and indirect species interactions (Pearce & Venier, 2006;

68 Maleque *et al.*, 2009). Specifically, ants are numerically dominant in most ecosystems, affecting

69 ecological processes through their nest building, predation, and mutualisms (Folgarait, 1998;

70 Crist, 2009); therefore, shifts in ant communities can have multifaceted impacts across trophic

71 levels. Similarly, spiders are obligate predators of other arthropods and may be more susceptible

72 to changes in landscape fragmentation, and loss of key predators is linked to trophic cascades

73 (Bonte *et al.*, 2004; Voigt *et al.*, 2007).

74   The mechanisms that might structure arthropod taxonomic and functional beta diversity

75 across spatial scales (e.g., region, site, and forest stand) include characteristics such as land use

76 and topography, management history, and habitat characteristics, respectively. Forest

77 management practices (e.g., logging, fire regimes, and patch size) affect arthropods across

78 multiple scales. At landscape and regional scales, forest fragmentation due to logging or land-use

79 changes lead to decreased habitat area and isolation as well as greater edge to area ratio and

80 altered biotic and abiotic conditions along edge boundaries (Gluck & Rempel, 1996; Fahrig,

81 2003; Haddad *et al.*, 2015). At the stand level, decreased forest area and increased edge cause

82 shifts in tree stand pattern, vegetation structure, and soil characteristics (e.g. moisture, organic

83 matter, texture; Johnston & Elliott, 1996). The effects of these changes on arthropods are many

84 and varied. Fragment size impacts both taxonomic and functional diversity of ants and spiders as

85   well as shifting community composition of these taxa (Pearce *et al.*, 2005). Forest habitats with

86   greater tree diversity and structural variability and complexity give rise to a greater variety of

87   niches, and, thus, species and roles to inhabit those niches (Tews *et al.*, 2004). Thus, vegetation

88   or habitat complexity can drive patterns of arthropod species richness through direct effects on

89   foraging success and resource availability and indirect effects on ant nest site selection via soil

90   moisture and shading (Mcnett & Rypstra, 2000; Wang *et al.*, 2001; Lassau & Hochuli, 2004).

91   Taken together, beta diversity and composition of key arthropod communities may be

92   affected at a range of spatial scales, potentially driven by several biotic and abiotic

93   characteristics. However, many studies of arthropod diversity focus on a single spatial scale and

94   on taxonomic diversity alone. In this study, we evaluated the role of spatial scale on the

95   taxonomic and functional diversity and the community composition of two arthropod groups

96   (ants and spiders). We quantified these measures across four spatial scales: trees, forest stands,

97   sites, and ecoregions. Specifically, we asked: 1) What spatial scales explain the greatest variation

98   in taxonomic and functional beta diversity and in the community composition of these two taxa?

99   and 2) What are potential mechanisms of scale-associated community structuring, including

100   variation in tree species, forest area and connectivity, and seasonality in climate? We

101   hypothesized that both taxonomic and functional diversity have greater variation at finer spatial

102   scales (tree and stand levels) than at broader spatial scales (site and ecoregion). We also expected

103   that spiders, with greater dispersal abilities, would exhibit greater levels of beta diversity at

104   broader spatial scales than ants, which are more dispersal limited. Similarly, we hypothesized that

105   the biotic and abiotic factors structuring these patterns of diversity differ for spiders and ants

106   given inherent differences in resource use and dispersal ability.

107

108 **2 METHODS**

109 *2.1 Sampling Design, Study Sites, and Arthropod Collection*

110   Samples were collected from tree canopies of southern Ohio and southeastern Indiana

111 using a hierarchically nested design with four levels. The broadest level – ecoregion – was

112 represented by the glaciated North-Central Till Plain and unglaciated Western Allegheny Plateau

113 (Figure S1). Each ecoregion varies in soil type, forest composition, and topography. The second

114 level – site – comprised 3 sites in each ecoregion for a total of 6 sites (Figure S1). The third level

115 – stand – comprised 4 forest stands within each site (24 total). Within each site, two stands were

116 located in uplands, and two stands were located in lowland topographic positions. The fourth

117 level – tree – included 8 individual trees (96 total) within a 1-ha area of each stand. Each tree was

118 sampled using canopy fogging and arthropods were collected in an array of 12 1-m^2 funnel arrays

119 placed under the crown of the fogged tree. Arthropods were knocked down by insecticidal

120 fogging (0.5 L of 0.5% pyrethrin-based insecticide) for 3 minutes using a Curtis Dyna-Fogger

121 hoisted into the tree crown and collected by funnels with attached vials of ethanol. Insecticidal

122 fogging is not dependent on arthropod activity and lethality is non-specific (Basset *et al.*, 1997;

123 Stork & Hammond, 1997). Sampling was completed during early (22 May-20 June 2000) and

124 late (2-25 August 2000) summer to capture seasonal variation, with early and late season samples

125 pooled for analyses. For more details on sampling methods, see Gering & Crist (2002). Ants were

126 identified to species using the *Ants of Ohio* (Coovert, 2005) and ant functional groups were trait-

127 based (see below) rather than explicitly based on taxonomy or behavior (Andersen, 1997; Crist,

128 2009). Spider adults were identified to species based on the *Spiders of North America* (American

129 Arachnological Society, 2005), Spiders of Connecticut (Kaston, 1981), and a provisional list of

130 Ohio spiders (Bradley, 2017), while juveniles were identified to family level when possible.

131   Spider families were used as an indicator of functional guild, based on foraging strategy, prey

132   range, habitat stratification, and circadian activity, as these traits are highly correlated with family

133   (Cardoso *et al.*, 2011).

134   We refer to these samples as canopy or arboreal arthropods because they were collected

135   by fogging tree crowns. Although some of the common species we recorded are primarily

136   arboreal (e.g., *Aphaenogaster mariae*, Table S3), most of the species of ants and spiders are

137   known to move between strata and nest or overwinter in the ground. Nonetheless, Crist and

138   Campbell (2017) recorded significant differences in the community composition of ants from

139   canopy fogging and pitfall traps samples at the same study sites in the North-Central Till Plain.

140

141   *2.2 Data Analyses*

142   2.2.1 Ant functional groups

143   To classify ants according to functional traits, we selected 10 binary, categorical, and

144   continuous traits that may influence the ecological role of ants (Table S1; (Del Toro *et al.*, 2015;

145   Record *et al.*, 2018; Mahon, 2019). We used trait definitions and data from Del Toro *et al.*

146   (2015), Record *et al.* (2018), Coovert (2005), and AntWiki (2022). Missing morphological data

147   were supplemented with measurements taken from 2-10 mounted specimens per species collected

148   during this study. Functional groups were formed from a dendrogram based on functional

149   dispersion and the Ward clustering method using the dbFD function (FD package, R; Laliberté &

150   Legendre, 2010); functional groups were delineated by setting six functional groups, where we

151   noted a clear break of functional groups (Table S1, Figure S2).

152

153   2.2.2. General patterns and species accumulation curves

154   For all statistical analyses, early and late sampling periods were pooled and all univariate

155   analyses were conducted in R v4.0.0 (R Core Team, 2022). We constructed sample-based

156   rarefaction curves of ants and spiders by tree species to assess differences in species richness

157   among the most common host trees. To determine the effectiveness of our overall sampling

158   effort, we also conducted species rarefaction and extrapolation curves for ants and spiders using

159   the iNEXT package in R (Chao *et al.*, 2014). We also estimated species richness by host trees and

160   overall richness using the Chao1 estimator (Chao, 1984; Colwell & Coddington, 1994).

161

162   2.2.3 Diversity partitioning

163   To analyze taxonomic diversity, we partitioned species richness and functional group

164   richness (q = 0) across hierarchical levels, with multiplicative partitioning methods based on the

165   PARTITION software developed by Crist *et al.* (2003) using the R package, PARTITIONR

166   (Mahon *et al.*, 2019). Multiplicative partitions express beta diversity as the effective number of

167   distinct communities, whereas alpha diversity is in units of species richness (Anderson *et al.*,

168   2011). Using hierarchical diversity partitioning, beta components can be separated into nested

169   hierarchical levels (i.e. spatial scale). Hierarchical multiplicative partitioning calculates beta

170   diversity at a given level (i) by dividing the average alpha at the i+1 level, $\beta_i = \alpha_{i+1}/\alpha_i$. We

171   tested the significance of α_1 (within trees), β_1 (among trees), β_2 (among stands), β_3 (among

172   sites), and β_4 (between ecoregions) against null, random distributions using 1000 sample-based

173   randomizations. This type of randomization preserves intraspecific aggregation at each

174   hierarchical level, and thus tests the null hypothesis that observed patterns of species diversity at

175 each level are similar to those expected by randomized aggregation of samples at each level of

176 the hierarchical design; alternatively, the null hypothesis is rejected if observed patterns are

177 significantly different from those expected from null distributions, supporting non-random

178 hierarchical species assemblages that are structured by ecological processes (Crist *et al.*, 2003).

179 Partitioning of alpha, beta diversity in this manner therefore accounts for issues of spatial

180 pseudoreplication that can arise in local-to-regional comparisons of species richness (Gering &

181 Crist, 2002). We used a two-tail probability of $p = 0.05$ ($p = 0.025$ for each tail of the null

182 distribution) to determine whether observed diversity patterns were higher or lower than expected

183 via randomizations. To compare relative deviations of the null distributions from the expected

184 values across hierarchical levels and endpoints, we calculated standard effect sizes (SES; also

185 termed beta and alpha deviations) from the mean and standard deviation of the null distributions

186 for each hierarchical level ($SES = (I_{obs} - I_{exp})/\sigma$) (Gotelli & McCabe, 2002; Kraft *et al.*, 2011).

187   To analyze variation in community composition across hierarchical levels, we conducted

188 analyses for multivariate location using PRIMER-E and PERMANOVA+ v6 (Anderson, 2001).

189 We used permutational multivariate analysis of variance (PERMANOVA) to partition the

190 variation in community composition across hierarchical levels. PERMANOVAs were conducted

191 using 9999 permutations of the data, with a nested design. Since multivariate analyses were

192 conducted on square-root transformed abundance data with a Bray-Curtis dissimilarity, variance

193 components of PERMANOVA can be interpreted as percent dissimilarity (Anderson, 2001).

194

195 2.2.4 Landscape and environmental variable analyses

196   To address potential mechanisms of diversity structuring, we compiled and evaluated

197   landscape, climactic, and vegetation variables for forest stands and surrounding areas. Landscape

198   variables were habitat fragmentation measures (estimated using ESRI arcGIS Dekstop v10.6.1

199   (ESRI, 2019), Fragstats v4.2.1 (McGarigal *et al.*, 2012)) and land use data (USDA NASS Crop

200   data layer for 2008, the closest year with most reliable data for both Indiana and Ohio (USDA

201   National Agricultural Statistics Service, 2022)). Land cover/land use composition and

202   configuration was collected for of 1.0, 3.0, 6.5, and 10.0 km buffers surrounding each stand to

203   accommodate the potential dispersal distances of both spiders and ants, and to minimize overlap

204   between stand buffers (Thomas *et al.*, 2003). Initial model selection (see methods below) was

205   conducted to determine which buffer size explained the most variation for both ants and spiders;

206   data at the 6.5 km buffer were used for the remainder of the statistical analyses. Each landscape

207   was analyzed using a "no-sampling" strategy and an 8-cell neighborhood rule for the following

208   class level metrics as specified in Fragstats: CLUMPY, PLAND, GYRATE_MN,

209   GYRATE_AM, and PARA (McGarigal *et al.*, 2012). CLUMPY (fragmentation index) is an

210   index of fragmentation of deciduous forest within the measured landscape where -1 is highly

211   fragmented forest and 1 is a complete, unfragmented forest; the CLUMPY index is not

212   confounded by changes in forest area. PLAND is the percentage of deciduous forest within the

213   landscape. GYRATE_MN is the mean distance (m) to forest edge from patch centroid.

214   GYRATE_AM (patch connectedness), is the area-weighted distance (m) to forest edge from

215   patch centroid, or patch connectedness. PARA (patch edge:area ratio) is the mean edge:area ratio

216   for all deciduous forest patches. We obtained 19 bioclimatic variables from WorldClim v2.0

217   (Fick & Hijmans, 2017); due to the relatively course resolution (~1 km^2) of the bioclimatic

218   variables, 2 of our stands (within Brookville) had identical climatic data, but all other stands and

219   sites varied. We included a stand-level vegetation measure of tree species richness (dbh ≥10 cm)

220   by recording all tree species present within the same 1-ha stands where trees were fogged (Crist

221   *unpublished data*).

222   We accounted for collinearity among landscape and environmental variables by removing

223   those that were highly correlated (Pearson $r \geq 0.80$). In total, 10 variables were included: 4

224   landscape variables, 5 climatic variables, and 1 vegetation variable (Table S2). Prior to all

225   analyses, variables were standardized to z-scores to aid in model fitting and inference. To

226   determine climatic, landscape, and vegetative influence on patterns of taxonomic and functional

227   richness, we used linear regression models (lm function, stats package, R; (R Core Team, 2022)

228   with response variables of mean alpha (α_1, within trees) and beta (β_1, among trees) diversity for

229   taxonomic and functional diversity at each stand. Model selection allowed for the additive term

230   of all environmental predictors. To identify best models, we used the lowest Akaike's

231   Information Criterion with bias-correction (AICc). For best models, we calculated AICc weights

232   (w) and appropriate R^2. We tested for spatial autocorrelation using Moran's I (Moran.I function,

233   ape package, (Paradis & Schliep, 2019), which indicated no spatial autocorrelation present in the

234   residuals of our univariate models.

235   Similarly, we used DISTLM and distance-based redundancy analyses (dbRDA) in

236   PRIMER and PERMANOVA+ (McArdle & Anderson, 2001) to assess influences of our

237   environmental variables on community composition at the stand level. We performed stepwise

238   model selection based on AIC values to examine the relationship between the explanatory

239   variables and community composition. We only included variables with significance of $p < 0.10$

240   in preliminary marginal tests to reduce likelihood of overfitting multivariate analyses.

241   Significance values and variance explained by selected predictors were found using bootstrap

242   tests based on 9999 iterations. Multivariate analyses were conducted on square-root transformed

243   abundance data with Bray-Curtis dissimilarity.

244

245   **3 RESULTS**

246   We collected 3,053 individual ants representing 23 species with 2 singleton species (Table

247   S3). Estimated Chao1 richness was 24 ± 2 species, with rarefaction curves indicating ant richness

248   had plateaued (Figure S3). We collected 5,221 individual spiders representing 23 families, 67

249   genera, and 97 species. Of these, 83.7% were juveniles, we identified the remaining 925 adults to

250   morphospecies (Table S3). Of these species, 15 were represented by a single specimen. Dominant

251   spider families were Araneidae (23%), Linyphiidae (17%), Salticidae (16%), Anyphaenidae

252   (12%), and Theridiidae (10%). Estimated Chao1 richness was 108 ± 6 species, with rarefaction

253   indicating spider richness began to plateau and likely would have been reached by 150 tree

254   samples (Figure S3).

255   *3.1 Hierarchical diversity partitioning*

256   Spider species alpha and beta diversity were higher than ant species diversity, ant

257   functional diversity, and spider functional diversity (Table 1). Multiplicative beta diversity based

258   on species richness ($q = 0$) exhibited similar patterns between taxa, with beta decreasing as scale

259   increased (Figure 1). For species richness, the observed β_{tree} components were 2x the α_{tree} of 4.8

260   species of ants per tree and 2.8x of 6.4 species of spiders per tree, respectively. The β_{stand} values

261   were 1.6x the combined of 9.5 species of ants per stand, and 2.4x the 17.9 species of spiders per

262   stand. The β_{site} components were 1.3x the 15.7 species of ants per site and 1.7x the 42.9 spider

263 species per site, and $\beta_{ecoregion}$ were <1.3x the mean richness of ants and spiders per ecoregion

264 (Table 1). The functional group diversity components mirrored those of species richness, except

265 that the α_{tree} and β_{tree} levels comprised most of variation in total functional diversity of ants with

266 additional variation explained by β_{stand} for spiders. Randomization tests of species richness

267 indicated α_{tree} was significantly lower than expected across taxa ($p < 0.001$), β_{tree} was higher than

268 expected across taxa ($p < 0.001$), β_{stand} was higher than expected for ant species and spiders ($p <$

269 0.001), β_{site} was higher for spider species ($p = 0.005$), and β_{region} was not different across taxa ($p >$

270 0.025, Table 1). These patterns emerged, despite having similar diversity across scales for

271 diversity for ant species, ant functional groups, and spider functional groups (Figure 1, Table 1).

272 At local scales (within and among trees), for both taxonomic and functional endpoints, the

273 deviations from observed diversity were greater for ants than spiders, but the opposite pattern

274 emerged at broader scales (stand, site, and region; Figure 1), indicating differential hierarchical

275 patterns of species diversity between ants and spiders.

276

277 *3.2 Community composition*

278   We tested for multivariate differences in ant and spider species composition across

279 hierarchical levels based on variation in Bray-Curtis dissimilarities (Table 2). For both taxa, a

280 greater proportion of the variation in dissimilarities was explained at site and ecoregion levels

281 than with univariate diversity partitions, but components still decreased with increasing spatial

282 scale (Table 2). Spiders also showed greater residual variability among trees (56%) compared to

283 ants (40%). Similarly, spider species composition showed greater variance among stands within

284 sites than ant species composition (Table 2). Ant assemblages showed significant variability

13

285 across all spatial scales; however, this was not the case for spiders, as the variance component for

286 ecoregion was not different from zero (Table 2).

287   For both ants and spiders, functional composition was less variable than taxonomic

288 composition across scales (Table 2). Ant and spider functional assemblages were significantly

289 variable at the stand and site levels, but the variance component for ecoregion was not different

290 from zero (Table 2). While spider functional composition showed reduced variance components

291 with increasing spatial scale, ant functional composition showed little differentiation among

292 stand, site, and ecoregion scales, but variance was highest among sites (Table 2), indicating

293 stronger variability across sites within ecoregion than among stands within sites. Nonetheless,

294 both ant and spider functional composition was most variable among trees within stands (Table

295 2), suggesting functional differentiation of these communities among tree species.

296

297 *3.3 Patterns of diversity and community composition*

298   Tree identity influenced spider and ant species richness. For ants, white oak (*Quercus*

299 *alba*), red oak (*Q. rubra*), American beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*),

300 and hickory (*Carya* spp.) hosted similar levels of richness, while tulip poplar (*Liriodendron*

301 *tulipifera*) maintained the lowest richness (Figure 2B). Ant richness began to plateau on most tree

302 species (but see hickory, Figure 2A). For spiders, white oak, sugar maple, and American beech

303 had greater richness than tulip poplar, red oak, and hickory, as indicated by rarefaction (Figure

304 2B). Unlike for ants, most tree species did not begin to plateau for spiders, except for red oak.

305   Average alpha (α_1, within trees) and beta (β_1, among trees within stand) diversity for

306 taxonomic and functional endpoints were driven by a combination of landscape and climatic

14

307   variables measured at the stand level. Temperature evenness (isothermality) and precipitation

308   seasonality were important predictors of alpha diversity of spider functional groups, ant species,

309   and ant functional groups as well as beta diversity of spider species, spider functional groups, and

310   ant species (Table 3). Specifically, precipitation seasonality was negatively associated with alpha

311   diversity, but positively associated with beta diversity (Table 3). This suggests that increased

312   variability in precipitation may simultaneously reduce average alpha within trees while increasing

313   differentiation of arthropod communities among tree species (beta). Stand-level richness of tree

314   species was positively associated with beta diversity of ant species, but negatively associated

315   with beta diversity of spider functional groups (Table 3). Finally, patch connectedness, size, and

316   shape were important predictors of alpha diversity of ant and spider functional groups and of beta

317   diversity of ant functional groups (Table 3).

318   Similar to univariate patterns of alpha and beta diversity, variation in multivariate

319   community composition using dbRDA was driven by a similar combination of landscape and

320   climatic drivers. Variation in ant community composition was best explained by precipitation

321   variability ($R^2 = 16.3\%$) (Figure 3A). Variation in ant functional group composition was best

322   explained by isothermality ($R^2 = 40\%$), patch connectedness (14.2%), and precipitation

323   seasonality (11.1%) (Figure 3B). Variation in spider community composition was best explained

324   by isothermality ($R^2 = 17.6\%$), maximum temperature (15.6%), and habitat fragmentation

325   (10.4%) (Figure 3C). Variation in spider functional guild composition was best explained by

326   patch connectedness ($R^2 = 25.2\%$), isothermality (16%), stand tree richness (9.6%), and habitat

327   fragmentation (8.9%) (Figure 3D).

328

4 DISCUSSION

4.1 Spatial structure of diversity

Our results indicate differential patterns of beta diversity and community structure between canopy-dwelling ants and spiders and that taxonomic diversity is more variable at larger spatial scales than functional diversity. In support of our hypothesis that spider diversity would be more affected by broader spatial scales than ants, we saw greater diversity and greater deviation from expected diversity (SES) at broader spatial scales for spiders than for ants, but there was more variation between ecoregions for ant communities than for spider communities. While functional and taxonomic diversity exhibited similar patterns across scales, taxonomic diversity exceeded functional diversity at coarser spatial scales (Site and Ecoregion), suggesting trait clustering and functional redundancy at broader spatial scales, consistent with the findings of Jarzyna & Jetz (2018). Essentially, the loss or addition of species at the site and ecoregion scales has little influence on the loss or addition of ecological functions – as determined by functional groups – at these same scales.

The finding that broad-scale (Ecoregion) beta components of diversity were not different than expected suggests the effects of ecoregions do not structure the taxonomic and functional diversity of canopy-dwelling ants and spiders. Our results contrast with the significant differentiation of beetle diversity between ecoregions from these same samples (Gering *et al.*, 2003) but are consistent with those of Summerville *et al.* (2003) who found no significant deviation from expected diversity in forest moth species richness among ecoregions. Nonetheless, both ant and spider communities showed similar patterns of decreasing community variation with increasing spatial scale, indicating strong differences in beta diversity at the tree and stand levels, consistent with the findings of Gering *et al.* (2003) and Summerville *et al.* (2003). Here, we also

352   conducted multivariate partitions of Bray-Curtis dissimilarity across scales, which showed

353   slightly larger components of variation at the site and ecoregion levels than univariate partitions.

354   This suggests that shifts in the relative abundance of species or functional group across sites and

355   ecoregions were more important than shifts in species or functional group composition.

356   Lower variation than expected at the individual tree-level implies that tree species support

357   distinct levels of species richness and, likely, functional diversity of arthropod taxa, as supported

358   by rarefactions of individual tree species for both ants and spiders. Differences in tree species-

359   arthropod species richness relationships (estimated and observed richness) indicate potential tree-

360   species specific constraints such as prey species abundance and competition/territoriality in ants

361   (Majer & Delabie, 1999; Yasuda & Koike, 2009) and nesting/web site limitations for spiders

362   (Nicolai, 1986; Larrivée & Buddle, 2010). Thus, the maintenance of temperate, canopy-dwelling

363   arthropod communities is, at least somewhat, dependent on maintaining the diversity of host

364   trees. As such, the subsequent emerald ash borer (*Agrilus planipennis*) driven loss of ash trees

365   (*Fraxinus* spp.; Herms & McCullough, 2014) and long-term declines of several oak species in

366   eastern forests (McEwan *et al.*, 2011) since the time of sampling has likely resulted in the loss of

367   distinct arboreal arthropod communities and, possibly, species since the early 2000s.

368

369   4.2 Landscape and environmental influences

370   Previous studies have found differential environmental drivers between taxonomic and

371   functional diversity (Longhi & Beisner, 2010; Pool *et al.*, 2010; Meynard *et al.*, 2011),

372   suggesting that different environmental filters act on taxonomic and functional diversity of the

373   same taxa. While we saw similar scaling patterns between ants and spiders, taxonomic and

374   functional diversity, and community structure, the climatic, landscape, and vegetation drivers of

375   these patterns did, indeed, differ (Table 3, Figure 3). Climatic characteristics showed strong

376   influence on alpha and beta diversity as well as both taxonomic and functional composition,

377   while landscape characteristics were important in explaining patterns of functional alpha diversity

378   and functional composition. Nonetheless, taxonomic and functional community composition was

379   explained by shared climatic variables (precipitation seasonality and isothermality), indicating

380   that both taxonomic and functional assemblages are partially driven by the same climatic

381   conditions.

382   Climate variables were more common than landscape variables in univariate (diversity)

383   and multivariate (community composition) ant and spider models. Precipitation seasonality was

384   the most common predictor in explaining variation in taxonomic and functional diversity (Table

385   3), while isothermality (temperature evenness) was the most common predictor for explaining

386   multivariate variation in taxonomic and functional community composition (Figure 3). These

387   differences in climate variables as predictors of univariate and multivariate variation in diversity

388   may also reflect variation in species distributions versus shifts in relative abundances. The

389   broader implication of climate variability as an important driver of diversity and composition of

390   canopy arthropod communities is that climate change mediated increases in climate variability

391   (increased precipitation seasonality and decreased isothermality) will likely greatly alter these

392   canopy-dwelling communities (Westerling, 2016; Jump *et al.*, 2017; Neumann *et al.*, 2017).

393   Habitat configuration was more important in explaining patterns of ant and spider alpha

394   and beta diversity and community structure than total habitat availability, but spider functional

395   richness was related to patch size and shape. In line with our results, previous research suggests

396   that ants show weak support for species-area relationships, while spiders tend to exhibit strong

397   positive species-area relationships (Crist, 2009; Cardoso *et al.*, 2010). Similarly, previous studies

398   have found higher ant richness in habitat fragments with higher connectivity, while habitat

399   connectivity does not influence spider species richness (Abensperg-Traun *et al.*, 1996; Suarez *et*

400   *al.*, 1998; Cardoso *et al.*, 2010). The disparities in the influence of habitat fragmentation and

401   patch size and shape between ants and spiders is likely due to differences in dispersal ability

402   (Thompson & Townsend, 2006). Our results suggest that patterns of arthropod diversity among

403   habitat patches is influenced by dispersal ability, with connectivity being an important predictor

404   of poor dispersing arthropods and patch size and shape being an important predictor of diversity

405   of stronger dispersing arthropods. Taken together, this suggests that the importance of habitat

406   configuration and area of habitat in determining species richness (Haddad *et al.*, 2017) may be

407   somewhat dependent upon the dispersal ability of organisms. Yet, connectivity and fragmentation

408   of habitat patches were important for composition of both taxa, suggesting that while spider

409   richness may not be influenced by habitat configuration, the identities of spider species is

410   influenced by habitat configuration. Therefore, conservation efforts should focus on increasing

411   both patch connectivity and size to provide the largest benefits to diversity of all arthropods.

412   Nevertheless, future research should expand upon the relative roles of habitat configuration and

413   patch size and shape in driving patterns of diversity for taxa across a dispersal gradient.

414   *4.3 Conclusions*

415   Our findings demonstrate stronger scaling patterns of taxonomic diversity than functional

416   diversity from local to regional scales, suggesting functional redundancy at broader spatial scales.

417   Further, taxonomic and functional diversity and community assemblages change along different

418   environmental gradients. The controls of climate and landscape fragmentation on the diversity

419   and structure of canopy-dwelling ants and spider communities indicate that climate change via

420   increased variability will likely further alter the diversity, composition, and function of arboreal

421   arthropods that are already threatened by forest fragmentation and land use changes. Our findings

422   provide further support for the consideration of functional components of diversity and multiple

423   measures of beta diversity in monitoring and conservation (Cadotte *et al.*, 2011; Socolar *et al.*,

424   2016; Isbell *et al.*, 2017; Jarzyna & Jetz, 2018).

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Code and Data accessibility: All data and R code are available on github: https://github.com/mahonmb/CanopyArthropodDiversity. PRIMER and PERMANOVA+ code is available by request.

Tables.

Table 1. Multiplicative partition of alpha and beta diversity components across a hierarchically nested study of canopy ant and spider diversity. *P* values <0.05 are bolded

Source	Observed Diversity	Expected Diversity	*p*	SES
Ant Species				
Ecoregion (β_{region})	1.10	1.10	0.687	-0.01
Site (β_{site})	1.34	1.33	0.386	0.52
Stands (β_{stand})	1.66	1.55	**0.001**	3.94
Among Trees (β_{tree})	1.98	1.57	**0.001**	24.67
Within Trees (α_{tree})	4.78	6.02	**0.001**	-19.6
Ant Functional Group				
Ecoregion (β_{region})	1.00	1.00	0.500	0.00
Site (β_{site})	1.06	1.04	0.348	1.27
Stands (β_{stand})	1.16	1.16	0.520	0.15
Among Trees (β_{tree})	1.56	1.33	**0.001**	15.23
Within Trees (α_{tree})	3.13	3.66	**0.001**	-13.01
Spider Species				
Ecoregion (β_{region})	1.30	1.28	0.291	0.92
Site (β_{site})	1.74	1.67	**0.003**	2.98
Stands (β_{stand})	2.40	2.23	**0.001**	5.97
Among Trees (β_{tree})	2.79	2.60	**0.001**	7.01
Within Trees (α_{tree})	6.42	6.88	**0.001**	-6.56
Spider Functional Group				
Ecoregion (β_{region})	1.15	1.15	0.803	0.19
Site (β_{site})	1.24	1.23	0.475	0.36
Stands (β_{stand})	1.32	1.26	**0.001**	4.27
Among Trees (β_{tree})	1.38	1.32	**0.001**	7.12
Within Trees (α_{tree})	8.89	9.32	**0.001**	-6.80

Table 2. Permutational multivariate analyses of variance (PERMANOVA) based on Bray-Curtis dissimilarity of square-root transformed abundance data for species and functional groups for both taxa. *P*-values are based on Monte-Carlo randomization, *p* values <0.05 are bolded. Variance is the square root of the estimated component of variance, to put values on the scale of Bray-Curtis dissimilarities (percent difference among assemblages).

Endpoint and Source of Variation	*df*	MS	Pseudo-F	*p*	Variance	Percent Variance Explained
Ant Species						
Ecoregion	1	14407	2.41	**0.042**	13.3	15.9%
Site(Ecoregion)	4	5970.3	2.31	**<0.001**	14.5	17.4%
Stand(Site(Ecoregion))	18	2589.7	1.65	**<0.001**	16.0	19.2%
Residual	72	1566.1			39.6	47.5%
Ant Functional Groups						
Ecoregion	1	10354	2.71	0.066	11.7	17.8%
Site(Ecoregion)	4	3821.6	2.61	**0.003**	12.1	18.5%
Stand(Site(Ecoregion))	18	1463.4	1.63	**0.003**	11.9	18.1%
Residual	72	899.2			30.0	45.7%
Spider Species						
Ecoregion	1	15822	1.82	0.058	12.2	11.7%
Site(Ecoregion)	4	8706	1.82	**<0.001**	15.7	15.1%
Stand(Site(Ecoregion))	18	4778.7	1.53	**<0.001**	20.4	19.6%
Residual	72	3120			55.9	53.7%
Spider Functional Groups						
Ecoregion	1	4849.3	2.01	0.089	7.1	13.5%
Site(Ecoregion)	4	2415.2	1.80	**0.023**	8.2	15.5%
Stand(Site(Ecoregion))	18	1343.8	2.42	**<0.001**	14.0	26.5%
Residual	72	554.9			23.6	44.5%

Table 3. Multiple regressions of tree-level alpha and beta diversity as predicted by stand-level measurements of climate, landscape structure and tree species richness. Regression coefficients of best models as indicated by AICc model selection. All predictor variables were converted to Z scores (SE) to allow for comparison of strength of effects.

	df	Patch Connectedness	Patch Edge:Area	Tree Richness	Isothermality	Temp Warm Month	Precipitation Seasonality	R^2
Alpha								
Ant Species	2						-0.73 (0.22)	0.53
Ant Func. Group	3	0.44 (0.18)					-0.60 (0.18)	0.72
Spider Species	1							---
Spider Func. Guild	3		-0.99 (0.25)				-1.27 (0.24)	0.70
Beta								
Ant Species	4	0.82 (0.21)		0.49 (0.20)			0.86 (0.21)	0.63
Ant Func. Group	2					-0.58 (0.26)		0.33
Spider Species	2				-0.54 (0.27)			0.29
Spider Func. Guild	3			-0.52 (0.23)			0.49 (0.23)	0.44

Figure 1. Standard effect sizes (SES) of the observed diversity partitions and the diversity deviations from a null model across the hierarchical scales (within trees, among trees, stand, site, and region) for taxonomic and functional diversity. Blue triangles are spiders, pink circles are ants.
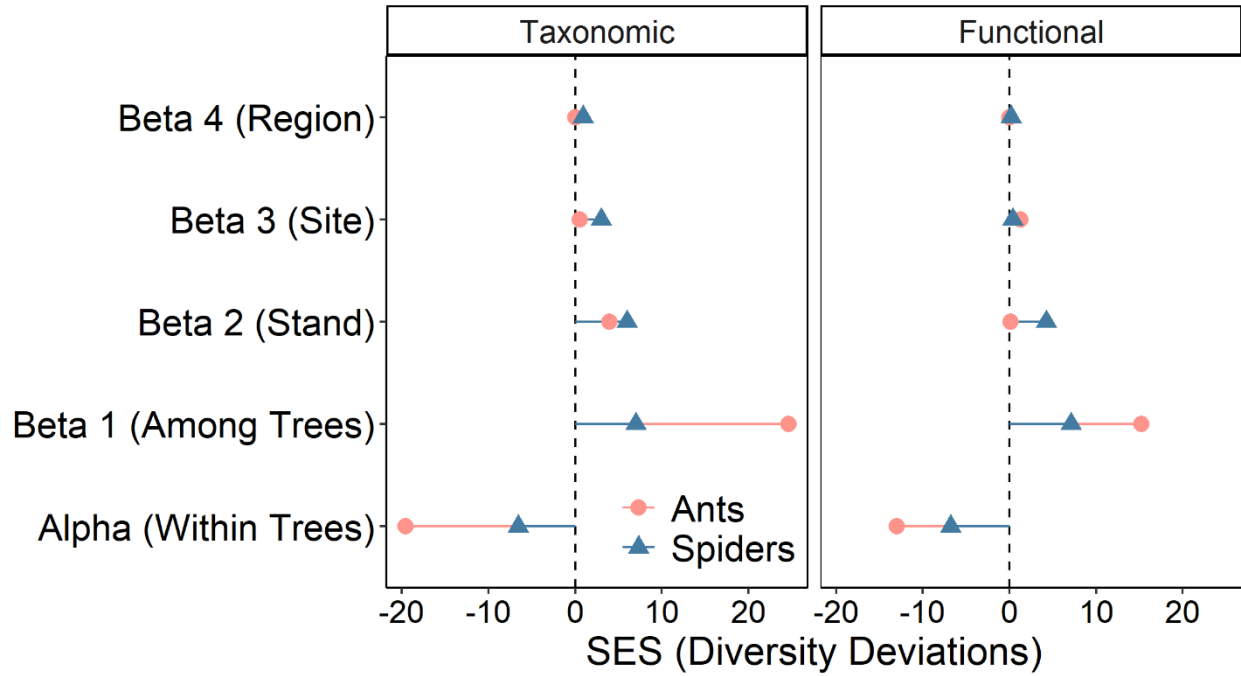
Figure 2. Sample-based rarefaction curves of ant (A) and spider (B) species by number of host trees sampled. Ash, Hackberry, Sycamore, and Walnut trees are not shown, because of few individual trees sampled (< 5 for each species). Number of points on a curve and length of the curve represent the number of individual trees fogged. Ants and spiders show differential patterns among tree species of observed (O) and Chao1 estimated (E) species richness.
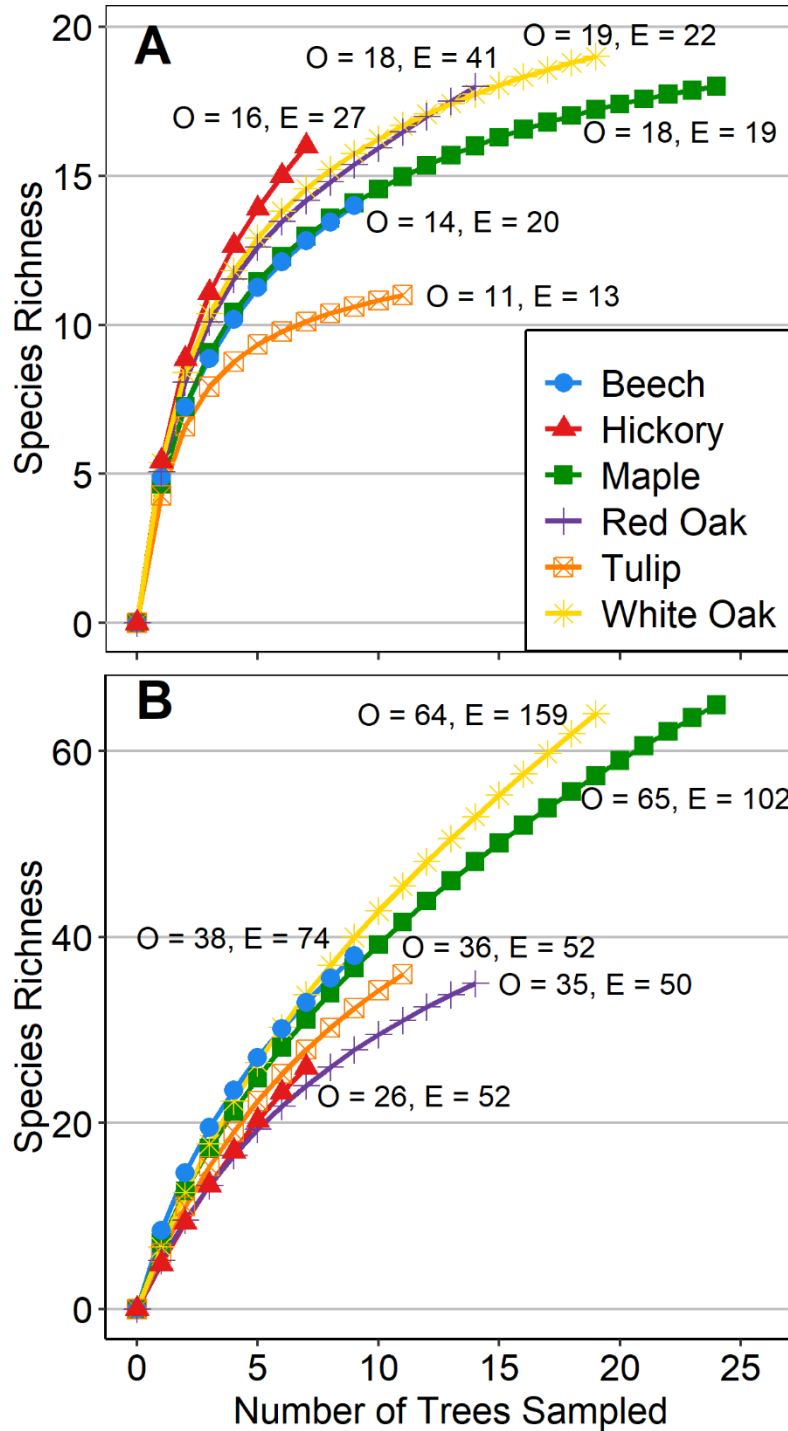
Figure 3. Distance-based redundancy analysis (dbRDA) of stand-level variation in composition based on Bray-Curtis dissimilarities of square-root transformed abundance of ant species (A), ant functional groups (B), spider species (C), and spider functional groups (D). Vectors correspond to predictor variables in best model as determined by model selection. The circles correspond to vector lengths that would have a correlation coefficient of 1 with a given axis, strength of correlation for vectors are scaled to this circle. Yellow symbols are stands within sites in the North-Central Till Plains and purple symbols are stands within sites in the Western Allegheny Plateau. Sites are designated by different symbol shapes.