

1 **Using remote camera traps to assess mammal and bird assemblages**  
2 **across a complex environmental landscape**

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32 **Abstract**

33           Animals must navigate a complex mosaic of habitat types, both natural and  
34 artificial. As artificial habitats (e.g., agricultural fields) become increasingly abundant in  
35 many landscapes, species will be affected differently, depending on their habitat  
36 preferences. We investigated the diversity, richness, abundance, and biomass of  
37 mammals and birds with remote camera traps that optimized the capture of both large and  
38 small animals. Camera traps allowed us to capture natural rates of mammals and birds,  
39 which is difficult to obtain using human observers who can affect the behavior of animals  
40 and are limited in their spatio-temporal scope and ability to assess nocturnal  
41 communities. Our camera trap arrays were established along two transects in a local  
42 conservation reserve; one transect ran from an agricultural field to an upland forest and  
43 another from a wetland to an upland forest. Over the 6-week study our cameras recorded  
44 2,245 images, within which we observed 483 individuals comprising 16 species of  
45 mammals and birds. Our data showed that species composition and abundances were  
46 only marginally different between the two transects, with species common to both  
47 transects not exhibiting any statistical difference in abundances. Coyotes and armadillos  
48 were unique to the riparian transect, and many more bird species were present along the  
49 riparian transect than the agricultural transect. Diversity, richness, and total community  
50 biomass did not differ significantly between the two transects nor along each transect but  
51 there were non-significant trends in predicted directions. Our results revealed that fewer  
52 species use the forest immediately adjacent to the agricultural field, but more species use  
53 the wetland and the forest immediately adjacent to the wetland. Our results corroborate  
54 other studies revealing that certain species are more common in forested areas but also  
55 that some species thought to prefer forested areas may actually be more habitat  
56 generalists than previously thought.

57

58 **Keywords**

59 diversity, edge effects, species composition, habitat heterogeneity, biomass, traits,  
60 riparian, agriculture, forest conversion

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## 63 **Introduction**

64           Animals must navigate landscapes composed of a heterogeneous mix of habitat  
65 types. As human activities modify and degrade habitats, landscapes are transforming into  
66 a mix of natural and artificial habitats [1]. More than 75% of deciduous forests in Eastern  
67 and Midwestern North America were cleared by 1850, primarily to create agricultural  
68 fields [2]. The clearing of these forests has changed the landscape matrix from primarily  
69 forested to agricultural fields [1-2]. This fragmentation of forests over the last two  
70 centuries has decreased landscape connectivity [3-4], isolated populations sensitive to  
71 these changes and increased inbreeding in those species [5-6], and produced more field-  
72 forest edges, thus increasing edge effects on forest interior species [7-9]. While these  
73 changes are detrimental to many habitat specialist species, habitat generalists often  
74 benefit from them [10]. As a result, changes in the landscape can affect species  
75 differently.

76           Eastern and Midwestern North American forests contain mammal and bird  
77 species that are both adversely and beneficially affected by landscape modifications. For  
78 example, white-tailed deer (*Odocoileus virginianus*) and nine-banded armadillos  
79 (*Dasypus novemcinctus*) are both forest interior species [11-14]. As such, we expect these  
80 species to be relatively infrequent in agricultural fields compared to upland and riparian  
81 forests. On the other hand, species such as raccoons (*Procyon lotor*), coyotes (*Canis*  
82 *latrans*), and grey squirrels (*Sciurus carolinensis*) are habitat generalists and will likely  
83 be equally common in forested and agricultural habitats [15-17]. Understanding exactly  
84 how these species respond to landscape changes and navigate a heterogeneous complex  
85 of habitat types is important for wildlife management [18].

86           Emerging technologies have advanced methodologies in ecology and wildlife  
87 monitoring. Automated computer imaging [19], drone technology [20-21], and motion-  
88 activated camera-traps [22-24] have provided high-throughput methods that decrease  
89 manual labor. Camera traps, for example, enable researchers to non-invasively record the  
90 abundances of a wide range of animals [25-26], including rare and endangered species  
91 [22, 27-28]. Camera traps require much less work than the manual labor required to  
92 extensively sample communities in order to properly measure species richness and  
93 abundances [23, 25], and these methods can greatly increase data throughput [19, 23, 29].

94 Furthermore, camera traps can provide information regarding an animal's phenotype,  
95 including traits such as body size and body condition [29].

96 In this study, we used camera trap arrays to examine diversity, richness, abundance,  
97 and biomass of mammals and birds along two transects that span different ecological  
98 gradients. The first transect ran from an agricultural field to an upland forest. The second  
99 transect ran from a wetland to an upland forest. We predicted that diversity, species  
100 richness, and biomass would be higher along the riparian transect, as species that are  
101 found in both upland forests and wetlands may be present. We predicted that species  
102 compositions and abundances would be different between the transects, with forest-  
103 oriented species (white-tailed deer, armadillos) more common on the riparian transect and  
104 species that are habitat generalists (coyote, raccoons, squirrels, and Virginia opossums)  
105 found equally between the transects.

106

## 107 **Materials and methods**

### 108 *Study site*

109 Our study was conducted at Lindenwood University's Daniel Boone Field Station,  
110 located in St. Charles County, MO (Lat: 38.652777; Long: -90.854376). This 404.7  
111 hectare field station (Fig. 1) maintains an annually harvested, 6.5 hectare hay field  
112 bordered by a mixed deciduous forest dominated by black oak (*Quercus velutina*), post  
113 oak (*Quercus stellata*), and white ash (*Fraxinus americana*). Ten small wetlands are  
114 interspersed throughout the forested area, providing an important local water resource for  
115 birds and mammals during drier summer months. Climate at the field station is highly  
116 seasonal, with the average temperature during the study of 24.2 °C and daily average  
117 precipitation of 1.68 cm.

118

119 **Fig 1: Map of the Lindenwood University's Daniel Boone Field Station.** Map shows  
120 the agricultural transect (orange) and the riparian transect (blue). The hay field is at the  
121 southern end of the agricultural transect and the small pond is at the western end of the  
122 riparian transect.

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127 *Data collection*

128 Remote camera traps were used to monitor mammal and bird assemblages along two 300  
129 m transects, both positioned to span distinct environmental gradients across the field  
130 station (Fig 1). Transect 1 ran from the edge of the 6.5 hectare hay field into the  
131 surrounding upland forest, while transect 2 ran from a small wetland (~125 m<sup>2</sup>) into the  
132 surrounding forest. The wetland at the beginning of transect 2 was bordered by forest on  
133 three sides, and by a small, mesic meadow to the north. Puddles often formed along  
134 transect 2 after heavy rains, primarily near 142 m (Fig 1). Transect 1 and transect 2 are  
135 referred to as the agricultural and riparian transects, respectively, throughout this study.

136 Monitoring of each transect was conducted over a 32-day period (8 June through  
137 10 July 2015). A total of 42 randomly-determined locations (plots) along each transect  
138 were monitored each for 48 or 72 h (depending on access to field site), with a total of  
139 three plots monitored simultaneously on each transect (the order in which plots were  
140 sampled was also randomly determined). At each plot, three infrared (IR) motion-sensor  
141 game cameras (Browning Model BTC-5) were positioned so that the fields of view  
142 overlapped, optimizing detection of small to large birds and mammals (Fig 2). Two of the  
143 cameras were attached to a single tree – one 20 cm and the other 50 cm above the  
144 substrate; both pointing in the same direction – while the third camera was placed 1–5  
145 meters away from the first two cameras at 50 cm above the ground on a tree so that its  
146 field of view was perpendicular to the other two cameras (Fig 2). All cameras were aimed  
147 parallel to the ground, and we assume that the total area covered by the three cameras in  
148 each plot was approximately the same for all 84 plots. Vegetation in front of the cameras  
149 was removed to prevent it from obscuring the field of view. Cameras were programmed  
150 to capture images immediately after motion was detected, with subsequent photos  
151 delayed five seconds to reduce multiple images of the same individual being recorded.  
152 The field of view for each camera was 55°. The limits of the IR trigger and the IR flash  
153 illumination were 13 m and 30.5 m, respectively. Image resolution was set at 1920 x  
154 1080 pixels, with each image also recording the time and date it was taken. This project  
155 conformed to the legal requirements for the use of vertebrates in research and was  
156 approved by the University of Illinois' Institutional Animal Care and Use Committee  
157 (Protocol Approval # 15074).

158

159 **Fig 2: Details of our 3-camera set up at each plot.** (A) Shows a photo of our field  
160 setup, with cameras circled in red. (B) Schematic of the setup from above, showing the  
161 overlap in the field of views of the three cameras at each plot. See main text for more  
162 details of our setup.

163

164 Additional environmental data was taken at each plot including: i) canopy cover  
165 (%) calculated with a spherical densiometer; ii) leaf-litter depth (mm) was the average of  
166 four random locations near the center of each plot measured with a hand ruler; and iii)  
167 environmental temperature ( $^{\circ}\text{C}$ ), which we measured with iButtons (Maxium Integrated,  
168 San Jose, CA) every hour. The iButtons were deployed for the duration that the camera  
169 traps were set at each plot and were used to determine the maximum and average  
170 temperatures of the plot.

171

### 172 *Image analysis*

173 The taxonomic identity of all birds and mammals in each image was determined  
174 using published literature and expert opinion. While most individuals could be identified  
175 to species, squirrels (*Sciurus* spp.) and mice (*Peromyscus* spp.) were only identified to  
176 genus (for simplicity, throughout the rest of the paper we refer to these taxonomic groups  
177 as species). Images of the same species (or genus for *Sciurus* and *Peromyscus*) taken  
178 within 10 min of each other at the same plot were considered the same individual, unless  
179 this was obviously untrue (e.g., different body sizes, antlered versus non-antlered deer).  
180 The body length of all mammals was estimated from each camera trap image by  
181 comparison to standardized images from each plot that included a human observed at  
182 specific distances from the cameras. Published length-weight regressions were used to  
183 estimate body mass; for deer we used  $W = 0.0287L^{3.03}$ , while for all other mammals we  
184 used  $W = 0.0374L^{2.92}$ , where  $W$  = weight and  $L$  = length [30]. We did not calculate the  
185 body weight of birds because it was often difficult to determine their lengths. Mammal  
186 biomass was calculated by summing all individuals at each plot and was standardized per  
187 day. For images in which body length could not be estimated, typically because the full  
188 length of the individual was obscured, an average for that species was used (this  
189 comprised a total of 52% of individuals).

190

191 *Statistical analyses*

192 *Environmental Variables:* Each plot was binned according to their distance from the hay  
193 field or wetland, with each bin spanning 50 m (i.e., bin 1 contained all plots between 1–  
194 50 m, bin 2 contained all plots between 51–100 m, etc., to 300 m). We then used one-way  
195 analysis of variance tests (ANOVA) to determine differences in environmental variables  
196 along each transect, where environmental variables (average temperature, maximum  
197 temperature, leaf litter depth, and percent canopy cover) were response variables, and bin  
198 number was the explanatory variable. We used two-tailed, Welch’s t-tests to determine  
199 differences in environmental variables between the two transects.

200 *Abundance and Composition:* To account for different sampling effort across plots,  
201 we calculated abundance as the number of individuals seen per day for each  
202 species/genus. To determine differences in species composition and abundances of each  
203 species both between and along transects we used a multi-response permutation  
204 procedure (MRPP) with a Bray-Curtis distance measure [31]. MRPP is more robust than  
205 discriminant analysis or MANOVA for species composition data, which are frequently  
206 non-normally distributed [31].

207 *Diversity, Richness, and Biomass:* We used general linear models (GLMs) in a  
208 model selection analysis to determine which ecological parameters best predict diversity,  
209 richness, and biomass. We used the per day abundances to estimate diversity using the  
210 Shannon-Wiener index [32]. Preliminary analysis using correlations and t-tests among  
211 the parameters revealed which factors and interaction terms were likely to be important in  
212 influencing diversity, richness, and biomass [33]. For each analysis (diversity, richness,  
213 and biomass), we began with models containing distance, transect type, maximum  
214 temperature, average temperature, litter depth, percent canopy cover, transect\*distance,  
215 transect\*maximum temperature, transect\*litter depth, transect\*percent canopy cover,  
216 distance\*litter depth, and distance\*percent canopy cover as explanatory variables. To  
217 determine which models best explained diversity, richness, and biomass, we used an  
218 information theoretic approach in which models were selected based on their Akaike’s  
219 information criterion corrected for small sample size (AIC<sub>c</sub>) [34-35]. We calculated AIC<sub>c</sub>  
220 values using the *AICcmodavg* package in R [36-37]. We used the *step()* function in R to

221 generate a subset of models [33, 37]. We considered models with the lowest  $AIC_c$  values  
222 to be the models of best fit, and we ranked models based on  $\Delta AIC_c$ , where  $\Delta AIC_c = AIC_i$   
223  $- AIC_m$  and  $AIC_i$  is the  $AIC_c$  value of model  $i$  and  $AIC_m$  is the  $AIC_c$  value of the model of  
224 best fit. When the  $\Delta AIC_c$  was less than two, indicating that both models substantially  
225 supported the data, we used the normalized Akaike model weights ( $w_{im}$ ) to determine the  
226 best model, where  $w_{im} = \exp(-0.5 \times \Delta AIC_i) / \sum_{i=1}^R \exp(-0.5 \times \Delta AIC_i)$  [35]. The normalized  
227 weight of each of the best models was less than 0.9, indicating other models were  
228 supported by the data, so we performed model averaging which provides more robust  
229 model variances and increases the reliability of parameter estimates [34]. We included a  
230 final subset of models that had cumulative model weights of  $\geq 0.95$  [38]. To determine  
231 the relative importance of each term in the models, we calculated the normalized Akaike  
232 weight for each parameter ( $w_{ip}$ ), which is the sum of the  $w_{im}$  in which that parameter is  
233 present ( $w_{ip} = 1$  indicates a parameter present in all models). We calculated the  
234 confidence intervals of the slopes between each parameter and diversity, species richness,  
235 and biomass to determine when those parameters may have significant effects.  
236 Additionally, we performed ANOVAs to determine if diversity, richness, and biomass  
237 differed along each transect (see above section “*environmental variables*” for binning  
238 procedure), and we used two-sided, Welch’s t-tests to determine differences between  
239 transects.

240

## 241 **Results**

### 242 *Environmental variables*

243 Average temperature was higher on the agricultural transect than on the riparian  
244 transect (t-test;  $t = 2.149$ ,  $df = 74.69$ ,  $p = 0.035$ ). Average temperature varied along the  
245 agricultural transect (Fig 3A; ANOVA:  $F = 3.124$ ,  $df = 5, 32$ ,  $p = 0.021$ ), with significant  
246 differences occurring between bin two (51–100 m) and bin six (251–300 m;  $p = 0.027$ )  
247 and between bin two and bin three (101–150 m;  $p = 0.030$ ). Average temperatures did not  
248 differ along the riparian transect (Fig 3A;  $F = 0.282$ ,  $df = 1, 37$ ,  $p = 0.598$ ). Maximum  
249 temperature was higher on the agricultural transect (Figure 3B; t-test:  $t = 2.893$ ,  $df =$   
250  $70.41$ ,  $p = 0.005$ ). Maximum temperature did not vary with distance along the  
251 agricultural (Fig 3B;  $F = 1.233$ ,  $df = 5, 32$ ,  $p = 0.317$ ) or the riparian transect (Figure 3B;



252 ANOVA:  $F = 1.218$ ,  $df = 1, 37$ ,  $p = 0.277$ ). Litter depth did not vary between the  
253 transects (Fig 3C; t-test:  $t = 0.428$ ,  $df = 74.99$ ,  $p = 0.670$ ). Litter depth did increase with  
254 distance from the hay field (Fig 3C; ANOVA:  $F = 4.533$ ,  $df = 5, 32$ ,  $p = 0.003$ ). Along  
255 the agricultural transect, a Tukey's Honest Significant Differences test found that litter  
256 depths were significantly different between bin one (1–50 m) and bin four (151–200 m;  $p$   
257 = 0.053), bin one and bin five (201–250 m;  $p = 0.007$ ), and bin one and bin six (251–300  
258 m;  $p = 0.003$ ). There was no change in litter depth along the riparian transect (Fig 3C;  
259 ANOVA:  $F = 2.554$ ,  $df = 1, 37$ ,  $p = 0.119$ ). The canopy cover was greater along the  
260 riparian transect (Fig 3D; t-test:  $t = -2.397$ ,  $df = 68.08$ ;  $p = 0.019$ ). Along the agricultural  
261 transect, canopy cover was lowest nearest the hay field (Fig 3D; ANOVA:  $F = 4.443$ ,  $df$   
262 = 5, 32,  $p = 0.003$ ). The canopy cover was significantly different between bin one and  
263 every other bin number (bin two:  $p = 0.021$ ; bin three:  $p = 0.002$ ; bin four:  $p = 0.013$ ; bin  
264 five:  $p = 0.038$ ; bin six:  $p = 0.007$ ). The canopy cover did not change along the riparian  
265 transect (Fig 3D; ANOVA:  $F = 0.446$ ,  $df = 1, 37$ ,  $p = 0.508$ ).

266

267 **Fig 3: Environmental variables along and between transects.** Box plots of  
268 environmental variables at different distances along the agricultural (left side) and  
269 riparian (right side) transect, with comparisons between the two transects in the middle.  
270

### 271 *Species Composition and Abundances*

272 We recorded at least one mammal or bird from 92 % of the plots we sampled; 38 of 42  
273 plots along the agricultural transect and 39 of 42 plots along the riparian transect. In total,  
274 we captured 2,245 images that included at least one mammal or bird, which we estimated  
275 to represent 483 individuals. For mammals, this consisted of 231 squirrels (*Sciurus* spp.),  
276 81 white-tailed deer (*Odocoileus virginianus*), 64 Virginia opossums (*Didelphis*  
277 *virginiana*), 36 deer mice (*Peromyscus* spp.), 38 raccoons (*Procyon lotor*), 6 armadillos  
278 (*Dasypus novemcinctus*), and 3 coyotes (*Canis latrans*). There were a total of 24 birds  
279 captured, with tufted titmouse (*Baeolophus bicolor*), wild turkeys (*Meleagris gallopavo*),  
280 and the northern cardinal (*Cardinalis cardinalis*), occurring on both transects and cooper's  
281 hawks (*Accipiter cooperii*), blue jays (*Cyanocitta cristata*), wood thrushes (*Hylocichla*  
282 *mustelina*), and barred owls (*Strix varia*) found only on the riparian transect. Due to their  
283 low numbers, all bird species were included as a single taxonomic group in subsequent

284 analyses. Using a MRPP, we found a marginally significant difference in species  
285 composition and abundances between the two transects ( $A = 0.0077$ ,  $p = 0.0706$ ).  
286 Squirrels (the most common species on both transects), white-tailed deer and raccoons  
287 exhibited similar per day abundances between our two transects (Table 1; Fig 4A, B).  
288 Virginia opossums and mice were both twice as abundant on the agricultural transect,  
289 whereas birds were over three times more abundant on the riparian transect (Table 1; Fig  
290 4A, B). Armadillos and coyotes were recorded only on the riparian transect (Table 1; Fig  
291 4A, B), and no species were found exclusively on the agricultural transect.

292

293 **Fig 4: Species abundances on along each transect.** Abundance per day ( $\pm$ SD) of each  
294 species/genus at different distances along the A) agricultural and B) Riparian transects.  
295 Each color represents a different distance along the transects. Red = 1-50m, orange = 51-  
296 100m, purple = 101-150m, green = 151-200m, blue = 201-250m, and yellow = 251-  
297 300m.

298

299 Along the agricultural transect, squirrels, white-tailed deer, raccoons, and birds  
300 were most abundant at intermediate distances from the hay field (Fig 4A). Virginia  
301 opossums were uncommon nearest the hay field edge, becoming more abundant moving  
302 away from the hay field (Fig 4A). Mice were most common farther from the hay field,  
303 although they also had relatively high abundances near the hay field (Fig 4A). Along the  
304 riparian transect, white-tailed deer, Virginia opossums, raccoons, and armadillos had the  
305 highest abundances at intermediate distances from the wetland (Fig 4B). Squirrels and  
306 mice had two distinct modes of abundance, near the wetland and at intermediate distances  
307 from the wetland (Fig 4B). Birds were most abundant near the wetland and at plots  
308 farthest from the wetland (Fig 4B). However, despite apparent systematic differences in  
309 the abundances of different species/genera at different distances along each transect, a  
310 MRPP found no difference in species composition and abundances at different distances  
311 along either the agricultural transect ( $A = -0.0079$ ,  $p = 0.6065$ ) or the riparian transect ( $A$   
312  $= 0.0021$ ,  $p = 0.6894$ ).

313

314 *Diversity, species richness and biomass*

315 The model selection process varied between diversity, species richness, and biomass  
316 (Table 1A, B, C, respectively). In the model selection for diversity, three models had

317 cumulative weights  $\geq 0.95$  (Table 1A), with the best-fitting model containing distance,  
318 transect, maximum temperature, average temperature, litter depth, transect\*maximum  
319 temperature, transect\*litter depth, and distance\*litter depth. The model weight was less  
320 than 0.9 for this model, but the next best-fitting model, which included canopy cover, had  
321 much lower weight and a  $\Delta AIC_c$  above two (Table 1A). In the model selection analysis  
322 for species richness, four models had cumulative weights of  $\geq 0.95$  (Table 1B), with the  
323 best-fitting model containing distance, litter depth, and the distance-litter depth  
324 interaction. The best-fitting model had a comparably low model weight than the second  
325 best-fitting model, which included average temperature, and the  $\Delta AIC_c$  value of the  
326 second best-fitting model was less than two. The model selection for biomass produced  
327 four models with cumulative model weights  $\geq 0.95$  (Table 1C), with the best-fitting  
328 model containing distance, transect, maximum temperature, average temperature,  
329 transect\*distance, transect\*maximum temperature (Table 1C). The second best-fitting  
330 model, which included litter depth, had a comparably high model weight and a  $\Delta AIC_c$   
331 value less than two. Distance is the only parameter common to the best fitting models for  
332 diversity, richness, and biomass. Common parameters between diversity and richness  
333 include distance, litter depth, and the distance-litter depth interaction.

334 The model selection analysis for diversity included eight explanatory parameters in  
335 the model of best fit (Table 1A). Diversity decreased at plots with higher average  
336 temperatures along both the agricultural and riparian transects (Fig 5A), but only  
337 decreased along the riparian transect for maximum temperature (Fig 5B). Diversity also  
338 decreased with increasing litter depth along both transects (Fig 5C). Despite being  
339 included in the best-fitting model, the slopes of these variables were not significantly  
340 different from zero (Table 1A). Likewise, diversity did not differ significantly between  
341 the agricultural and riparian transects (Fig 6A; t-test:  $t = 0.214$ ,  $df = 74.08$ ,  $p = 0.831$ ).  
342 Diversity did differ by bin number along the agricultural transects (Fig 6A; ANOVA:  $F =$   
343  $2.742$ ,  $df = 5, 32$ ,  $p = 0.036$ ). Follow-up Tukey Honest Significant Difference tests found  
344 differences in diversity between bins three and six (101–151 m and 251–300 m from the  
345 hay field;  $p = 0.048$ ). Diversity did not differ among bin numbers on the riparian transect  
346 (Fig 6A:  $F = 0.278$ ,  $df = 5, 32$ ,  $p = 0.922$ ).

347

348 **Fig 5: Effects of environmental variables on diversity, species richness, and biomass.**

349 The effects of average temperature, maximum temperature, litter depth, and percent  
350 canopy cover on diversity (A-D) and species richness (E-H), and biomass (I-L) of birds  
351 and mammals. Solid circles denote individuals observed on the agricultural transect, and  
352 open triangles denote individuals observed on the riparian transect. Lines represent the  
353 best-fit GLM for agricultural (solid) and riparian (dashed) transects.

354

355 The model selection analysis for species richness included three parameters for the  
356 model of best fit (Table 1B). Species richness increased slightly with increased litter  
357 depth along the riparian transect but not the agricultural transect (Figure 5G). The  
358 difference in these slopes was not significant though (Table 1B). Species richness did not  
359 differ between the agricultural and riparian transects (Fig 6B; t-test:  $t = -0.171$ ,  $df =$   
360  $73.93$ ,  $p = 0.864$ ). Species richness did not differ with bin number along either the  
361 agricultural (Figure 6B; ANOVA:  $F = 2.017$ ,  $df = 5, 32$ ,  $p = 0.103$ ) or riparian transects  
362 (Fig 6B; ANOVA:  $F = 0.352$ ,  $df 5, 32$ ,  $p = 0.877$ ).

363

364 **Figure 6: Diversity, species richness, and biomass along and between each transect.**

365 A) Diversity, B) species richness, and C) Biomass along the agricultural and riparian  
366 transects (left and right columns, respectively) and between the agricultural and riparian  
367 transects (middle column).

368

369 The model selection analysis for biomass included six parameters in the model of  
370 best fit (Table 1C). Biomass decreased at plots with maximum temperatures along the  
371 agricultural transect but increased with maximum temperature on the riparian transect  
372 (Fig 6C). The difference in these slopes was not significant however (Table 1C). Biomass  
373 did not differ between the agricultural and riparian transects (Fig 6C; t-test:  $t = 0.182$ ,  $df$   
374  $= 43.77$ ,  $p = 0.856$ ) did not differ with bin number along either the agricultural (Fig 6C;  
375 ANOVA:  $F = 0.447$ ,  $df = 5, 25$ ,  $p = 0.811$ ) or the riparian transects (Fig 6C; ANOVA:  $F$   
376  $= 2.173$ ,  $df = 5, 24$ ,  $p = 0.091$ ).

377

378 **Discussion**

379 Using remote camera traps, we estimated the abundance, diversity, and biomass of  
380 mammals and birds along two transects that traversed two distinct environmental  
381 gradients. Our use of multiple cameras per plot – positioned at different heights above the

382 forest floor – increased our ability to record both small and large species. Cameras placed  
383 at standard heights above the ground (~50 cm) often do not capture small mammals and  
384 birds [39,40], while cameras placed lower can miss larger mammals [40]. Having  
385 multiple cameras with overlapping fields of view also reduced the probability of missing  
386 animals due to failure of a single camera to trigger, which occurs for a variety of reasons  
387 [27, 41]. Thus, our multiple-camera setup (Fig 2) allowed us to estimate abundance,  
388 diversity, and biomass across a wider range of mammal and bird species than would be  
389 possible with just a single camera at each plot.

390 There were no differences in the abundances of species that were found on both  
391 transects. The marginally significant difference in species composition and abundance  
392 found by the MRPP between the transects was likely driven by the presence of armadillos  
393 and coyotes on the riparian transect but not on the agricultural transect as well as by the  
394 increased number of birds on the riparian transect. Several of our predictions regarding  
395 species-specific trends in abundances were supported, despite no significant differences  
396 in the abundances of most mammal species between the two transects (Fig 4A, B).

397 Armadillos were only present on the riparian transect, corroborating studies that found  
398 armadillos avoid open habitats and grasslands [11, 14]. The two species of squirrels at  
399 our site are considered habitat generalists and are quite adaptable to novel environments  
400 [15, 42-45] so it was unsurprising they occurred in high abundance on both transects  
401 (Table 1). Similarly, raccoons are a common habitat generalist in the Midwestern United  
402 States [17] and were found nearly equally between the transects.

403 Several of our other predictions regarding abundances were not supported. White-  
404 tailed deer, a species often associated with forests [12-13], were captured about equally  
405 on the two transects. While white-tailed deer prefer forested habitats, they will still use a  
406 wide range of habitats, including open fields [45]. Our study site is outside the range of  
407 mule deer, *Odocoileus hemionus*, which are closely related to white-tailed deer and found  
408 in more open areas in the western half of North America. Without the presence of mule  
409 deer, white-tailed deer may utilize open habitats and forests adjacent to open habitats  
410 more frequently than when in the presence of mule deer. Coyotes were found only on the  
411 riparian transect in our study. Coyotes are habitat generalists that will use habitats  
412 associated with their prey [16-17]. Coyotes have been shown to be one of the few species

413 that did not avoid agricultural fields [8], and it was therefore surprising that they were not  
414 captured on the agricultural transect, where their prey were equally abundant as on the  
415 riparian transect. However, coyotes may avoid cameras [39], making it difficult to  
416 conclude any patterns in their habitat use. Even on the riparian transect, coyotes were  
417 captured only three times. Virginia opossums tended to be more abundant along the  
418 agricultural transect, contrary to our prediction that they would be found about equally  
419 between the transects (Fig 4A, B).

420 Contrary to our prediction and despite higher species richness on the riparian  
421 transect, diversity was nearly equal between the two transects (Fig 6A). Two main  
422 reasons explain this pattern of diversity. First, the distribution of species is more even  
423 along the agricultural transect (Fig 4A, B). Squirrels dominate in abundance on both  
424 transects, but are relatively more dominant on the riparian transect than on the  
425 agricultural transect (Fig 4A, B). This unevenness in species abundances likely overrides  
426 the presence of two more species on the riparian transect. Second, two species of  
427 squirrels and many species of birds were respectively lumped into squirrel or bird groups  
428 in the diversity analysis. Lumping birds into a single group results in a greater  
429 underestimation in diversity on the riparian transect than on the agricultural transect. On  
430 the agricultural transect, the only birds captured were the tufted titmouse, wild turkeys,  
431 and the northern cardinal. In addition to those species, several cooper's hawks, blue jays,  
432 wood thrushes, and barred owls were found on the riparian transect.

433 The parameters in the best-fitting model for diversity included distance, transect,  
434 maximum and average temperature, leaf-litter depth, transect\*maximum temperature,  
435 transect\*leaf-litter depth, and distance\*leaf-litter depth. Of those parameters, average  
436 temperature and the distance\*leaf-litter depth had the strongest effects, in which the 95%  
437 CI of the slopes for each parameter did not cross zero (Table 1A). Diversity decreased  
438 with increased average and maximum temperatures (Fig 5A, B), a trend that is often  
439 found with increasing temperatures [46-47]. Fewer species may be able to tolerate  
440 warmer temperatures and therefore warmer plots had fewer species. Diversity also  
441 decreased with leaf-litter depth, particularly on the riparian transect (Fig 5C). This may  
442 be driven by squirrel abundances at sites with more leaf litter [44]. Where squirrel  
443 abundances are highest, they may dominate in the diversity index and result in lower

444 diversity at those sites. Mice may be less abundant where leaf litter is deep because they  
445 avoid dry hardwood litter to reduce the risk of auditory detection by predators [49].

446 The parameters in the best-fitting model for biomass included distance, transect,  
447 maximum and average temperature, transect\*distance, and transect\*maximum  
448 temperature. The slopes of all these parameters had 95% CI that included zero, indicating  
449 that none of the parameters significantly affected biomass. However, biomass increased  
450 gradually from the hay field to the upland forest (Fig 6E), a pattern we would expect if  
451 fewer species are using the hay field [8]. The diversity of mammals and birds found near  
452 the hay field was relatively low (Fig 6B). The concentration of biomass farther from the  
453 hay field and the lower species diversity supports the idea that the field may not be used  
454 by many species. On the other hand, biomass on the riparian transect was higher near the  
455 wetland and at intermediate distances (Fig 6F), and the diversity on the riparian transect  
456 decreased with distance from the wetland (Fig 6C), supporting the idea that many species  
457 are using the wetlands or areas adjacent to the wetlands. Wetlands are likely more useful  
458 for many organisms than the hay field. The wetland provides water, potentially a greater  
459 diversity of plants for herbivores to consume, and a greater diversity and abundance of  
460 prey for predator species. In fact, only on the riparian transect did we observe carnivores.

461 The relationship between biomass and temperature was opposite between the  
462 transects (Fig 5E, F). Biomass decreased with temperature on the agricultural transects  
463 and increased with temperature on the riparian transect. This pattern was more  
464 pronounced for maximum temperature (Table 3; Fig 5E, F), which varied more between  
465 the transects than average temperature (Fig 3D, E). Biomass was likely lower at warmer  
466 temperatures along the agricultural transects because plots with higher maximum  
467 temperatures were found near the hay field, where biomass was low.

468 An important caveat in the use of camera traps for wildlife studies is that it can be  
469 difficult to accurately determine density and abundances of animals that cannot be  
470 individually identified. Species with unique individual markings (e.g., tigers and jaguars)  
471 can be used in mark-recapture methods [22, 49]. When researchers are unable to identify  
472 individuals from markings, it becomes impossible to determine if each photograph  
473 represents separate individuals. However, researchers can take measures to reduce  
474 counting an individual more than once. We set our camera traps to have a five second

475 delay after a photo was taken and when more than one image of the same species (or  
476 genus for *Sciurus* and *Peromyscus*) were taken within 10 min of each other at the same  
477 plot, they were considered the same individual, unless they were obviously different  
478 individuals (e.g., different body size, antlered versus non-antlered deer). Many  
479 researchers have compared camera-trapping methods with traditional methods and have  
480 found that camera trapping provides comparable and reliable results [23-24, 50]. Others  
481 have found that camera traps under-estimated abundances and richness compared to  
482 traditional methods but these under-estimations were not significantly different from  
483 traditional methods [28, 51]. When researchers are only interested in detecting species  
484 presence and determining species richness, camera trapping is often the better method  
485 [25-26]. As such, the risk of resampling the same individuals more than once does not  
486 appear to affect the results any more than it does with traditional methods.

487 Camera traps are proving to be an invaluable tool in the toolbox of ecologists and  
488 wildlife biologists. They represent a cost-effective method for determining abundances,  
489 diversity, and richness [25, 52]. Camera traps provide the best results when they are  
490 applied to animals that can be individual identified, but still provide comparably reliable  
491 estimates on “unmarked” individuals. Indeed, their ability to capture rare and cryptic  
492 species far out-stripes traditional methods. Finally, while camera traps have been less  
493 utilized to non-invasively determine phenotypic traits, their ability to do so can greatly  
494 increase their capabilities as an ecological tool [29]. In our study, we used camera traps to  
495 estimate body size and, hence, the amount of biomass moving through each of the plots.  
496 As far as we know, this is the first study to utilize camera traps to obtain body sizes, and  
497 we conclude that future studies using camera traps can obtain body size and incorporate  
498 that information into their analyses.

499 In conclusion, we found that camera traps worked to estimate diversity, richness,  
500 abundance, and biomass of large and small mammals and birds. We found slight, non-  
501 significant differences in diversity, abundances, and biomass between a transect that  
502 traverses from a wetland to an upland forest and a transect that traverses from an  
503 agricultural field to an upland forest in eastern Missouri. Fewer species were found near  
504 the hay field while more species were found near the wetland. Armadillos and coyotes  
505 were unique to the riparian transect, while birds were more common and diverse on the



506 riparian transect. Virginia opossums were more common along the agricultural transects,  
507 but no species were unique to the agricultural transect.

508

### 509 **Author Contributions**

510 CSC contributed to the investigation, methodology, supervision, formal analysis,  
511 visualization, validation, and writing of the manuscript (both the original draft and  
512 review/editing).

513 LRC contributed to the investigation and methodology.

514 DAT contributed to the investigation and methodology.

515 JAC contributed to funding acquisition, methodology, resources, validation, and  
516 reviewing/editing the manuscript.

517 AID contributed to funding acquisition, methodology, resources, validation, and  
518 reviewing/editing the manuscript.

519

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527

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## AIC Model Selection Analyses

### A) Shannon-Wiener Diversity

Parameter	Model Rank			$\beta$	95% CI	$w_{ip}$
	1	2	3			
Constant	■	■	■	4.433	0.595 – 8.271	
Distance	■	■	■	0.002	-0.002 – 0.005	1
Transect	■	■	■	2.373	-0.796 – 5.543	1
Max Temp	■	■	■	0.020	-0.008 – 0.047	1
Ave Temp	■	■	■	-0.078	-0.136 – -0.021	1
Litter Depth	■	■	■	0.191	-0.008 – 0.390	1
% Canopy Cover		■	■	-0.001	-0.008 – 0.007	1
Transect*Max Temp	■	■	■	-0.028	-0.067 – 0.011	0.015
Transect*Litter Depth	■	■	■	-0.185	-0.434 – 0.063	1
Transect*% Canopy Cover			■	-0.003	-0.191 – 0.135	0.68
Distance*Litter Depth	■	■	■	-0.002	-0.003 – -0.001	1
AIC <sub>c</sub>	120.85	123.48	126.48			
$\Delta$ AIC <sub>c</sub>	0	2.63	5.28			
$w_{im}$	0.735	0.197	0.052			

### B) Species Richness

Parameter	Model Rank				$\beta$	95% CI	$w_{ip}$
	1	2	3	4			
Constant	■	■	■	■	1.794	-0.272 – 3.860	
Distance	■	■	■	■	0.002	-0.002 – 0.006	1
Transect			■	■	-0.006	-0.082 – 0.070	0.180
Ave Temp		■	■	■	-0.014	-0.030 – 0.445	0.464
Litter Depth	■	■	■	■	0.208	-0.002 – 0.002	1
% Canopy Cover				■	< 0.001	< -0.001 – < 0.001	0.064
Distance*Leaf Litter	■	■	■	■	< -0.001	-0.003 – < 0.001	1
AIC <sub>c</sub>	139.1	140.4	142.2	144.6			
$\Delta$ AIC <sub>c</sub>	0	1.27	3.05	5.48			
$w_{im}$	0.536	0.284	0.117	0.035			

### C) Biomass

Parameter	Model Rank				$\beta$	95% CI	$w_{ip}$
	1	2	3	4			
Constant	■	■	■	■	174280.760	-36281.94 – 384843.46	
Distance	■	■	■	■	85.485	-42.58 – 213.55	1
Transect	■	■	■	■	-138846.185	-316728.09 – 39035.72	1
Max Temp	■	■	■	■	103.712	-1265.62 – 1472.04	1
Ave Temp	■	■	■	■	-2471.299	-5545.64 – 603.05	1
Litter Depth		■	■	■	-1545.937	-5090.25 – 1998.37	1
% Canopy Cover			■	■	-117.438	-382.87 – 148.00	0.173
Transect*Distance	■	■	■	■	-123.424	-287.52 – 40.67	0.456
Transect* Max Temp	■	■	■	■	1984.147	-251.04 – 4219.33	1
Distance*Litter Depth				■			
AIC <sub>c</sub>	1412.20	1413.50	1415.2	1417.3	-0.074	-0.33 – 0.19	0.013
			5	5			
$\Delta$ AIC <sub>c</sub>	0	1.301	3.05	5.156			
$w_{im}$	0.544	0.284	0.118	0.041			

**Table 1. AIC<sub>c</sub> model selection analysis for A) Shannon-Wiener diversity indices, B) Species Richness, and Biomass for the subset of models that have a cumulative model weight of 0.95 and model-averaged parameter analysis. The black symbols indicate the presence of that parameter in the model. The AIC<sub>c</sub> values,  $\Delta$ AIC<sub>c</sub>, model weights ( $w_{im}$ ) are found on the lower part of the table. We used model-averaging to obtain parameter estimates, which are displayed on the right section of the table.**



## Figure Legends:

**Fig 1: Map of the Lindenwood University's Daniel Boone Field Station.** Map shows the agricultural transect (orange) and the riparian transect (blue). The hay field is at the southern end of the agricultural transect and the small pond is at the western end of the riparian transect.

**Fig 2: Details of our 3-camera set up at each plot.** (A) Shows a photo of our field setup, with cameras circled in red. (B) Schematic of the setup from above, showing the overlap in the field of views of the three cameras at each plot. See main text for more details of our setup.

**Fig 3: Environmental variables along and between transects.** Box plots of environmental variables at different distances along the agricultural (left side) and riparian (right side) transect, with comparisons between the two transects in the middle.

**Fig 4: Species abundances on along each transect.** Abundance per day ( $\pm$ SD) of each species/genus at different distances along the A) agricultural and B) Riparian transects. Each color represents a different distance along the transects. Red = 1-50m, orange = 51-100m, purple = 101-150m, green = 151-200m, blue = 201-250m, and yellow = 251-300m.

**Fig 5: Effects of environmental variables on diversity, species richness, and biomass.** The effects of average temperature, maximum temperature, litter depth, and percent canopy cover on diversity (A-D) and species richness (E-H), and biomass (I-L) of birds and mammals. Solid circles denote individuals observed on the agricultural transect, and open triangles denote individuals observed on the riparian transect. Lines represent the best-fit GLM for agricultural (solid) and riparian (dashed) transects.

**Figure 6: Diversity, species richness, and biomass along and between each transect.** A) Diversity, B) species richness, and C) Biomass along the agricultural and riparian transects (left and right columns, respectively) and between the agricultural and riparian transects (middle column).

Agricultural  
Transect



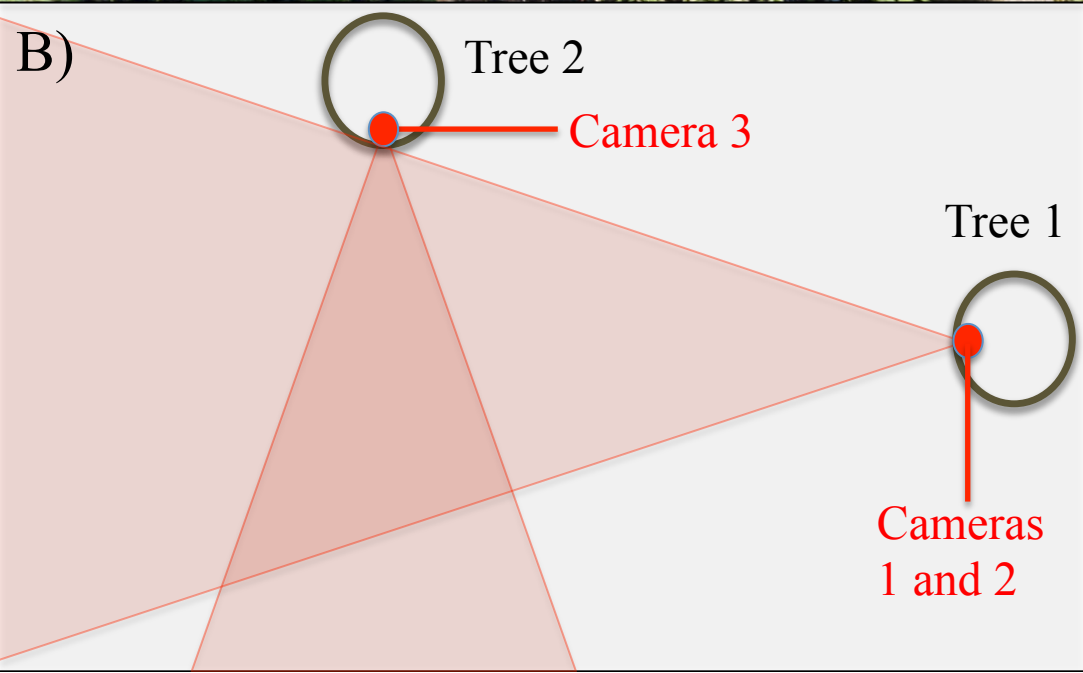
Hay Field

Pond



Riparian  
Transect



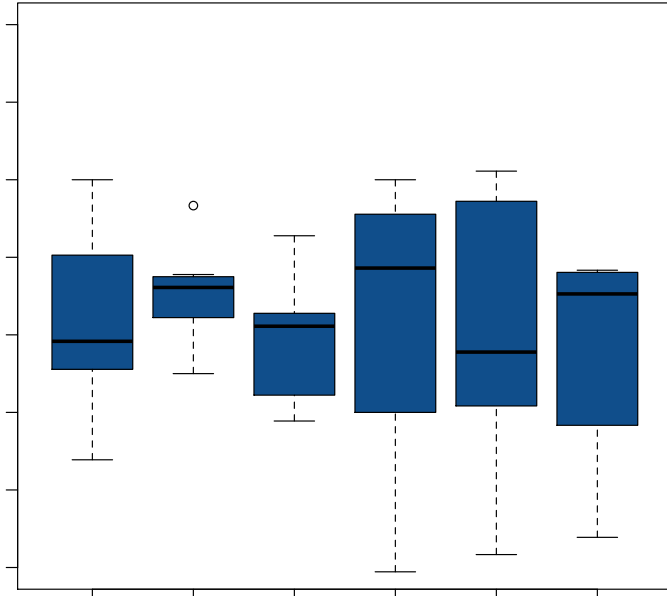
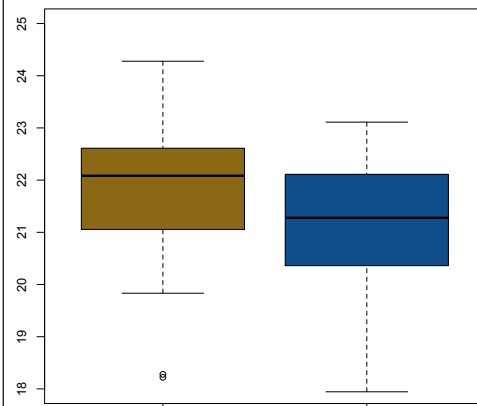
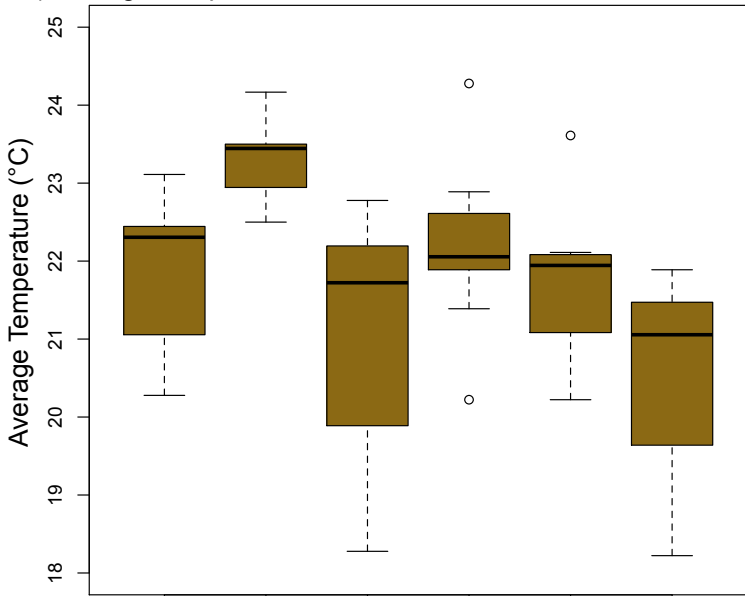


Agricultural

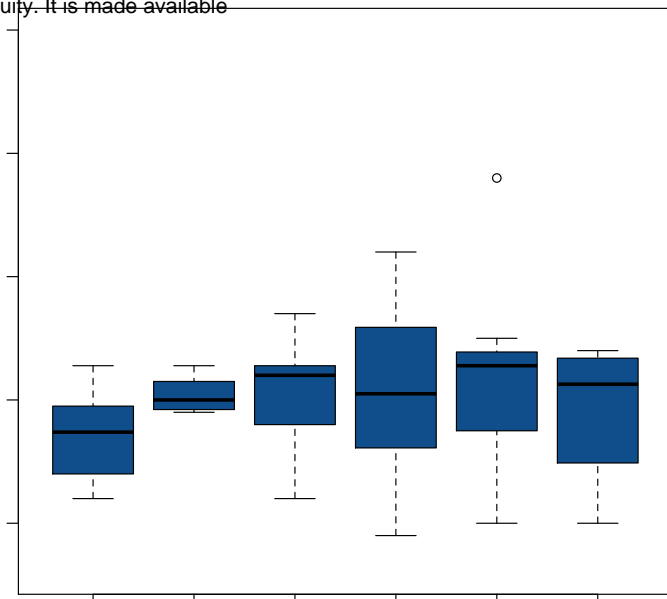
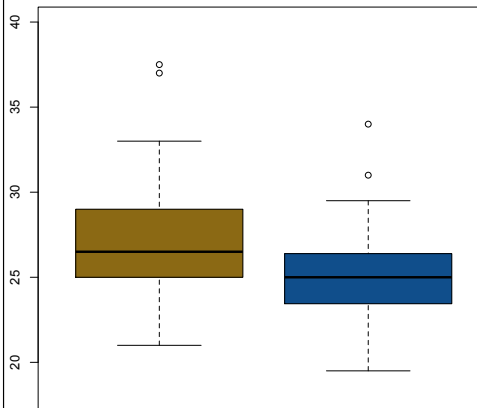
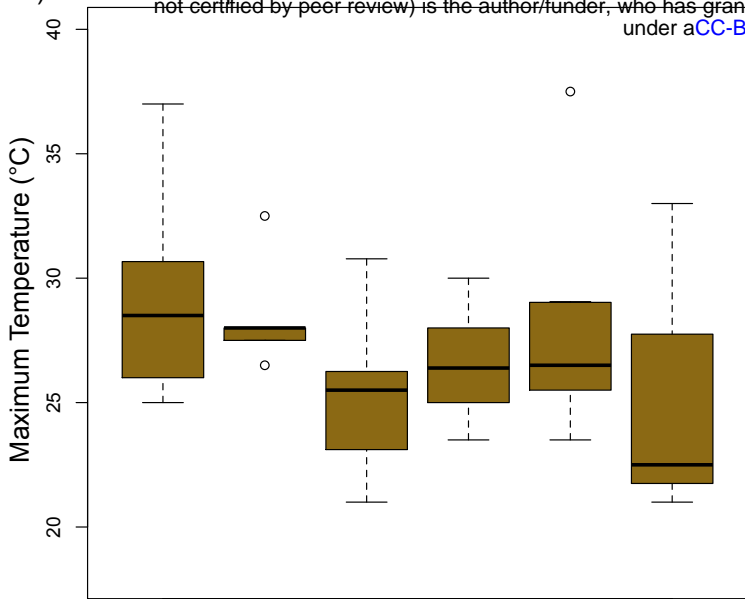
Riparian

Transect Averages  
(Agricultural/Riparian)

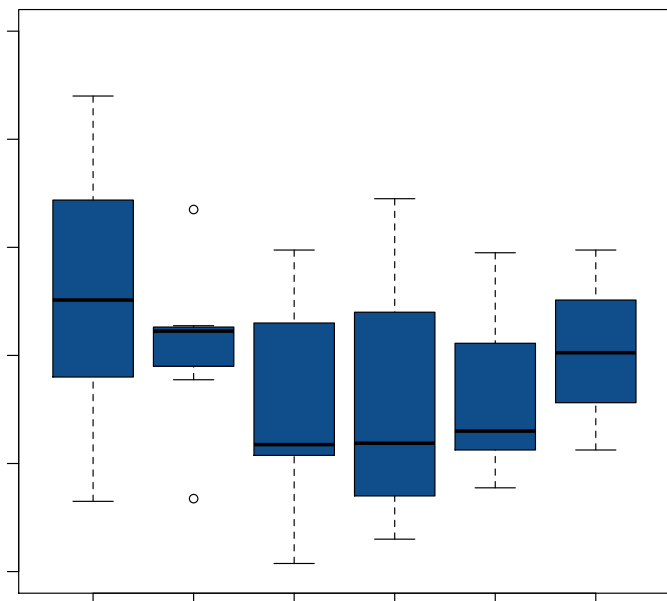
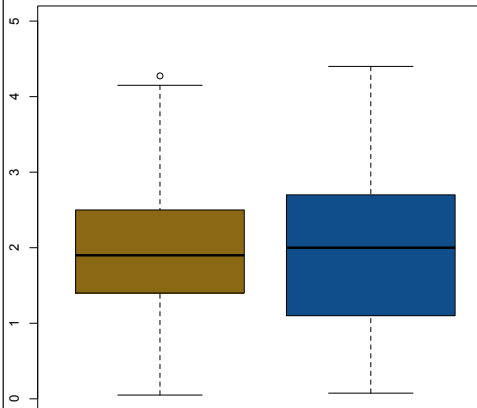
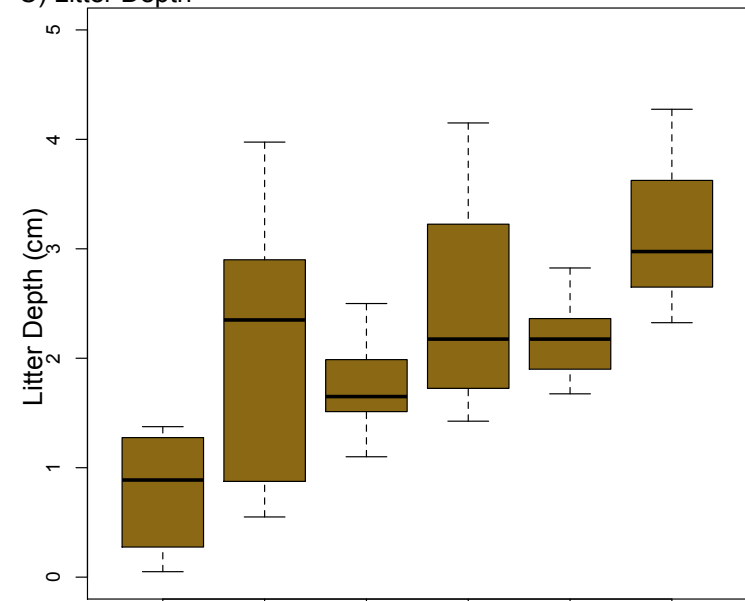
A) Average Temperature



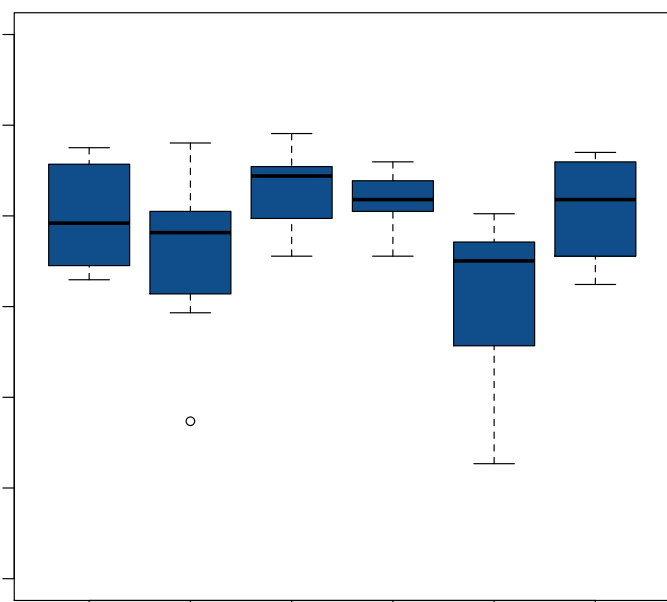
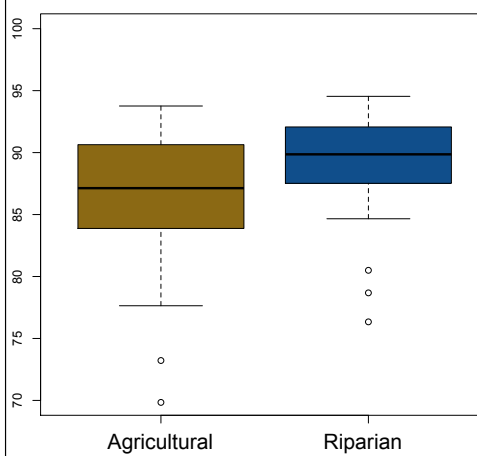
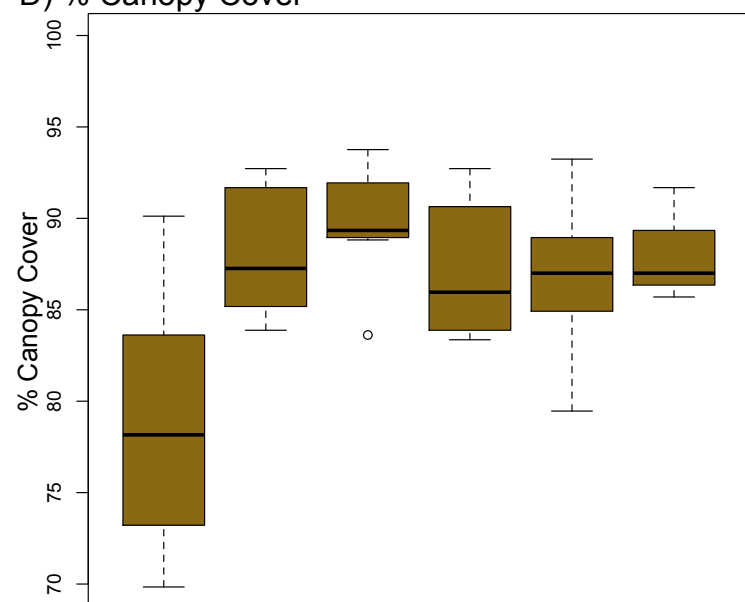
B) Maximum Temperature: <https://doi.org/10.1101/109538>; this version posted February 17, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.



C) Litter Depth



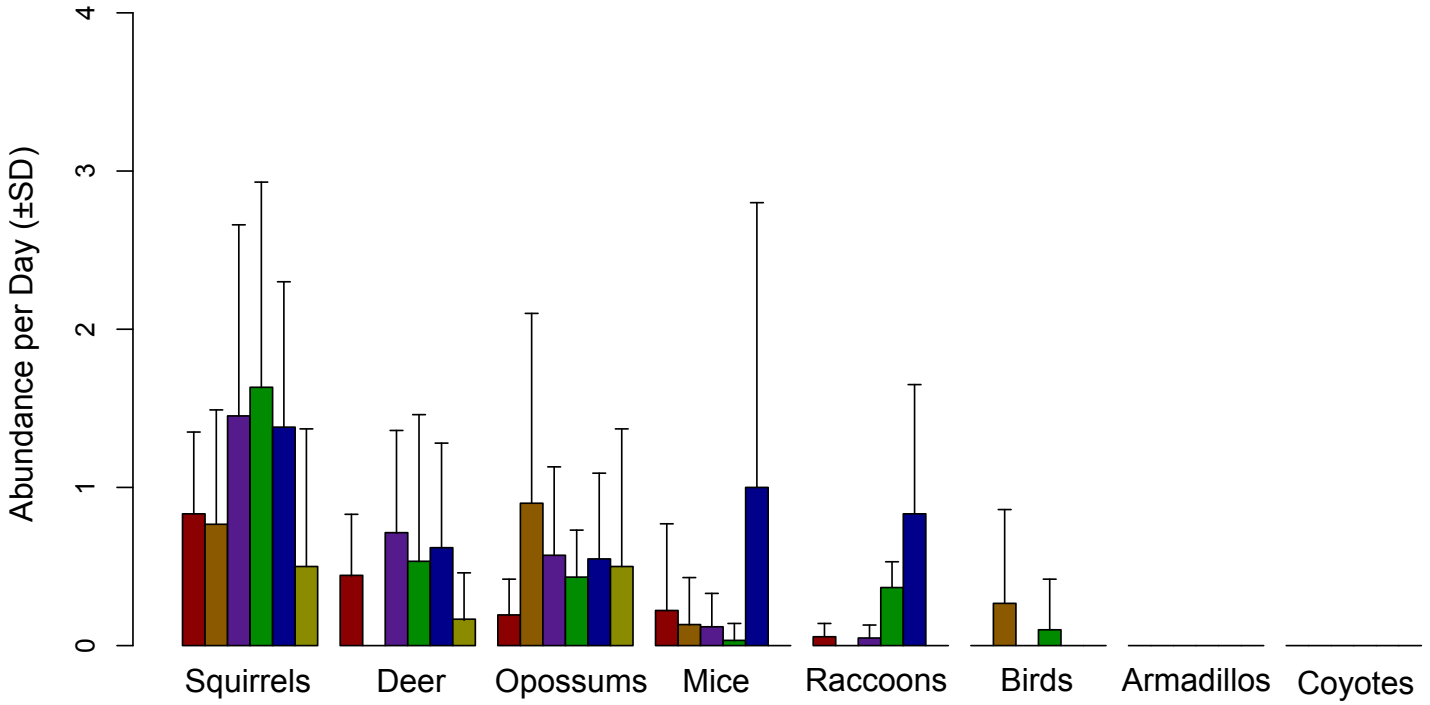
D) % Canopy Cover



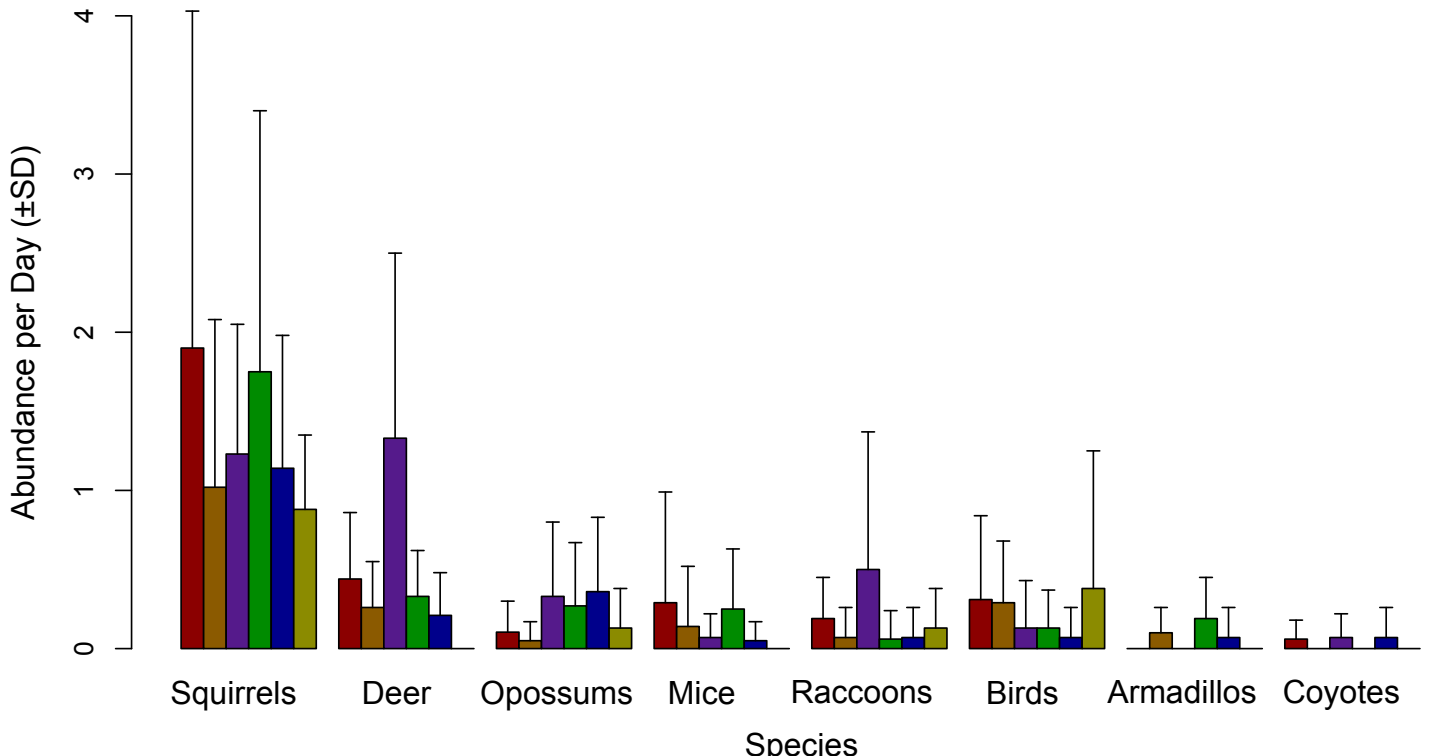
Distance from Hay Field (m)

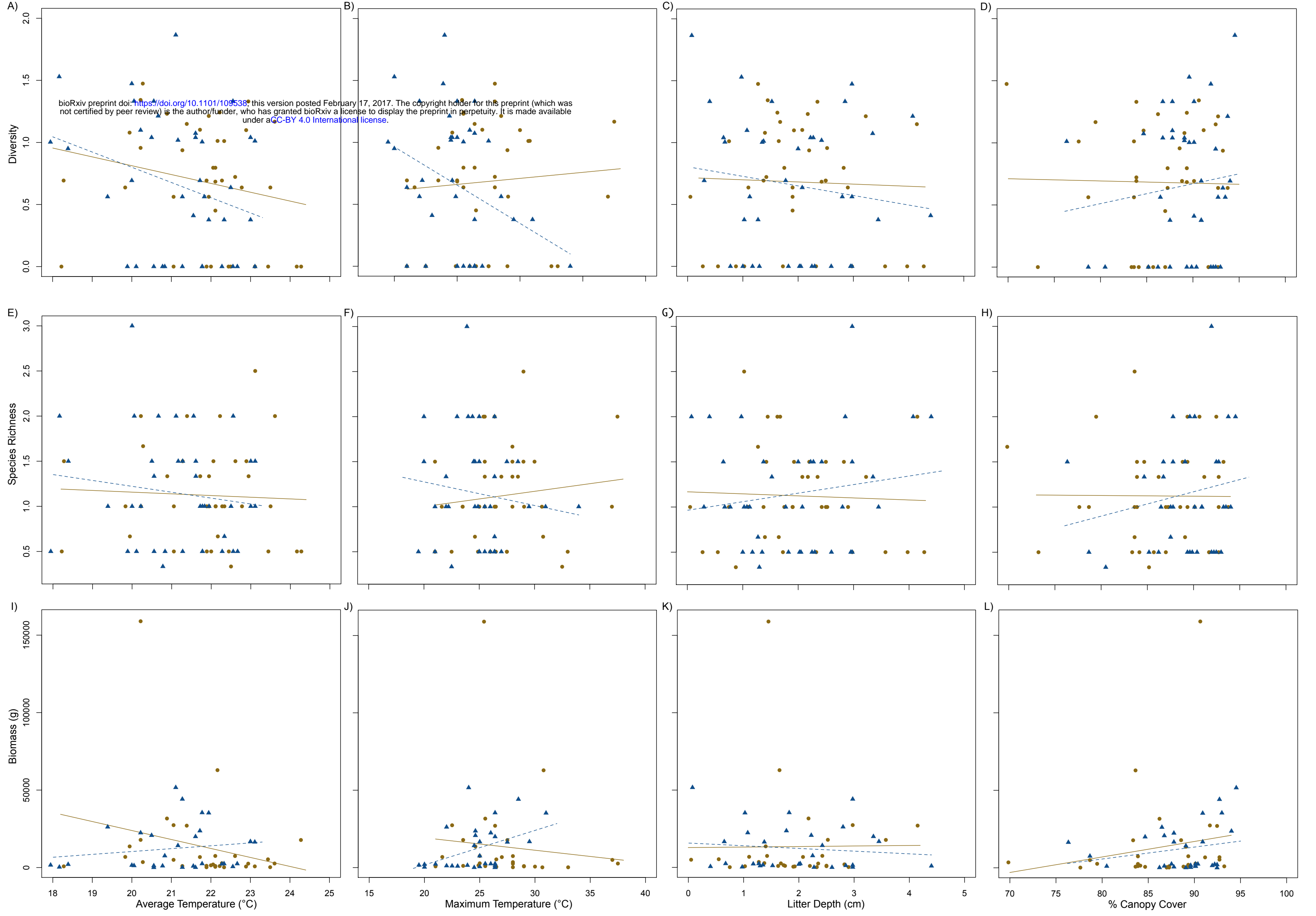
Distance from Wetland (m)

A) Agricultural



B) Riparian





## Transect Averages

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