

**1 Response of Bat Activity to Land-Cover and Land-Use Change in Savannas is Scale-,  
2 Season-, and Guild-Specific**

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23 **Abstract**

24 Tropical savannas are biomes of global importance that are under severe pressure from  
25 anthropogenic change, including land-cover and land-use change. Bats, the second-most diverse  
26 group of mammals, are critical to ecosystem functioning, but may be vulnerable to such  
27 anthropogenic stresses. However, there is little information on the response of savanna bats to  
28 land-cover and land-use change, especially in Africa. This limits our ability to develop  
29 conservation strategies for bats and maintain the ecosystem functions and services they provide  
30 in this biome. Using acoustic monitoring, we measured how guild-specific (aerial, edge, and  
31 clutter forager) bat activity responded to both fine-scale metrics of vegetation structure and  
32 landscape-scale metrics of land-cover composition and configuration across the wet and dry  
33 seasons in a savanna in southern Africa undergoing rapid land-cover and land-use change. We  
34 found that all three guilds responded more strongly to landscape metrics than fine-scale  
35 vegetation structure, although the specific metrics varied between guilds. Aerial and edge bats  
36 responded most strongly to the percent savanna cover and savanna fragmentation in both seasons  
37 while clutter bats responded to percent rural cover in the wet season and percent water cover in  
38 the dry. All three guilds responded more strongly to the landscape in the dry season than the wet  
39 season. Our results show it is possible to conserve bats, and the ecosystem services they can  
40 provide, in savannas undergoing anthropogenic land-use and land-cover change but strategies to  
41 do so must consider foraging guild, large spatial scales, and seasonal variation in bat activity.

42

43 **Key words:** Agriculture, Chiroptera, landscape ecology, savanna

44 **Highlights**

- 45 • Bats in savannas respond to land-cover and land-use change on large spatial scales
- 46 • Landscape had a greater influence on bat activity in the dry season than the wet
- 47 • Aerial and edge forager activity responded to savanna cover and fragmentation
- 48 • Clutter forager activity was best explained by rural and water cover
- 49 • Minimizing fragmentation and maintaining water promotes bat activity in modified
- 50 savannas

## 51 **1. Introduction**

52 Tropical savannas are biomes of global importance for people and wildlife (Bond and Parr, 2010;  
53 Murphy et al., 2016; Parr et al., 2014). They contain high levels of biodiversity, provide essential  
54 habitat for endemic and endangered species (Murphy et al., 2016), account for a large amount of  
55 terrestrial net primary productivity, and store carbon (Parr et al., 2014). Savannas also provide  
56 essential resources to people, especially in developing countries, such as pasture for livestock,  
57 firewood, thatching materials, and medicinal plants (Egoh et al., 2009; Fensham et al., 2005;  
58 Hoffmann et al., 2012; Parr et al., 2014; van der Werf et al., 2010).

59  
60 Despite their importance, tropical savannas are generally underappreciated, understudied and  
61 under-protected (Laurance et al., 2014; Parr et al., 2014), with less than 13% under any kind of  
62 official protection (Jenkins and Joppa, 2009). Globally, one of the principal threats to tropical  
63 savannas is land-cover change, particularly the conversion of savanna to agriculture, including  
64 both low-intensity croplands and high intensity commercial production (Aleman et al., 2016;  
65 Laurance et al., 2014).

66  
67 Land-cover change has profound, often negative, impacts on wildlife (Foord et al., 2018;  
68 Reynolds et al., 2018; Sala et al., 2000). At fine spatial scales, land-cover change alters the type  
69 and structure of vegetation, eliminating foraging habitat or shelter (Fahrig et al., 2011; Goodwin  
70 et al., 2002; Tschardt et al., 2012). On larger scales, landscape composition (the different types  
71 of land cover) and configuration (the spatial pattern of land cover) affect wildlife through  
72 different mechanisms. Changes in landscape composition typically lead to reductions in native  
73 habitats and the loss of resources located in them (Fischer and Lindenmayer, 2006; Tschardt et al.,  
74 2012). In contrast, changes in landscape configuration, regardless of the amount of cover,  
75 affect wildlife through edge effects, patch isolation, and loss of connectivity across the landscape  
76 (Fahrig, 2003).

77  
78 Bats in savannas appear to respond to land cover changes (Mtsetfwa et al., 2018; Weier et al.,  
79 2018) and may serve as bioindicators (Jones et al., 2009). They are the second most diverse order  
80 of mammals (Burgin et al., 2018) and provide important ecosystem services such as pest control,  
81 pollination, and seed dispersal (Boyles et al., 2011; Kunz et al., 2011; Maas et al., 2013; Taylor  
82 et al., 2017; Williams-Guillén et al., 2008). There is growing evidence that in savannas in  
83 particular, some bat species exhibit strong preferences for agricultural landscapes (Noer et al.,  
84 2012; Toffoli and Rughetti, 2017) where they play an important role in consuming pest insects  
85 (Bohmann et al., 2011; Puig-Montserrat et al., 2015; Taylor et al., 2013, 2018, 2017).

86  
87 Conserving bats, and therefore maintaining the ecosystem services and functions that they  
88 provide, requires an understanding of how bats are affected by land-cover change and at what  
89 spatial scale these changes most affect them. Although we know that bats respond to changes in  
90 both fine-scale vegetation structure and landscape-scale composition and configuration (Brigham

91 et al., 1997; Fuentes-Montemayor et al., 2013; Gehrt and Chelsvig, 2003; Kalda et al., 2015;  
92 Monadjem and Reside, 2008) these relationships are often a function of spatial scale (Gorresen et  
93 al., 2005; Mendes et al., 2017; Pinto and Keitt, 2008). Additionally, bats' response to land cover  
94 varies greatly between regions, biomes, seasons (Ferreira et al., 2017; Klingbeil and Willig,  
95 2010; Mendes et al., 2014), and species or guilds (Gorresen et al., 2005; Klingbeil and Willig,  
96 2009; Mendes et al., 2017; Müller et al., 2012).

97  
98 To date, most research on the impacts of land-cover change on bats has been conducted in forest  
99 biomes (Estrada-Villegas et al., 2010; Ferreira et al., 2017; Pinto and Keitt, 2008; Williams-  
100 Guillén and Perfecto, 2011), limiting our ability to generalize patterns. Our understanding of how  
101 land-cover change affects bats in savannas, particularly in Africa, is far more limited (Meyer et  
102 al., 2016; Monadjem and Reside, 2008; Mtsetfwa et al., 2018; Weier et al., 2018). There is  
103 evidence that high intensity agriculture in southern African savannas can negatively affect some  
104 bat species (Mtsetfwa et al., 2018), while remnant natural and semi-natural vegetation (Mtsetfwa  
105 et al., 2018; Weier et al., 2018) and wetlands (Sirami et al., 2013) in these landscapes can  
106 promote bat activity. However, the role of landscape configuration has not been considered. In  
107 addition, the relative effects of fine-scale vegetation compared to landscape composition and  
108 configuration have not been directly compared. Finally, studies in this region have only  
109 compared the effects of savanna and commercial agriculture on bats (Mtsetfwa et al., 2018;  
110 Sirami et al., 2013; Weier et al., 2018), while the role of rural areas and villages has been largely  
111 neglected, although they comprise a large, and growing, component of the landscape (Bailey et  
112 al., 2015).

113  
114 In order to understand the effects of land-cover change on bats in tropical savannas, we measured  
115 guild-level responses in bat activity across the wet and dry seasons to both fine-scale metrics of  
116 vegetation structure and landscape-scale metrics of land cover composition and configuration  
117 across northeastern Eswatini (formerly Swaziland). This region is part of the Maputaland-  
118 Albany-Pondoland biodiversity hotspot (Steenkamp et al., 2005) and undergoing rapid land-  
119 cover change, primarily as a result of agricultural expansion and intensification (Bailey et al.,  
120 2015). Our objectives were to: 1) quantify the response of bats to variation in fine-scale  
121 vegetation structure and landscape-scale land-cover composition and configuration; 2) compare  
122 the variation in responses by foraging guild; 3) determine the most relevant spatial scale of the  
123 response for each guild; and 4) ascertain how responses vary by season. We expected to see  
124 guild-specific responses to both fine- and landscape-scale characteristics, with bats that use  
125 denser vegetation and fly shorter distances responding more strongly to fine-scale vegetation  
126 structure while bats that forage in open areas and fly longer distances were expected to respond  
127 more strongly to landscape-scale characteristics (Ferreira et al., 2017; Fuentes-Montemayor et  
128 al., 2013; Pinto and Keitt, 2008). In general, we expected to see a greater effect of landscape  
129 composition than configuration on bats, as has been reported in previous studies (Arroyo-  
130 Rodríguez et al., 2016; Meyer and Kalko, 2008). We also expected to see strong seasonal

131 variation in response from all guilds (Monadjem and Reside, 2008; Mtsetfwa et al., 2018; Taylor  
132 et al., 2013).

133

## 134 **2. Materials and Methods**

### 135 *2.1 Study Area*

136 This study was conducted across an area of approximately 2,300 km<sup>2</sup> in the eastern low-lying  
137 region of Eswatini referred to as the “Lowveld” which is bordered by the Drakensberg  
138 Mountains in the west and the Lubombo Mountains in the east (Figure 1). The area is a part of  
139 the Maputaland-Pondoland-Albany biodiversity hotspot (Steenkamp et al., 2005), which  
140 stretches from southern Mozambique, through eastern Eswatini, and into South Africa. This  
141 region has been subject to rapid land-cover change, mainly from expansion of commercial and  
142 small-holder croplands (Bailey et al., 2015). Elevation ranges from approximately 150 m to 600  
143 m above sea level. The Lowveld is characterized by a warm, semi-arid subtropical climate  
144 (Matondo et al. 2004). The annual mean temperature is 20–22° C, with a mean monthly  
145 temperature of 26° C in January and 18° C in July (Monadjem and Garcelon, 2005). Annual  
146 rainfall is 500–700 mm per year, concentrated in the summer months of October to March  
147 (Matondo et al. 2004; Monadjem and Reside 2008; Knox et al. 2010).

148

### 149 *2.2 Land-Cover Classification*

150 Land cover at our site is savanna vegetation (open savanna and woodland), commercial  
151 sugarcane plantations, and rural settlements, which included buildings, subsistence crops  
152 (primarily maize) and pasture for domestic livestock (Bailey et al., 2015; Monadjem and Reside,  
153 2008). Several perennial rivers run through the study area and a number of dams occur here,  
154 mostly acting as reservoirs for the commercial plantations. Therefore, we classified land cover  
155 across the study region into four categories: rural settlements (hereafter “rural”), savannas,  
156 sugarcane plantations (hereafter “sugarcane”), and water. We used these four categories to create  
157 a classified raster of the region. First we carried out supervised classification in Google Earth  
158 Engine ([www.earthengine.google.com](http://www.earthengine.google.com)) using a cloud-free Landsat 8 8-day raw composite image  
159 from March 21 – 29, 2016 at 30 m resolution. We then trained a voting support vector machine  
160 (voting SVM) classifier using 193 manually drawn polygons including each of the four land-  
161 cover categories. Resampling of the classified raster yielded an overall validity of 99.97%.

162

163 Because the rural land-cover class included crops and pasture that may have a similar spectral  
164 signature to savanna vegetation (Prestele et al., 2016), we incorporated population density to  
165 further distinguish rural areas from savanna. We used the population count raster for Eswatini  
166 from WorldPop projected for 2015 (WorldPop, 2013) to identify rural areas (Linard et al., 2012).  
167 We resampled this population count raster to the resolution of the classified raster using the  
168 nearest-neighbor algorithm. We overlaid the population raster on the classified raster and  
169 reclassified any cells with population count >1 as rural (Figure 1).

170

### 171 2.3 Acoustic Sampling

172 To capture variation in landscape cover across our study site we created a grid of 3 km<sup>2</sup> (~1.73  
173 km × ~1.73 km) blocks (hereafter “block”). We then overlaid this grid on the classified raster.  
174 We randomly selected 30 blocks (out of a possible 780) for acoustic surveys. These blocks were  
175 stratified between the three land-cover categories, with ten blocks for each type (10 rural, 10  
176 savanna, 10 sugarcane). Within each block, we deployed five Anabat Express detectors (Titley,  
177 Inc., Ballina, Australia) at randomly placed points (hereafter “points”) from November 2015 –  
178 July 2016 (Figure 1). Each detector was attached to a tree trunk or electric pole at 1.5 m above  
179 the ground. Anabat detectors were set to record starting half an hour before sunset and continued  
180 recording for six hours. Each block was surveyed twice per season (wet: November – March;  
181 dry: May – July) for a total of four survey nights.

182

### 183 2.4 Classification of Bat Calls

184 We first trained a support vector machine (SVM) algorithm to classify bat calls based on calls  
185 from hand-released bats in the region (Monadjem et al., 2017). Five bat species (*Mops midas*,  
186 *Neoromicia nana*, *Scotophilus dinganii*, *Miniopterus natalensis*, and *Hipposideros caffer*) have  
187 calls that are distinctive and do not overlap in parameters with other species in the region. These  
188 species could be individually identified by the SVM algorithm. Several other species exhibit  
189 overlap in their call parameters (Monadjem et al., 2017) and were therefore grouped together into  
190 the following three “sono-species” during classification:

- 191 1. *Chaerephon pumilus* – *Mops condylurus* – *Taphozous mauritanus*
- 192 2. *Neoromicia zuluensis* – *Nycticeinops schlieffeni* – *Pipstrellus hesperidus* – *Scotophilus*  
193 *viridis*
- 194 3. *Rhinolophus blasii* – *R. darlingi* – *R. simulator*

195

196 In addition, we manually searched through bat files to identify calls from the two *Myotis* species  
197 from the region (*Myotis bocagii* and *M. tricolor*), which are visually distinctive from other bat  
198 species in the region, but have highly variable call parameters (Monadjem et al., 2017).

199

200 We examined the echolocation calls recorded at each point with the program ANALOOK (Chris  
201 Corben, version 4.8, <http://www.hoarybat.com>). Calls were first filtered to remove files with  
202 only noise and no bat calls. We then extracted the call parameters from those Anabat files that  
203 passed the noise filter. These parameters describe each bat pulse within a pass. The SVM  
204 algorithm classified bat calls at the level of the bat pulse within a pass. In order to be counted,  
205 four consecutive pulses had to be classified as the same sono-species. We validated the classifier  
206 by comparing a manual identification to the SVM classifier for 639 calls. SVM classification and  
207 manual identification were in agreement for 98.3% of the 639 validation calls.

208

209 We standardized the number of calls per sono-species by counting each species a maximum of  
210 once per minute (Miller, 2001). Finally, we grouped classified calls from each species or species

211 group into three foraging guilds based on their wing morphology, echolocation, and foraging  
212 ecology: aerial foragers, edge foragers, and clutter foragers (Arita and Fenton, 1997; Meyer et  
213 al., 2004; Monadjem et al., 2010; Monadjem and Reside, 2008; Schnitzler and Kalko, 2001).  
214 Aerial foragers are adapted to fast, less maneuverable flight in open areas, while clutter foragers  
215 are adapted to slower, more maneuverable flight within dense vegetation; edge foragers are  
216 intermediate in terms of flight speed and maneuverability and often use vegetation at the edge of  
217 more open areas (Arita and Fenton, 1997; Meyer et al., 2004; Monadjem et al., 2010; Monadjem  
218 and Reside, 2008; Schnitzler and Kalko, 2001) (Table 1).

219

### 220 *2.5 Fine- and Landscape-Scale Metrics*

221 We quantified the environment at two spatial scales: a fine scale around each sampling point and  
222 the landscape scale within each sampling block. At the fine scale, we measured vegetation cover  
223 and structure. In order to do so, we established a 30 m transect in each of the cardinal directions  
224 from the sampling point. We evaluated canopy and ground cover at the sampling point where the  
225 Anabat detector was placed and at points at 10 m intervals along each 30 m transect (total of  
226 thirteen measurements) while shrub cover was measured along the length of each 10 m interval  
227 within each transect (total of twelve measures). We measured the canopy cover using a spherical  
228 densiometer (Forestry Suppliers, Inc., Jackson MS) (Lemmon, 1956). We visually estimated  
229 ground cover in  $1 \times 1$  m quadrats. We classified ground cover as: sugarcane, crop (all crops other  
230 than sugarcane), grass, bare ground, and water. We measured shrub cover, woody vegetation  $<2$   
231 m in height (Edwards, 1983), using the line intercept method (Canfield, 1941). For each  
232 sampling point, we took the mean canopy cover and ground cover from the thirteen points where  
233 we took these measures and the mean shrub cover from the twelve transects around the sampling  
234 point. We also measured the distance from each Anabat sampling point to the nearest water  
235 source because bats are known to use and forage around water bodies and riparian corridors  
236 (Monadjem and Reside, 2008; Pinto and Keitt, 2008; Sirami et al., 2013), using the function  
237 “gDistance” in the package rgeos (Bivand et al., 2017).

238

239 We calculated a variety of land-cover composition and configuration metrics within each  
240 sampling block (Gustafson, 1998). To account for land-cover composition, we measured the  
241 percent cover of savanna, rural, sugarcane, and water. For configuration metrics, we used  
242 savanna edge density because many bats use edges of natural vegetation (Chambers et al., 2016;  
243 Ethier and Fahrig, 2011; Mendes et al., 2017; Müller et al., 2012) and the savanna splitting index  
244 (hereafter “savanna splitting”), to account for the connectivity of savanna land cover, which may  
245 also be important for bats (Frey-Ehrenbold et al., 2013). We calculated all land-cover  
246 composition and configuration metrics using the “ClassStat” function in the SDMTools package  
247 (VanDerWal et al., 2014) in R version 3.3.3 (R Core Team, 2013).

248



249 We calculated pairwise correlations between all fine-scale metrics and all landscape-scale  
250 metrics using the function “rcorr” in the package Hmisc (Harrell, 2006). We found no  
251 correlations  $>0.7$  among either the fine- or landscape-scale metrics that we used in our models.  
252

## 253 *2.6 Statistical Analysis*

### 254 *2.6.1 Bat activity*

255 We measured the response of aerial, edge, and clutter foragers’ activity at two scales: fine scale  
256 and landscape scale. At the fine scale, we summed the total number of calls at each Anabat point  
257 over all the sampling nights per season. For the landscape scale, we summed the number of bat  
258 calls per season from all Anabat detectors within the block. We measured bat response separately  
259 for each season (wet vs. dry) at both spatial scales because levels of bat activity are known to  
260 vary between seasons due to changes in temperature, precipitation, prey abundance and water  
261 availability (Cisneros et al., 2015; Ferreira et al., 2017; Klingbeil and Willig, 2010; Mendes et  
262 al., 2014).

263  
264 We evaluated *a priori* suites of models to explain bat activity at both the fine and landscape  
265 scales. Each fine scale model included one of the fine-scale measures of vegetation structure:  
266 canopy cover, shrub cover, sugarcane cover, bare ground cover, water cover, and distance to  
267 water. We also included a null model (Table 2). To evaluate these models, we used generalized  
268 linear mixed models with the function “glmer” in the package lme4 (Bates et al., 2015), with a  
269 Poisson distribution to measure the response to fine-scale covariates. We used an offset term to  
270 account for the different number of sampling nights per point (Warton et al., 2015), due to  
271 occasional equipment failure. We used “block” as a random effect in order to account for spatial  
272 autocorrelation between points within the same block (Bailey et al., 2017).

273  
274 Landscape-scale models included one measure of landscape composition or configuration: rural,  
275 sugarcane, savanna, and water cover, edge density of savanna, or savanna splitting index. We  
276 also included two models with interactive effects between savanna composition and  
277 configuration: savanna cover  $\times$  savanna edge density and savanna cover  $\times$  savanna splitting  
278 (Table 2). We included interaction terms in order to determine whether savanna configuration  
279 may exacerbate or mitigate the effects of reduced savanna cover (composition). We used  
280 generalized linear models in base R v. 3.3.3 ([www.r-project.org](http://www.r-project.org)) with a Poisson distribution to  
281 measure the response to covariates at the landscape scale. Because the landscape response was  
282 aggregated at the block level, we did not include a random term to account for block. We used an  
283 offset term that was the sum of the number of sampling nights from all detectors within the block  
284 (Warton et al., 2015).

285  
286 Within each scale and for each season, we compared models using Akaike Information Criterion  
287 corrected for small sample size (AICc) using the function “model.sel” in the package MuMIn  
288 (Barton, 2017). We considered models within 2 AICc units to be competing models. We then

289 compared the point response models to each other and the best block response models to each  
290 other, using AICc. We evaluated the parameters of the top models by examining their 95%  
291 Confidence Intervals (CIs) and considered those that did not cross 0 to be relevant. We then  
292 graphed relevant parameters to understand how activity changes across variables of interest.  
293

294 Finally, we compared the fit of the overall best fine-scale models to the overall best landscape-  
295 scale models using Pseudo  $R^2$  (McFadden, 1974). Pseudo  $R^2$  measures the deviance explained by  
296 a given model compared to the null model. We used Pseudo  $R^2$  because the local and landscape  
297 models had different responses (e.g. activity at Anabat points vs. activity summed across all  
298 Anabat points within a block, respectively) and are therefore not directly comparable.  
299

### 300 **3. Results**

301 We recorded acoustic data for a total of 3,408 hours during 120 sampling nights across the 30  
302 sampling blocks. During this period, we identified a total of 69,897 bat calls. These calls were  
303 predominantly from aerial bats (n=48,466), followed by edge bats (n=21,361), and finally clutter  
304 bats (n=70). In general, we found that all three guilds responded more to the landscape scale than  
305 the fine scale and this response was stronger in the dry season than the wet season, but each guild  
306 responded differently to the landscape (Table 3).  
307

#### 308 *3.1 Aerial foraging guild*

309 At the fine scale, the best model to explain activity of aerial foragers during both seasons was  
310 water cover. Activity increased with increasing water cover during both the wet season ( $\beta = 0.09$ ,  
311 [95% confidence interval: 0.08, 0.10]) and dry season ( $\beta = 0.14$  [0.13, 0.16]). There were no  
312 other competing models (Table 3, Table S1, Fig. 2). The Pseudo  $R^2$  for top models in both  
313 seasons was relatively low, though higher in the dry (0.07 vs. 0.04) (Table 3).  
314

315 At the landscape scale, the best model to explain activity in both seasons was a model with  
316 interactive effects of savanna cover and savanna splitting (Table 3). There was a positive  
317 relationship with activity in the wet season (savanna cover:  $\beta = 0.09$  [0.03, 0.15]; savanna  
318 splitting:  $\beta = 0.66$  [0.36, 0.95]; interaction:  $\beta = 0.19$  [0.02, 0.36]) and negative relationship in the  
319 dry season ([-1.13, -0.87]; savanna splitting:  $\beta = -3.97$  [-4.63, -3.31]; interaction:  $\beta = -2.47$  [-  
320 2.85, -2.08]). During the wet season, activity increased more quickly with increasing savanna  
321 splitting where there was greater savanna cover. In the contrast, in the dry season, activity  
322 decreased with increasing savanna splitting, with a more rapid decline when savanna cover was  
323 higher (Fig. 2). There were no other competing models (Table 3, Table S1). Pseudo  $R^2$  was over  
324 twice as high for dry season models as the wet (0.28 vs. 0.12) (Table 3).  
325

#### 326 *3.2 Edge foraging guild*

327 At the fine scale, the best model explaining activity of edge bats during the wet season was a  
328 model with percent shrub cover. Shrub cover was a relevant predictor of bat activity, which

329 decreased with increasing cover ( $\beta = -0.23$  [-0.25, -0.20]). The best model to explain bat activity  
330 in the dry season was a model with distance to water. Bat activity increased with decreasing  
331 distance from water ( $\beta = -0.77$  [-0.88, -0.67]). There were no other competing models to explain  
332 edge bat activity during either season (Table 3, Table S1). Similar to aerial bats, Pseudo  $R^2$  was  
333 twice as high for dry season models as the wet (0.08 vs. 0.04) (Table 3, Table S2, Figure 3).

334  
335 At the landscape scale, the best model to explain the activity of edge bats was a model with the  
336 interaction between savanna cover and splitting (Table 3, Table S1). The response was similar in  
337 both seasons, activity decreased with splitting and cover (wet: savanna cover:  $\beta = -1.87$  [-1.98, -  
338 1.76]; savanna splitting:  $\beta = -8.6$  [-9.16, -8.05]; dry: savanna cover:  $\beta = -1.57$  [-1.78, -1.36];  
339 savanna splitting:  $\beta = -6.73$  [-7.78, -5.70]). However, the decrease in bat activity with savanna  
340 splitting was reduced on blocks with less savanna (wet: interaction:  $\beta = -5.1$  [-5.42, -4.78]; dry;  
341 interaction:  $\beta = -4.05$  [-4.66, -3.45]) (Fig. 3). There were no competing models (Table 3, Table  
342 S1). The dry season model (Pseudo  $R^2=0.18$ ) fit the data better than the wet season model  
343 (Pseudo  $R^2=0.09$ ). (Table 3).

### 344 345 *3.3 Clutter foraging guild*

346 The best model of activity of clutter bats at the fine scale in the wet season was a model with the  
347 variable grass cover, but with a 95% CI that included 0 and hence it was not a relevant predictor  
348 ( $\beta = 0.50$  [-0.04, 1.07]). The null model and a model with bare ground cover were also  
349 competing models but bare ground was also not a relevant predictor ( $\beta = -0.50$  [-1.31, 0.17]) In  
350 the dry season the best model included the variable sugarcane cover, which was a relevant  
351 predictor ( $\beta = 0.36$  [0.09, 0.62]); bat activity increased with increasing sugarcane cover. A model  
352 including the variable water cover was also a competing model, but it was not a relevant  
353 predictor ( $\beta = -0.53$  [-0.71, 0.55]) (Table 3, Table S3, Figure 4). The model fit for the top models  
354 in both seasons was comparable (Pseudo  $R^2=0.04$ ).

355  
356 At the landscape scale, the best model to explain the activity of clutter bats during the wet season  
357 was the amount of rural land cover. Bat activity decreased as the amount of rural land in a block  
358 increased ( $\beta = -1.36$  [-3.37, -0.32]). During the dry season the best model explaining bat activity  
359 was water cover, with activity increasing with increasing water ( $\beta = 1.03$  [0.85, 1.22]). There  
360 were no competing models at the landscape scale in either season. The top dry season model for  
361 clutter foragers (Pseudo  $R^2=0.48$ ) fit data better than our top wet season model (Pseudo  $R^2=0.21$ )  
362 (Table 3, Table S3, Figure 4).

## 363 364 **4. Discussion**

365 This study demonstrates the role of both fine-scale vegetation structure and landscape-scale  
366 composition and configuration in shaping bat activity within a savanna undergoing rapid land-  
367 use and land-cover change (Bailey et al., 2015). Across all three bat foraging guilds, we found  
368 that activity was best explained by landscape-scale characteristics rather than fine-scale

369 vegetation parameters. Previous studies have reported that bats with larger home ranges respond  
370 more strongly to broad-scale features of the landscape, while bats with smaller home ranges  
371 respond more to fine-scale vegetation structure (Ferreira et al., 2017; Fuentes-Montemayor et al.,  
372 2013; Klingbeil and Willig, 2010; Pinto and Keitt, 2008). Although clutter bats have much  
373 smaller home ranges than edge or aerial bats, they may still fly up to 2 km per night, which may  
374 explain the relevance of broader scale landscape features as reported here and elsewhere (Fenton,  
375 1990; Fenton and Rautenbach, 1986; Monadjem et al., 2009). Our results suggest any  
376 conservation planning or assessment of bat biodiversity in tropical African savannas should  
377 consider land cover at broad scale ( $>3 \text{ km}^2$ ). The use of inappropriate spatial scales may limit the  
378 effectiveness of conservation actions or mitigation measures. Indeed, there is evidence that  
379 mitigations (such as agro-environmental measures) that are implemented only at fine scales, such  
380 as leaving hedgerows or small patches of natural vegetation, may be ineffective in promoting or  
381 maintaining bat activity (Fuentes-Montemayor et al., 2011).

382  
383 We found that these landscape characteristics explained more of the bat activity response in the  
384 dry season than the wet season for all three foraging guilds. Seasonal responses in bat activity are  
385 common and have been found in tropical savannas of this region (Mtsetfwa et al., 2018; Taylor  
386 et al., 2013) as well as other parts of the world (Cisneros et al., 2015; Ferreira et al., 2017;  
387 Klingbeil and Willig, 2010; Mendes et al., 2014). During the wet season, essential resources,  
388 such as insect prey and water, are more abundant (Fukui et al., 2006; Hagen and Sabo, 2012;  
389 Salsamendi et al., 2012) and therefore bats might be less constrained or affected by landscape  
390 composition and configuration. The effect of landscape may be more pronounced in the dry  
391 season because resources, particularly water, become scarce (Korine et al., 2016).

392  
393 While we predicted that bats would respond more strongly to landscape composition than  
394 configuration, we found that both composition and configuration, particularly fragmentation of  
395 savanna land cover, were important for aerial and edge foraging bats. Bats have been shown to  
396 exhibit both negative and positive responses to fragmentation; these responses are often species-  
397 or guild-specific (Cosson et al., 1999; Estrada-Villegas et al., 2010; Ethier and Fahrig, 2011;  
398 Meyer et al., 2016). While some studies have found that the amount of natural cover is more  
399 important than fragmentation for bats (Meyer and Kalko, 2008), here we find an interactive  
400 effect between savanna cover and fragmentation. This interaction suggests that the effect  
401 fragmentation has on aerial and edge foraging bats depends on the amount of savanna cover.  
402 When savanna cover is high ( $>50\%$ ), fragmentation results in a steep decline in bat activity. At  
403 lower savanna cover (20%), fragmentation still has a negative effect, but the reduction in bat  
404 activity is less pronounced, perhaps because at this level the remaining savanna essentially exists  
405 in small fragments only. Alternatively, the decline in bat activity may be less pronounced at  
406 lower savanna cover because the other land-cover types (e.g. sugarcane and rural) in the  
407 landscape provide adequate resources, such as food, water, or roost sites.

408

409 Bat activity tends to increase in lower intensity agricultural systems, such as agroforestry and  
410 organic farms, at least in the few studies that have investigated this relationship (Cleary et al.,  
411 2016; Park, 2015; Wickramasinghe et al., 2003). However, we found that clutter bats responded  
412 negatively to rural cover, which is comprised of low-intensity small-holder crops, homes, pasture  
413 and dirt roads. These areas are typically very open, with large areas of bare ground and few trees  
414 or shrubs. The lack of dense vegetation likely limits the ability of clutter forager bats to use rural  
415 areas (Monadjem and Reside, 2008; Schnitzler and Kalko, 2001). On the other hand, we found  
416 that sugarcane had a significant, positive effect on clutter bats at the fine scale in the dry season.  
417 During this season, sugarcane plantations may offer resources, such as water from dams or  
418 irrigation canals and insects that are scarce in savannas or rural areas. In addition, sugarcane is  
419 densely planted and may reach two meters in height and therefore may provide suitable habitat  
420 for clutter foragers. The resemblance of vegetation structure to native vegetation in areas of  
421 agricultural land use may be more important for bats than the production intensity.

422  
423 We found that water was important for all three foraging guilds in the dry season, although there  
424 was variation in the spatial scale at which water drove activity for each guild. Water availability  
425 is important for bats in general, providing both water for drinking and insect foraging (Adams,  
426 2010; Adams and Hayes, 2008; Monadjem and Reside, 2008; Sherwin et al., 2013; Sirami et al.,  
427 2013). Water may play an even more important role in savannas, where availability might be  
428 lower than other tropical biomes, especially during dry seasons (Korine et al., 2016), and may  
429 drive bat movement and activity across the landscape (Geluso and Geluso, 2012; Rainho and  
430 Palmeirim, 2011). Because savannas, especially in arid and semi-arid areas, are at risk of future  
431 droughts and desertification (Engelbrecht et al., 2015; Stringer et al., 2009), water will likely  
432 become increasingly scarce for bats. Artificial water sources which are available year-round,  
433 such as the dams and canals within commercial agriculture areas and some villages, may provide  
434 an especially important resource for bats in this human-altered landscape (Sirami et al., 2013).

435  
436 There are some limitations to the use of acoustic monitoring in this study. A number of  
437 echolocating species found in the region, such as *Nycteris thebaica* and *Kerivoula lanosa* cannot  
438 be detected by our acoustic detectors (Monadjem et al., 2017). Similarly, non-echolocating  
439 species such as the fruit bat *Epomophorus wahlbergi* (Shapiro and Monadjem, 2016) could also  
440 not be included. In addition, many species in the region cannot be distinguished from acoustic  
441 calls alone due to similarity in call parameters (Monadjem et al., 2017). While we see clear  
442 patterns by foraging guild, there could also be species-specific responses within guilds (Ethier  
443 and Fahrig, 2011; Fuentes-Montemayor et al., 2011; Gorresen et al., 2005; Gorresen and Willig,  
444 2004; Pinto and Keitt, 2008), which we were unable to take into account.

445  
446 Increasing levels of anthropogenic land-cover change around the world are cause for concern for  
447 many wildlife species and biodiversity as a whole (Foley et al., 2005; Jetz et al., 2007; Venter et  
448 al., 2016), including those in savannas (Laurance et al., 2014; Parr et al., 2014). However,

449 despite the pressures of land-cover and land-use change, it is possible to conserve bats, and the  
450 ecosystem services they provide (Kunz et al., 2011; Taylor et al., 2018), in these changing  
451 savanna landscapes. Bats in savannas have a complex relationship with the landscape that varies  
452 by guild, season, and spatial scale. Therefore, any conservation or management strategies for  
453 bats in tropical savannas should consider the landscape at large scales ( $\geq 3$  km), minimize  
454 fragmentation of existing savanna, especially in areas of high remaining coverage ( $>50\%$ ), and  
455 maintain water sources, both natural and artificial. Doing so can promote activity of aerial, edge,  
456 and clutter foragers across spatial and temporal scales.

457

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466

#### 467 **References**

- 468 Adams, R.A., 2010. Bat reproduction declines when conditions mimic climate change  
469 projections for western North America. *Ecology* 91, 2437–2445. doi:10.1890/09-0091.1
- 470 Adams, R.A., Hayes, M.A., 2008. Water availability and successful lactation by bats as related to  
471 climate change in arid regions of western North America. *J. Anim. Ecol.* 77, 1115–1121.  
472 doi:10.1111/j.1365-2656.2008.01447.x
- 473 Aleman, J.C., Blarquez, O., Staver, C.A., 2016. Land-use change outweighs projected effects of  
474 changing rainfall on tree cover in sub-Saharan Africa. *Glob. Chang. Biol.* 22, 3013–3025.  
475 doi:10.1111/gcb.13299
- 476 Arita, H.T., Fenton, M.B., 1997. Flight and echolocation in the ecology and evolution of bats.  
477 *Trends Ecol. Evol.* 12, 53–58. doi:10.1016/S0169-5347(96)10058-6
- 478 Arroyo-Rodríguez, V., Rojas, C., Saldaña-Vázquez, R.A., Stoner, K.E., 2016. Landscape  
479 composition is more important than landscape configuration for phyllostomid bat  
480 assemblages in a fragmented biodiversity hotspot. *Biol. Conserv.* 198, 84–92.  
481 doi:10.1016/J.BIOCON.2016.03.026
- 482 Bailey, A.M., Ober, H.K., Sovie, A.R., McCleery, R.A., 2017. Impact of land use and climate on  
483 the distribution of the endangered Florida bonneted bat. *J. Mammal.* 98, 1586–1593.  
484 doi:10.1093/jmammal/gyx117
- 485 Bailey, K.M., McCleery, R.A., Binford, M.W., Zweig, C., 2015. Land-cover change within and  
486 around protected areas in a biodiversity hotspot. *J. Land Use Sci.* 1–23.  
487 doi:10.1080/1747423X.2015.1086905
- 488 Barton, K., 2017. MuMIn: Multi-Model Inference. R package version 1.40.0.
- 489 Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using  
490 lme4. *J. Stat. Softw.* 67, 1–48. doi:10.18637/jss.v067.i01
- 491 Bivand, R., Rundel, C., Pebesma, E., Stuetz, R., Hufthammer, K.O., Giraudoux, P., Davis, M.,  
492 Santilli, S., 2017. rgeos: Interface to geometry engine . Version 0.3-27].

- 493 Bohmann, K., Monadjem, A., Noer, C.L., Rasmussen, M., Zeale, M.R.K., Clare, E., Jones, G.,  
494 Willerslev, E., Gilbert, M.T.P., 2011. Molecular diet analysis of two African free-tailed bats  
495 (Molossidae) using high throughput sequencing. *PLoS One* 6.  
496 doi:10.1371/journal.pone.0021441
- 497 Bond, W.J., Parr, C.L., 2010. Beyond the forest edge: Ecology, diversity and conservation of the  
498 grassy biomes. *Biol. Conserv.* 143, 2395–2404. doi:10.1016/J.BIOCON.2009.12.012
- 499 Boyles, J.G., Cryan, P.M., McCracken, G.F., Kunz, T.K., 2011. Economic importance of bats in  
500 agriculture. *Science* (80-. ). 332, 41–42. doi:10.1126/science.1201366
- 501 Brigham, R.M., Morissette, J.L., Brigham, R.M., Grindal, S.D., Firman, M.C., 1997. The  
502 influence of structural clutter on insectivorous bats. *Artic. Can. J. Zool.* 75, 131–136.  
503 doi:10.1139/z97-017
- 504 Burgin, C.J., Colella, J.P., Kahn, P.L., Upham, N.S., 2018. How many species of mammals are  
505 there? *J. Mammal.* 99, 1–14. doi:10.1093/jmammal/gyx147
- 506 Canfield, R.H., 1941. Application of the line interception method in sampling range vegetation.  
507 *J. For.* 39, 388–394. doi:10.1093/jof/39.4.388
- 508 Chambers, C.L., Cushman, S.A., Medina-Fitoria, A., Martínez-Fonseca, J., Chávez-Velásquez,  
509 M., 2016. Influences of scale on bat habitat relationships in a forested landscape in  
510 Nicaragua. *Landsc. Ecol.* 31, 1299–1318. doi:10.1007/s10980-016-0343-4
- 511 Cisneros, L.M., Fagan, M.E., Willig, M.R., 2015. Effects of human-modified landscapes on  
512 taxonomic, functional and phylogenetic dimensions of bat biodiversity. *Divers. Distrib.* 21,  
513 523–533. doi:10.1111/ddi.12277
- 514 Cleary, K.A., Waits, L.P., Finegan, B., 2016. Agricultural intensification alters bat assemblage  
515 composition and abundance in a dynamic Neotropical landscape. *Biotropica* 48, 667–676.  
516 doi:10.1111/btp.12327
- 517 Cosson, J.-F., Pons, J.-M., Masson, D., 1999. Effects of forest fragmentation on frugivorous and  
518 nectarivorous bats in French Guiana. *J. Trop. Ecol.* 15, 515–534.
- 519 Edwards, D., 1983. A broad-scale structural classification of vegetation for practical purposes.  
520 *Bothalia* 14, 705–712.
- 521 Egoh, B., Reyers, B., Rouget, M., Bode, M., Richardson, D.M., 2009. Spatial congruence  
522 between biodiversity and ecosystem services in South Africa. *Biol. Conserv.* 142, 553–562.  
523 doi:10.1016/J.BIOCON.2008.11.009
- 524 Engelbrecht, F., Adegoke, J., Bopape, M.-J., Naidoo, M., Garland, R., Thatcher, M., McGregor,  
525 J., Katzfey, J., Werner, M., Ichoku, C., Gatebe, C., 2015. Projections of rapidly rising  
526 surface temperatures over Africa under low mitigation. *Environ. Res. Lett.* 10, 085004.  
527 doi:10.1088/1748-9326/10/8/085004
- 528 Estrada-Villegas, S., Meyer, C.F.J., Kalko, E.K.V., 2010. Effects of tropical forest fragmentation  
529 on aerial insectivorous bats in a land-bridge island system. *Biol. Conserv.* 143, 597–608.  
530 doi:10.1016/J.BIOCON.2009.11.009
- 531 Ethier, K., Fahrig, L., 2011. Positive effects of forest fragmentation, independent of forest  
532 amount, on bat abundance in eastern Ontario, Canada. *Landsc. Ecol.* 26, 865–876.  
533 doi:10.1007/s10980-011-9614-2
- 534 Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. *Annu. Rev. Ecol. Evol. Syst.*  
535 34, 487–515. doi:10.1146/annurev.ecolsys.34.011802.132419
- 536 Fahrig, L., Baudry, J., Brotons, L., Oise, F., Burel, G., Crist, T.O., Fuller, R.J., Sirami, C.,  
537 Siriwardena, G.M., Martin, J.-L., 2011. Functional landscape heterogeneity and animal  
538 biodiversity in agricultural landscapes. *Ecol. Lett.* 14, 101–112. doi:10.1111/j.1461-

- 539 0248.2010.01559.x  
540 Fensham, R.J., Fairfax, R.J., Archer, S.R., 2005. Rainfall, land use and woody vegetation cover  
541 change in semi-arid Australian savanna. *J. Ecol.* 93, 596–606. doi:10.1111/j.1365-  
542 2745.2005.00998.x  
543 Fenton, M.B., 1990. The foraging behaviour and ecology of animal-eating bats. *Can. J. Zool.* 68,  
544 411–422. doi:10.1139/z90-061  
545 Fenton, M.B., Rautenbach, I.L., 1986. A comparison of the roosting and foraging behavior of 3  
546 species of African insectivorous bats (Rhinolophidae, Vespertilionidae, and Molossidae).  
547 *Can. J. Zool.* 64, 2860–2867. doi:10.1139/z86-412  
548 Ferreira, D.F., Rocha, R., López-Baucells, A., Farneda, F.Z., Carreiras, J.M.B., Palmeirim, J.M.,  
549 Meyer, C.F.J., 2017. Season-modulated responses of Neotropical bats to forest  
550 fragmentation. *Ecol. Evol.* 7, 4059–4071. doi:10.1002/ece3.3005  
551 Fischer, J., Lindenmayer, D.B., 2006. Beyond fragmentation: the continuum model for fauna  
552 research and conservation in human-modified landscapes. *Oikos* 112, 473–480.  
553 doi:10.1111/j.0030-1299.2006.14148.x  
554 Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe,  
555 M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik,  
556 C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N., Snyder, P.K., 2005. Global  
557 consequences of land use. *Science* (80-. ). 309, 570–574. doi:10.1126/science.1111772  
558 Foord, S.H., Swanepoel, L.H., Evans, S.W., Schoeman, C.S., Erasmus, B.F.N., Schoeman, M.C.,  
559 Keith, M., Smith, A., Mauda, E.V., Maree, N., Nembudani, N., Dippenaar-Schoeman, A.S.,  
560 Munyai, T.C., Taylor, P.J., 2018. Animal taxa contrast in their scale-dependent responses to  
561 land use change in rural Africa. *PLoS One* 13, e0194336.  
562 doi:10.1371/journal.pone.0194336  
563 Frey-Ehrenbold, A., Bontadina, F., Arlettaz, R., Obrist, M.K., 2013. Landscape connectivity,  
564 habitat structure and activity of bat guilds in farmland-dominated matrices. *J. Appl. Ecol.*  
565 50, 252–261. doi:10.1111/1365-2664.12034  
566 Fuentes-Montemayor, E., Goulson, D., Cavin, L., Wallace, J.M., Park, K.J., 2013. Fragmented  
567 woodlands in agricultural landscapes: The influence of woodland character and landscape  
568 context on bats and their insect prey. *Agric. Ecosyst. Environ.* 172, 6–15.  
569 doi:10.1016/j.agee.2013.03.019  
570 Fuentes-Montemayor, E., Goulson, D., Park, K.J., 2011. Pipistrelle bats and their prey do not  
571 benefit from four widely applied agri-environment management prescriptions. *Biol.*  
572 *Conserv.* 144, 2233–2246. doi:10.1016/j.biocon.2011.05.015  
573 Fukui, D., Murakami, M., Nakano, S., Aoi, T., 2006. Effect of emergent aquatic insects on bat  
574 foraging in a riparian forest. *J. Anim. Ecol.* 75, 1252–1258. doi:10.1111/j.1365-  
575 2656.2006.01146.x  
576 Gehrt, S.D., Chelvig, J.E., 2003. Bat activity in an urban landscape: Patterns at the landscape  
577 and microhabitat scale. *Ecol. Appl.* 13, 939–950. doi:10.1890/02-5188  
578 Geluso, K.N., Geluso, K., 2012. Effects of environmental factors on capture rates of  
579 insectivorous bats, 1971–2005. *J. Mammal.* 93, 161–169. doi:10.1644/11-MAMM-A-107.1  
580 Goodwin, B.J., Fahrig, L., Goodwin, B.J., Fahrig, L., 2002. How does landscape structure  
581 influence landscape connectivity? *Oikos* 99, 552–570.  
582 Gorresen, P.M., Willig, M.R., 2004. Landscape responses of bats to habitat fragmentation in  
583 Atlantic forest of Paraguay. *J. Mammal.* 85, 688–697. doi:10.1644/bwgf-125  
584 Gorresen, P.M., Willig, M.R., Strauss, R.E., 2005. Multivariate analysis of scale-dependent



- 585 associations between bats and landscape structure. *Ecol. Appl.* 15, 2126–2136.  
586 doi:10.1890/04-0532
- 587 Gustafson, E.J., 1998. Quantifying landscape spatial pattern: What is the state of the art?  
588 *Ecosystems* 2, 143–156.
- 589 Hagen, E.M., Sabo, J.L., 2012. Influence of river drying and insect availability on bat activity  
590 along the San Pedro River, Arizona (USA). *J. Arid Environ.* 84, 1–8.  
591 doi:10.1016/J.JARIDENV.2012.03.007
- 592 Harrell, F.E.J., 2006. Hmisc: Harrell Miscellaneous. R package version 3.0-12.
- 593 Hoffmann, W.A., Geiger, E.L., Gotsch, S.G., Rossatto, D.R., Silva, L.C.R., Lau, O.L.,  
594 Haridasan, M., Franco, A.C., 2012. Ecological thresholds at the savanna-forest boundary:  
595 how plant traits, resources and fire govern the distribution of tropical biomes. *Ecol. Lett.* 15,  
596 759–768. doi:10.1111/j.1461-0248.2012.01789.x
- 597 Jenkins, C.N., Joppa, L., 2009. Expansion of the global terrestrial protected area system. *Biol.*  
598 *Conserv.* 142, 2166–2174. doi:10.1016/j.biocon.2009.04.016
- 599 Jetz, W., Wilcove, D.S., Dobson, A.P., 2007. Projected impacts of climate and land-use change  
600 on the global diversity of birds. *PLoS Biol.* 5, e157. doi:10.1371/journal.pbio.0050157
- 601 Jones, G., Jacobs, D.S., Kunz, T.H., Willig, M.R., Racey, P.A., 2009. Carpe noctem: the  
602 importance of bats as bioindicators. *Endanger. Species Res.* 8, 93–115.  
603 doi:10.3354/esr00182
- 604 Kalda, O., Kalda, R., Liira, J., 2015. Multi-scale ecology of insectivorous bats in agricultural  
605 landscapes. *Agric. Ecosyst. Environ.* 199, 105–113. doi:10.1016/J.AGEE.2014.08.028
- 606 Klingbeil, B.T., Willig, M.R., 2010. Seasonal differences in population-, ensemble- and  
607 community-level responses of bats to landscape structure in Amazonia. *Oikos* 119, 1654–  
608 1664. doi:10.1111/j.1600-0706.2010.18328.x
- 609 Klingbeil, B.T., Willig, M.R., 2009. Guild-specific responses of bats to landscape composition  
610 and configuration in fragmented Amazonian rainforest. *J. Appl. Ecol.* 46, 203–213.  
611 doi:10.1111/j.1365-2664.2008.01594.x
- 612 Korine, C., Adams, R., Russo, D., Fisher-Phelps, M., Jacobs, D., 2016. Bats and water:  
613 Anthropogenic alterations threaten global bat populations, in: *Bats in the Anthropocene:  
614 Conservation of Bats in a Changing World*. Springer International Publishing, Cham,  
615 Switzerland, pp. 215–241. doi:10.1007/978-3-319-25220-9\_8
- 616 Kunz, T.H., Braun de Torrez, E., Bauer, D., Lobo, T., Fleming, T.H., 2011. Ecosystem  
617 services provided by bats. *Ann. N. Y. Acad. Sci.* 1223, 1–38. doi:10.1111/j.1749-  
618 6632.2011.06004.x
- 619 Laurance, W.F., Sayer, J., Cassman, K.G., 2014. Agricultural expansion and its impacts on  
620 tropical nature. *Trends Ecol. Evol.* 29, 107–116. doi:10.1016/J.TREE.2013.12.001
- 621 Lemmon, P.E., 1956. A spherical densiometer For estimating forest overstory density. *For. Sci.*  
622 2, 314–320. doi:10.1093/forestscience/2.4.314
- 623 Linard, C., Gilbert, M., Snow, R.W., Noor, A.M., Tatem, A.J., 2012. Population distribution,  
624 settlement patterns and accessibility across Africa in 2010. *PLoS One* 7, e31743.  
625 doi:10.1371/journal.pone.0031743
- 626 Maas, B., Clough, Y., Tscharntke, T., 2013. Bats and birds increase crop yield in tropical  
627 agroforestry landscapes. *Ecol. Lett.* 16, 1480–1487. doi:10.1111/ele.12194
- 628 McCleery, R., Monadjem, A., Baiser, B., Fletcher, R., Vickers, K., Kruger, L., 2018. Animal  
629 diversity declines with broad-scale homogenization of canopy cover in African savannas.  
630 *Biol. Conserv.* 226, 54–62. doi:10.1016/J.BIOCON.2018.07.020

- 631 McFadden, D., 1974. Conditional logit analysis of qualitative choice behavior, in: Zarembka, P.  
632 (Ed.), *Frontiers in Econometrics*. Academic Press, New York, pp. 105–142.
- 633 Mendes, E., Fonseca, C., João, M., Pereira, R., Mendes, E.S., Marques, S.F., 2014. A mosaic of  
634 opportunities? Spatio-temporal patterns of bat diversity and activity in a strongly humanized  
635 Mediterranean wetland. *Eur. J. Wildl. Res.* 60, 651–664. doi:10.1007/s10344-014-0832-1
- 636 Mendes, E.S., Fonseca, C., Marques, S.F., Maia, D., Ramos Pereira, M.J., 2017. Bat richness and  
637 activity in heterogeneous landscapes: guild-specific and scale-dependent? *Landsc. Ecol.* 32,  
638 295–311. doi:10.1007/s10980-016-0444-0
- 639 Meyer, C.F.J., Kalko, E.K. V., 2008. Assemblage-level responses of phyllostomid bats to  
640 tropical forest fragmentation: Land-bridge islands as a model system. *J. Biogeogr.* 35,  
641 1711–1726. doi:10.1111/j.1365-2699.2008.01916.x
- 642 Meyer, C.F.J., Schwarz, C.J., Fahr, J., 2004. Activity patterns and habitat preferences of  
643 insectivorous bats in a West African forest–savanna mosaic. *J. Trop. Ecol.* 20, 397–407.  
644 doi:10.1017/S0266467404001373
- 645 Meyer, C.F.J., Struebig, M.J., Willig, M.R., 2016. Responses of tropical bats to habitat  
646 fragmentation, logging, and deforestation, in: Christian C. Voigt, Tigga Kingston (Eds.),  
647 *Bats in the Anthropocene: Conservation of Bats in a Changing World*. Springer  
648 International Publishing, Cham, Switzerland, pp. 63–103. doi:10.1007/978-3-319-25220-  
649 9\_4
- 650 Midgley, G.F., Bond, W.J., 2015. Future of African terrestrial biodiversity and ecosystems under  
651 anthropogenic climate change. *Nat. Clim. Chang.* 5, 823–829.  
652 doi:10.1038/NCLIMATE2753
- 653 Miller, B.W., 2001. A method for determining relative activity of free flying bats using a new  
654 activity index for acoustic monitoring. *Acta Chiropterologica* 3, 93–105.
- 655 Monadjem, A., Garcelon, D.K., 2005. Nesting distribution of vultures in relation to land use in  
656 Swaziland. *Biodivers. Conserv.* 14, 2079–2093. doi:10.1007/s10531-004-4358-9
- 657 Monadjem, A., Reside, A., 2008. The influence of riparian vegetation on the distribution and  
658 abundance of bats in an African savanna. *Acta Chiropterologica* 10, 339–348.  
659 doi:10.3161/150811008x414917
- 660 Monadjem, A., Reside, A., Cornut, J., Perrin, M.R., 2009. Roost selection and home range of an  
661 African insectivorous bat *Nycteris thebaica* (Chiroptera, Nycteridae). *Mammalia* 73, 353–  
662 359. doi:10.1515/mamm.2009.056
- 663 Monadjem, A., Shapiro, J.T., Mtsetfwa, F., Reside, A.E., McCleery, R.A., 2017. Acoustic call  
664 library and detection distances for bats of Swaziland. *Acta Chiropterologica* 19.  
665 doi:10.3161/15081109ACC2017.19.1.014
- 666 Monadjem, A., Taylor, P.J., Cotterill, F.P.D., Schoeman, M.C., 2010. *Bats of Southern and*  
667 *Central Africa: A Biogeographic and Taxonomic Synthesis*. Wits University Press,  
668 Johannesburg.
- 669 Mtsetfwa, F., McCleery, R.A., Monadjem, A., 2018. Changes in bat community composition and  
670 activity patterns across a conservation-agriculture boundary. *African Zool.* 53, 99–106.  
671 doi:10.1080/15627020.2018.1531726
- 672 Müller, J., Mehr, M., Bäessler, C., Fenton, M.B., Hothorn, T., Pretzsch, H., Klemmt, H.-J.,  
673 Brandl, R., 2012. Aggregative response in bats: prey abundance versus habitat. *Oecologia*  
674 169, 673–684. doi:10.1007/s00442-011-2247-y
- 675 Murphy, B.P., Andersen, A.N., Parr, C.L., 2016. The underestimated biodiversity of tropical  
676 grassy biomes. *Philos. Trans. R. Soc. London. Ser. B Biol. Sci.* 371, 20150319.

- 677 doi:10.1098/rstb.2015.0319
- 678 Noer, C.L., Dabelsteen, T., Bohmann, K., Monadiem, A., 2012. Molossid bats in an African  
679 agro-ecosystem select sugarcane fields as foraging habitat. *African Zool.* 47, 1–11.
- 680 Park, K.J., 2015. Mitigating the impacts of agriculture on biodiversity: bats and their potential  
681 role as bioindicators. *Mamm. Biol. - Zeitschrift für Säugetierkd.* 80, 191–204.  
682 doi:10.1016/J.MAMBIO.2014.10.004
- 683 Parr, C.L., Lehmann, C.E.R., Bond, W.J., Hoffmann, W.A., Andersen, A.N., 2014. Tropical  
684 grassy biomes: misunderstood, neglected, and under threat. *Trends Ecol. Evol.* 29, 205–213.  
685 doi:10.1016/j.tree.2014.02.004
- 686 Pinto, N., Keitt, T.H., 2008. Scale-dependent responses to forest cover displayed by frugivore  
687 bats. *Oikos* 117, 1725–1731.
- 688 Prestele, R., Alexander, P., Rounsevell, M.D.A., Arneith, A., Calvin, K., Doelman, J., Eitelberg,  
689 D.A., Engström, K., Fujimori, S., Hasegawa, T., Havlik, P., Humpenöder, F., Jain, A.K.,  
690 Krisztin, T., Kyle, P., Meiyappan, P., Popp, A., Sands, R.D., Schaldach, R., Schüngel, J.,  
691 Stehfest, E., Tabeau, A., Van Meijl, H., Van Vliet, J., Verburg, P.H., 2016. Hotspots of  
692 uncertainty in land-use and land-cover change projections: a global-scale model  
693 comparison. *Glob. Chang. Biol.* 22, 3967–3983. doi:10.1111/gcb.13337
- 694 Puig-Montserrat, X., Torre, I., López-Baucells, A., Guerrieri, E., Monti, M.M., Ràfols-García,  
695 R., Ferrer, X., Gisbert, D., Flaquer, C., 2015. Pest control service provided by bats in  
696 Mediterranean rice paddies: Linking agroecosystems structure to ecological functions.  
697 *Mamm. Biol.* 80, 237–245. doi:10.1016/J.MAMBIO.2015.03.008
- 698 R Core Team, 2013. R: A language and environment for statistical computing. R Found. Stat.  
699 Comput. Vienna, Austria.
- 700 Rainho, A., Palmeirim, J.M., 2011. The importance of distance to resources in the spatial  
701 modelling of bat foraging habitat. *PLoS One* 6, e19227. doi:10.1371/journal.pone.0019227
- 702 Reynolds, C., Fletcher, R.J., Carneiro, C.M., Jennings, N., Ke, A., LaScaleia, M.C., Lukhele,  
703 M.B., Mamba, M.L., Sibiya, M.D., Austin, J.D., Magagula, C.N., Mahlaba, T., Monadjem,  
704 A., Wisely, S.M., McCleery, R.A., 2018. Inconsistent effects of landscape heterogeneity  
705 and land-use on animal diversity in an agricultural mosaic: a multi-scale and multi-taxon  
706 investigation. *Landsc. Ecol.* 33, 241–255. doi:10.1007/s10980-017-0595-7
- 707 Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E.,  
708 Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A.,  
709 Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M., Wall, D.H., 2000.  
710 Global biodiversity scenarios for the year 2100. *Science (80-. )*. 287, 1770–1774.  
711 doi:10.1126/science.287.5459.1770
- 712 Salsamendi, E., Arostegui, I., Aihartza, J., Almenar, D., Goiti, U., Garin, I., 2012. Foraging  
713 ecology in Mehely’s horseshoe bats: Influence of habitat structure and water availability.  
714 *Acta Chiropterologica* 14, 121–132. doi:10.3161/150811012X654330
- 715 Schnitzler, H.U., Kalko, E.K. V, 2001. Echolocation by insect-eating bats. *Bioscience* 51, 557–  
716 569. doi:10.1641/0006-3568(2001)051[0557:ebieb]2.0.co;2
- 717 Shapiro, J.T., Monadjem, A., 2016. Two new bat species for Swaziland and a revised list for the  
718 country. *Mammalia*. doi:10.1515/mammalia-2014-0174
- 719 Sherwin, H.A., Montgomery, W.I., Lundy, M.G., 2013. The impact and implications of climate  
720 change for bats. *Mamm. Rev.* 43, 171–182. doi:10.1111/j.1365-2907.2012.00214.x
- 721 Sirami, C., Jacobs, D.S., Cumming, G.S., 2013. Artificial wetlands and surrounding habitats  
722 provide important foraging habitat for bats in agricultural landscapes in the Western Cape,

- 723 South Africa. *Biol. Conserv.* 164, 30–38. doi:10.1016/j.biocon.2013.04.017
- 724 Steenkamp, Y., Van Wyk, B., Victor, J., Hoare, D., Smith, G.F., Dold, T., Cowling, R.M., 2005.
- 725 Maputaland-Pondoland-Albany, in: Mittermeier, R.A., Robles Gil, P., Hoffman, M.,
- 726 Pilgrim, J., Brooks, T., Goettsch Mittermeier, C., Lamoreux, J., Da Fonseca, G.A.B. (Eds.),
- 727 Hotspots Revisited: Earth’s Biologically Richest and Most Endangered Terrestrial
- 728 Ecoregions. Chicago, pp. 219–228.
- 729 Stringer, L.C., Dyer, J.C., Reed, M.S., Dougill, A.J., Twyman, C., Mkwambisi, D., 2009.
- 730 Adaptations to climate change, drought and desertification: Local insights to enhance policy
- 731 in southern Africa. *Environ. Sci. Policy* 12, 748–765. doi:10.1016/j.envsci.2009.04.002
- 732 Taylor, P.J., Grass, I., Alberts, A.J., Joubert, E., Tscharrntke, T., 2018. Economic value of bat
- 733 predation services – A review and new estimates from macadamia orchards. *Ecosyst. Serv.*
- 734 30, 372–381. doi:10.1016/J.ECOSER.2017.11.015
- 735 Taylor, P.J., Matamba, E., Steyn, J.N., Nangammbi, T., Zepeda-Mendoza, M.L., Bohmann, K.,
- 736 2017. Diet determined by Next Generation Sequencing reveals pest consumption and
- 737 opportunistic foraging by bats in macadamia orchards in South Africa. *Acta*
- 738 *Chiropterologica* 19, 239–254. doi:10.3161/15081109ACC2017.19.2.003
- 739 Taylor, P.J., Monadjem, A., Steyn, J.N., 2013. Seasonal patterns of habitat use by insectivorous
- 740 bats in a subtropical African agro-ecosystem dominated by macadamia orchards. *Afr. J.*
- 741 *Ecol.* 51, 552–561. doi:10.1111/aje.12066
- 742 Taylor, P.J., Steyn, J.N., Schoeman, C., 2013. Bats eat pest green vegetable stink bugs (*Nezara*
- 743 *viridula*): Diet analyses of seven insectivorous species of bats roosting and foraging in
- 744 macadamia orchards. *South. African Macadamia Grow. Assoc. Yearb.* 21, 45–52.
- 745 Toffoli, R., Rughetti, M., 2017. Bat activity in rice paddies: Organic and conventional farms
- 746 compared to unmanaged habitat. *Agric. Ecosyst. Environ.* 249, 123–129.
- 747 doi:10.1016/J.AGEE.2017.08.022
- 748 Tscharrntke, T., Tylianakis, J.M., Rand, T.A., Didham, R.K., Fahrig, L., Batáry, P., Bengtsson, J.,
- 749 Clough, Y., Crist, T.O., Dormann, C.F., Ewers, R.M., Fründ, J., Holt, R.D., Holzschuh, A.,
- 750 Klein, A.M., Kleijn, D., Kremen, C., Landis, D.A., Laurance, W., Lindenmayer, D.,
- 751 Scherber, C., Sodhi, N., Steffan-Dewenter, I., Thies, C., Van Der Putten, W.H., Westphal,
- 752 C., 2012. Landscape moderation of biodiversity patterns and processes -eight hypotheses.
- 753 *Biol. Rev.* 87, 661–685. doi:10.1111/j.1469-185X.2011.00216.x
- 754 van der Werf, G.R., Randerson, J.T., Giglio, L., Collatz, G.J., Mu, M., Kasibhatla, P.S., Morton,
- 755 D.C., DeFries, R.S., Jin, Y., van Leeuwen, T.T., 2010. Global fire emissions and the
- 756 contribution of deforestation, savanna, forest, agricultural, and peat fires (1997–2009).
- 757 *Atmos. Chem. Phys.* 10, 11707–11735. doi:10.5194/acp-10-11707-2010
- 758 VanDerWal, J., Falconi, L., Januchowski, S., Shoo, L., Storlie, C., 2014. Package “SDMTools.”
- 759 Venter, O., Sanderson, E.W., Magrath, A., Allan, J.R., Beher, J., Jones, K.R., Possingham, H.P.,
- 760 Laurance, W.F., Wood, P., Fekete, B.M., Levy, M.A., Watson, J.E.M., 2016. Sixteen years
- 761 of change in the global terrestrial human footprint and implications for biodiversity
- 762 conservation. *Nat. Commun.* 7. doi:10.1038/ncomms12558
- 763 Warton, D.I., Shipley, B., Hastie, T., 2015. CATS regression - a model-based approach to
- 764 studying trait-based community assembly. *Methods Ecol. Evol.* 6, 389–398.
- 765 doi:10.1111/2041-210X.12280
- 766 Weier, S.M., Grass, I., Linden, V.M.G., Tscharrntke, T., Taylor, P.J., 2018. Natural vegetation
- 767 and bug abundance promote insectivorous bat activity in macadamia orchards, South
- 768 Africa. *Biol. Conserv.* 226, 16–23. doi:10.1016/J.BIOCON.2018.07.017

- 769 Wickramasinghe, L.P., Harris, S., Jones, G., Vaughan, N., 2003. Bat activity and species  
770 richness on organic and conventional farms: Impact of agricultural intensification. *J. Appl.*  
771 *Ecol.* 40, 984–993.
- 772 Williams-Guillén, K., Perfecto, I., 2011. Ensemble composition and activity levels of  
773 insectivorous bats in response to management intensification in coffee agroforestry systems.  
774 *PLoS One* 6, e16502. doi:10.1371/journal.pone.0016502
- 775 Williams-Guillén, K., Perfecto, I., Vandermeer, J., 2008. Bats limit insects in a neotropical  
776 agroforestry system. *Science* (80-. ). 320, 70. doi:10.1126/science.1152944
- 777 WorldPop, 2013. Swaziland 100m Population [WWW Document].  
778 doi:10.5258/SOTON/WP00259  
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781 Table 1. Definition of foraging guilds and classification of bat species by foraging guild

Foraging guild	Wing morphology	Echolocation	Foraging ecology	Species / Species Group
Aerial	Long and narrow, high wing-loading	Low duty-cycle - Quasi-constant frequency	Open spaces, high altitudes	<i>Chaerephon pumilus</i> – <i>Mops condylurus</i> – <i>Taphozous mauritanus</i> group <i>Mops midas</i>
Edge	Intermediate length, width, and wing loading	Low duty-cycle frequency-modulated or frequency-modulated-quasi-constant frequency	Edges of dense vegetation	<i>Neoromicia nana</i> <i>Scotophilus dinganii</i> <i>Neoromicia zuluensis</i> – <i>Nycticeinops schlieffeni</i> – <i>Pipstrellus hesperidus</i> – <i>Scotophilus viridis</i> group <i>Myotis bocagii</i> – <i>Myotis tricolor</i> group <i>Miniopterus natalensis</i>
Clutter	Short and broad, low wing-loading	Constant frequency	Dense, cluttered vegetation	<i>Rhinolophus blasii</i> – <i>R. darlingi</i> – <i>R. simulator</i> group

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785 Table 2. List of models used for each spatial scale. “×” indicates interactive term in models.

Scale of bat response	Spatial scale of model covariates	Model covariates
Fine	30 m	Canopy cover (percent) Shrub cover (percent) Bare ground cover (percent) Grass cover (percent) Sugarcane cover (percent) Water cover (percent) Distance to water (m) Null
Landscape	3 km <sup>2</sup>	Rural cover (percent) Savanna cover (percent) Sugarcane cover (percent) Water cover (percent) Savanna edge density Savanna splitting Savanna cover × Savanna edge density Savanna cover × Savanna splitting Null

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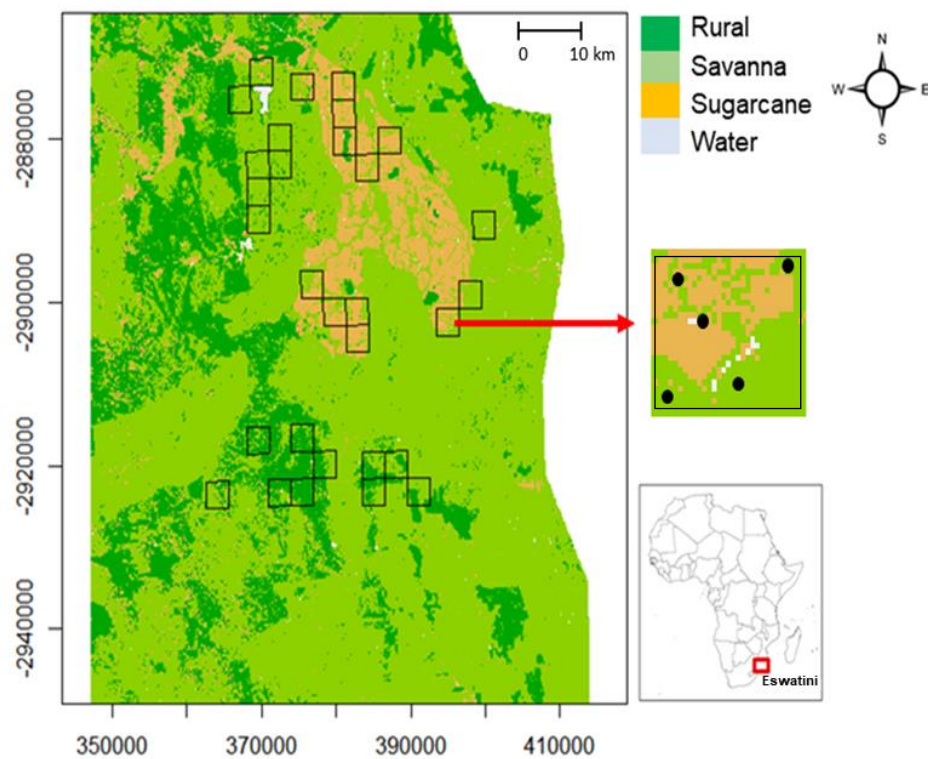
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788 Table 3. Top model and any competing models for each guild at each spatial scale in each  
 789 season. See Supplemental Information for full model selection tables.

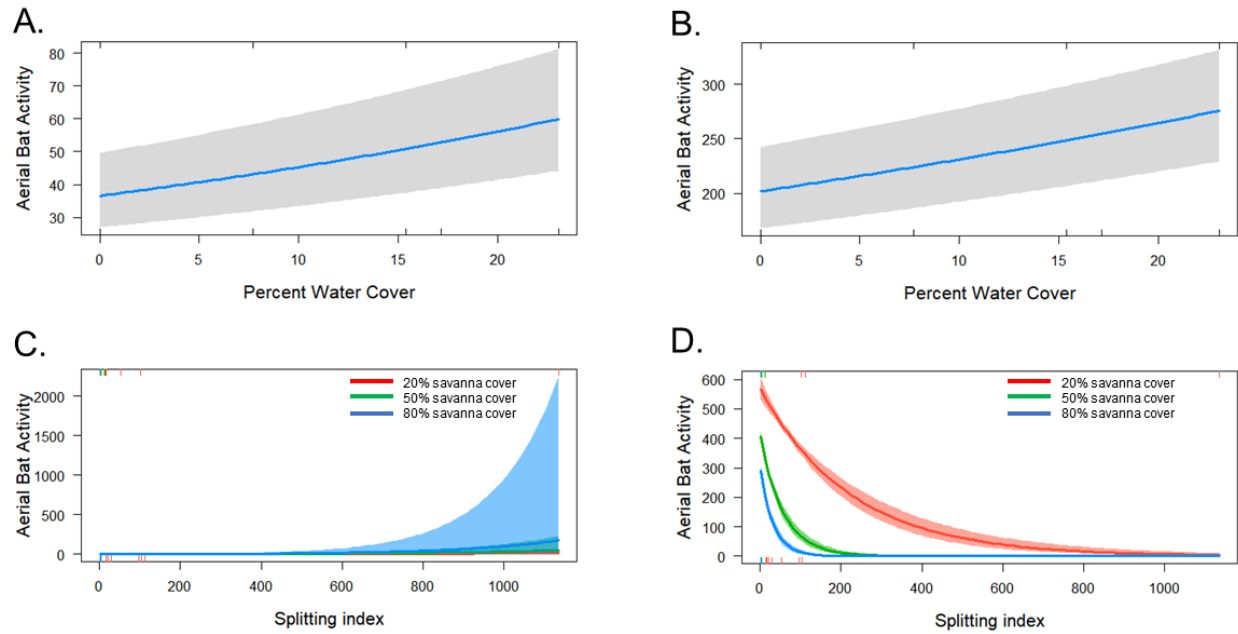
Guild	Scale	Season	Top Model	Pseudo $R^2$	Competing models
Aerial	Fine	Wet	Water cover	0.04	None
		Dry	Water cover	0.07	None
	Landscape	Wet	Savanna cover × Savanna splitting	0.12	None
		Dry	Savanna cover × Savanna splitting	0.28	None
Edge	Fine	Wet	Shrub cover	0.04	None
		Dry	Distance to water	0.08	None
	Landscape	Wet	Savanna cover × Savanna splitting	0.09	None
		Dry	Savanna cover × Savanna splitting	0.18	None
Clutter	Fine	Wet	Grass cover	0.04	Bare ground cover Null model
		Dry	Sugarcane cover	0.04	Water cover
	Landscape	Wet	Rural cover	0.21	None
		Dry	Water cover	0.48	None

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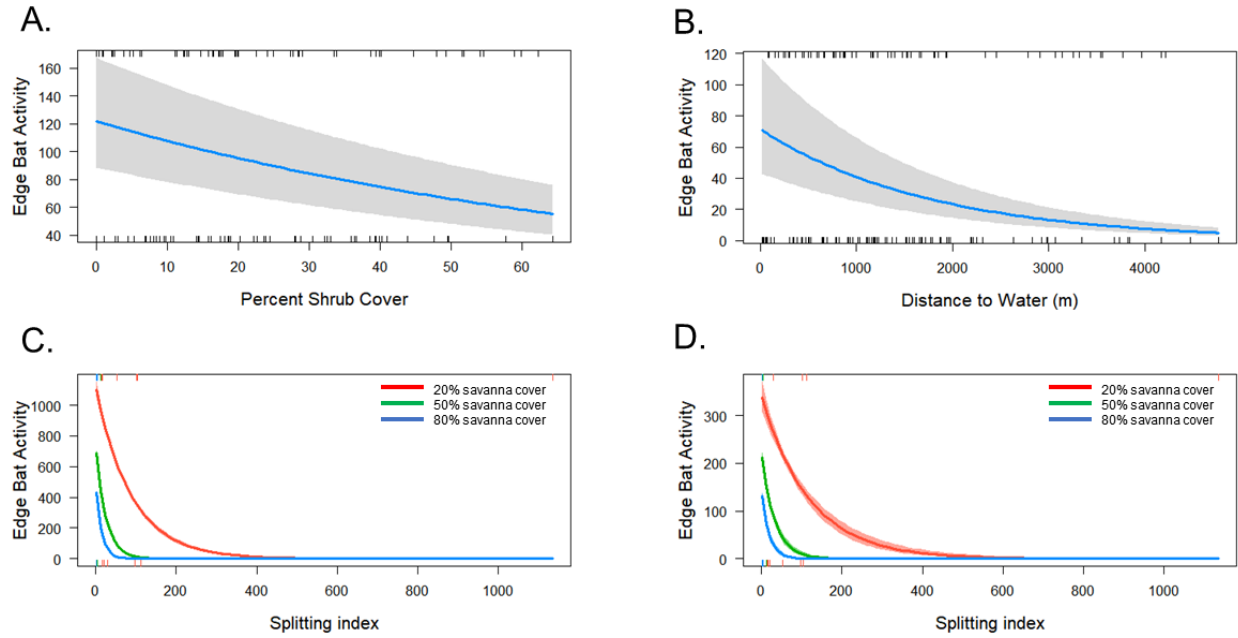


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792 Figure 1. Map of the study region with sampling blocks outlined in black. The inset shows a  
793 close-up of one block, with Anabat points indicated by the black circles.  
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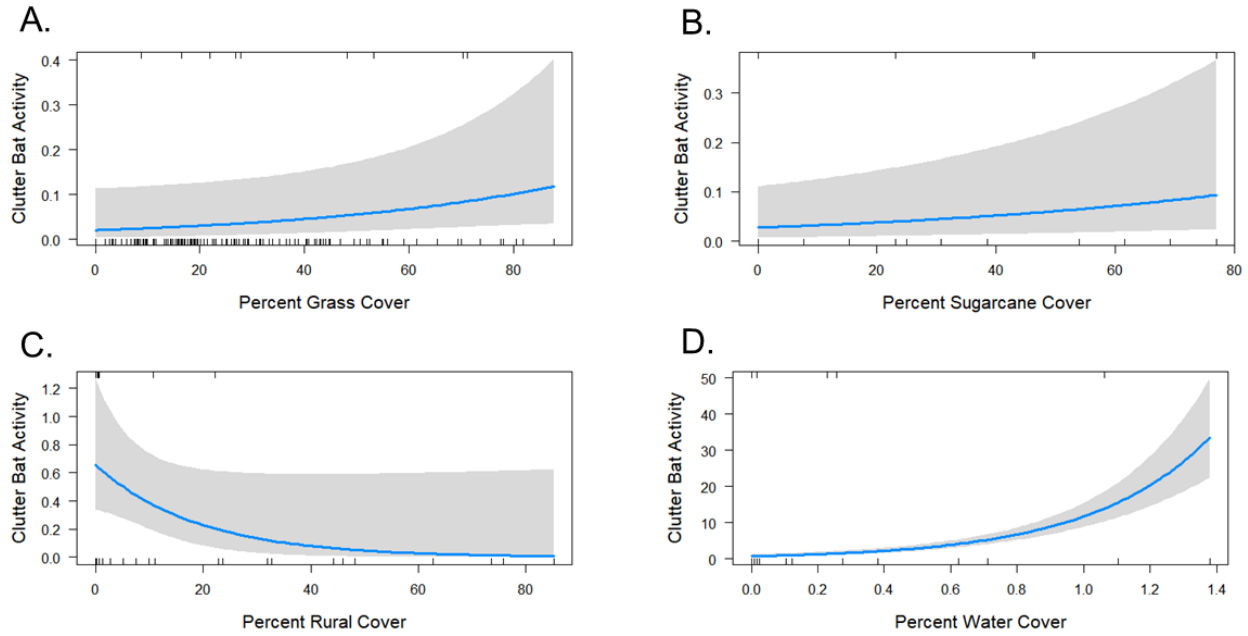
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Figure 2. Response of aerial foraging guild bats at the fine scale in the A. wet season, B. dry season and at the landscape scale in the C. wet season and D. dry season.



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Figure 3. Response of edge foraging guild bats at the fine scale in the A. wet season, B. dry season and at the landscape scale in the C. wet season and D. dry season.



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Figure 4. Response of clutter foraging guild bats at A. wet season, B. dry season and at the landscape scale in the C. wet season and D. dry season.