1   **Response of Bat Activity to Land-Cover and Land-Use Change in Savannas is Scale-,**
2   **Season-, and Guild-Specific**
3
4   Julie Teresa Shapiro[a,b,1*], Ara Monadjem[c,d], Timo Röder[e,2], Robert A. McCleery[a,b]
5

6   [a] School of Natural Resources and Environment, University of Florida; 103 Black Hall,
7   Gainesville FL USA; julie.teresa.shapiro@gmail.com; ramccleery@ufl.edu
8   [b] Department of Wildlife Ecology and Conservation, University of Florida; Newins-Ziegler Hall,
9   Gainesville FL USA
10   [c] Department of Biological Sciences, University of Eswatini, Private Bag 4, Kwaluseni,
11   Eswatini; aramonadjem@gmail.com
12   [d] Mammal Research Institute, Department of Zoology & Entomology, University of Pretoria,
13   Private Bag 20, Hatfield 0028, Pretoria, South Africa
14   [e] Centre for GeoGenetics, Natural History Museum of Denmark, University of Copenhagen,
15   Øster Voldgade 5-7, 1350 Copenhagen, Denmark; tiro@food.dtu.dk
16
17   Present address:
18   [1] Centre International de Recherche en Infectiologie, Institut national de la santé et recherche
19   médicale, 46 Allée d'Italie, 69364 Lyon, France
20   [2] National Food Institute, Technical University of Denmark, 2800 Lyngby, Denmark
21
22   [*] Corresponding author: julie.teresa.shapiro@gmail.com, +33 85 (0)6 99 23 03

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

2

Highlights

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

1. Introduction

51
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; Tscharntke 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; Tscharntke et
74 al., 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

4

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

5

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^2 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) 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^2 (~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 mauritianus*

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 1×1 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 × savanna edge density and savanna cover × 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) 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 (β = 0.09,
311 [95% confidence interval: 0.08, 0.10]) and dry season (β = 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: β = 0.09 [0.03, 0.15]; savanna
318 splitting: β = 0.66 [0.36,0.95]; interaction: β = 0.19 [0.02,0.36]) and negative relationship in the
319 dry season ([-1.13, -0.87]; savanna splitting: β = -3.97 [-4.63, -3.31]; interaction: β = -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 (β = -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 (β = -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: β = -1.87 [-1.98, -
338   1.76]; savanna splitting: β = -8.6 [-9.16, -8.05]; dry: savanna cover: β = -1.57 [-1.78, -1.36];
339   savanna splitting: β = -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: β = -5.1 [-5.42, -4.78]; dry;
341   interaction: β = -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   (β = 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 (β = -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 (β = 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 (β = -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 (β = -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 (β = 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 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 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,

13

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 (≥ 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

458 **Acknowledgements**

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 echlocation 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].

14

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. Can. 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., Chelsvig, 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/bwg-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., Lobova, 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

17

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., Bässler, 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., Arneth, 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,

19

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., Tscharntke, 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 Tscharntke, 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., Magrach, 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., Tscharntke, 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
779
780

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	*Chaerephon pumilus – Mops condylurus – Taphozous mauritianus* group *Mops midas*
Edge	Intermediate length, width, and wing loading	Low duty-cycle frequency-modulated or frequency-modulated-quasi-constant frequency	Edges of dense vegetation	*Neoromicia nana* *Scotophilus dinganii* *Neoromicia zuluensis – Nycticeinops schlieffeni – Pipstrellus hesperidus – Scotophilus viridis* group *Myotis bocagii – Myotis tricolor* group *Miniopterus natalensis*
Clutter	Short and broad, low wing-loading	Constant frequency	Dense, cluttered vegetation	*Rhinolophus blasii – R. darlingi – R. simulator* group

782

783

784

22

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^2	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

786
787

23

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.

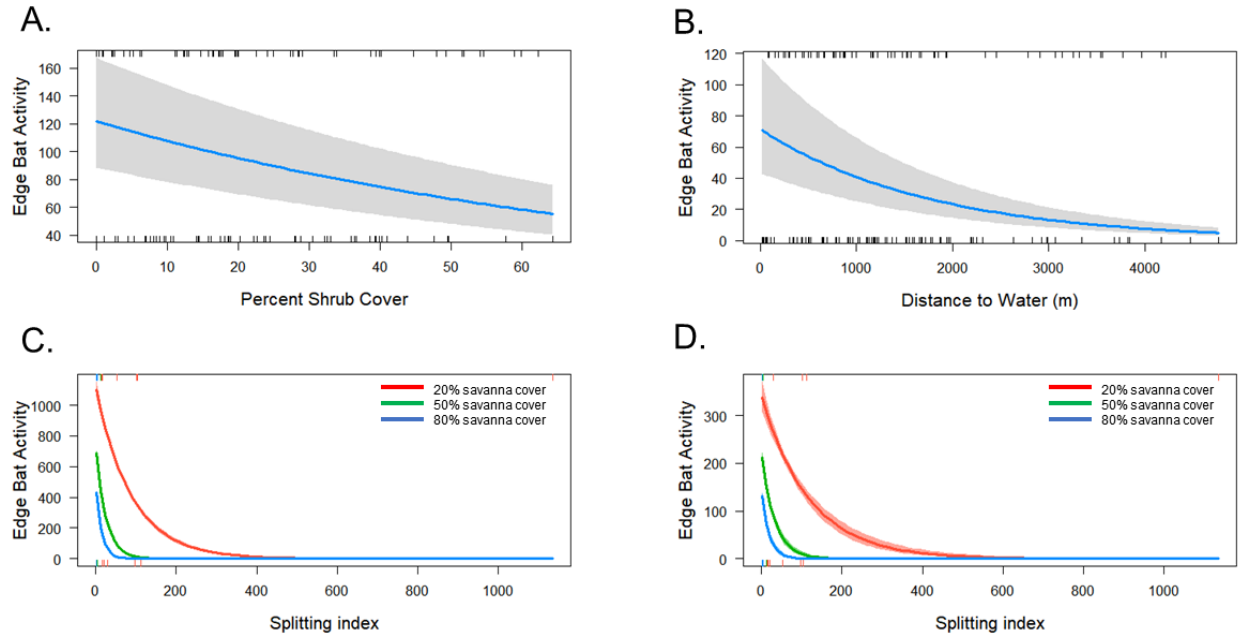| Guild	Scale	Season	Top Model	Pseudo R^2	Competing models
Aerial	Fine	Wet	Water cover	0.04	None
		Dry	Water cover	0.07	None
	Landscape	Wet	Savanna cover × Savanna splitting	0.12	None
		Dry	Savanna cover × Savanna splitting	0.28	None
Edge	Fine	Wet	Shrub cover	0.04	None
		Dry	Distance to water	0.08	None
	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

790
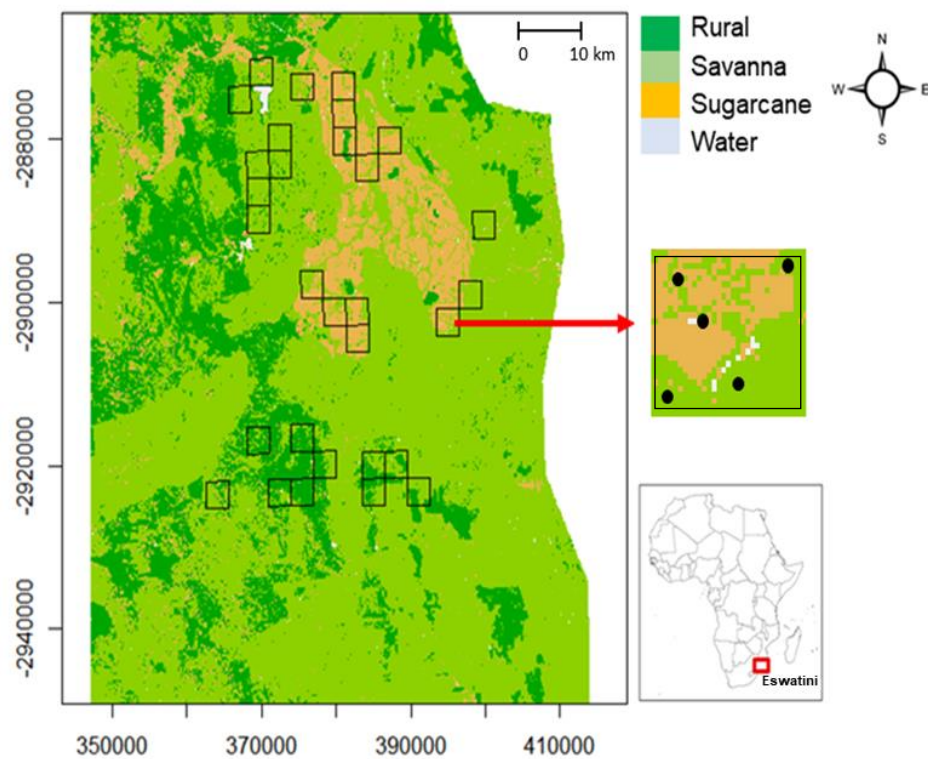
791
792   Figure 1. Map of the study region with sampling blocks outlined in black. The inset shows a
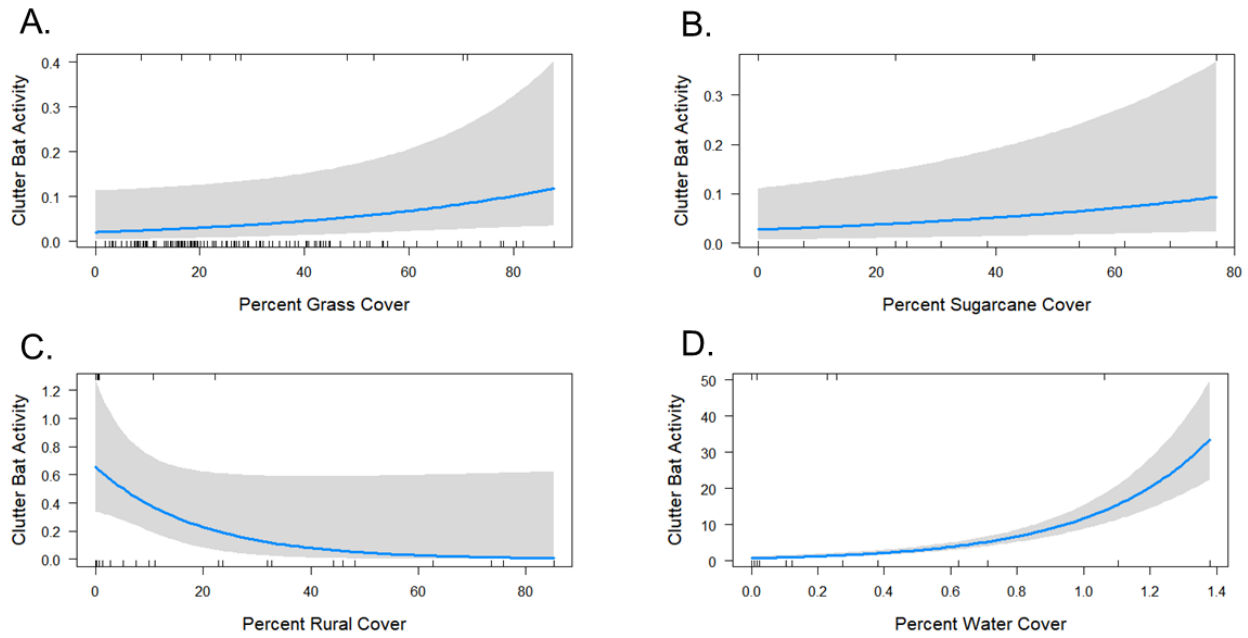793   close-up of one block, with Anabat points indicated by the black circles.
794
795
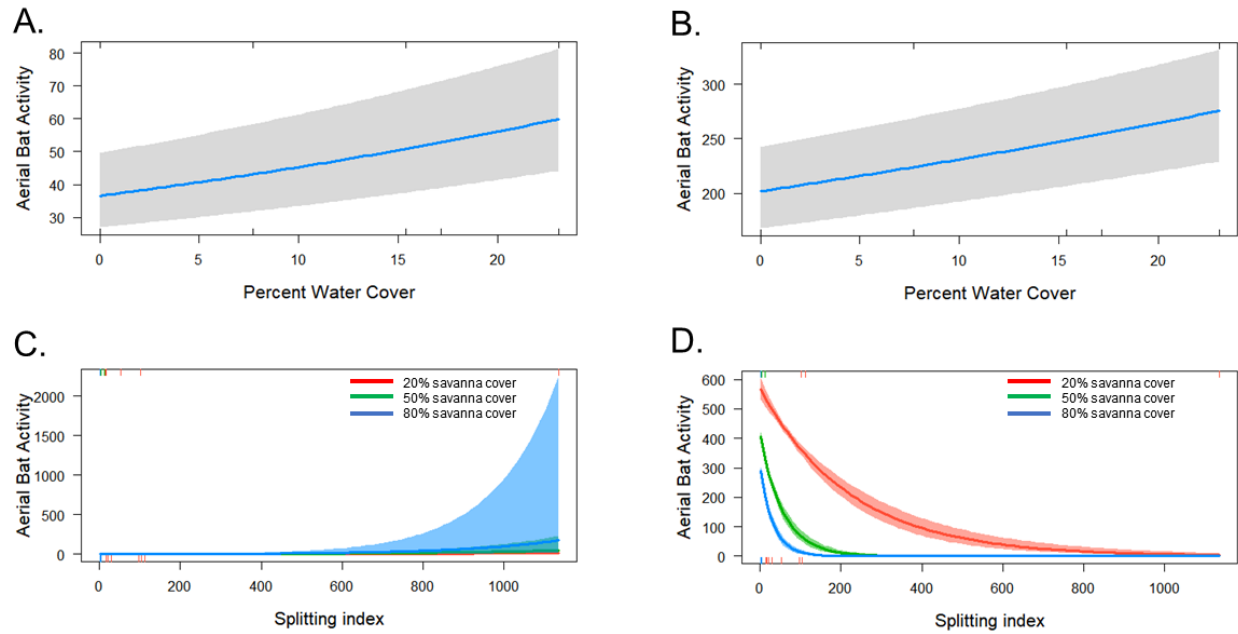
796
797 Figure 2. Response of aerial foraging guild bats at the fine scale in the A. wet season, B. dry
798 season and at the landscape scale in the C. wet season and D. dry season.
799
800

801
802 Figure 3. Response of edge foraging guild bats at the fine scale in the A. wet season, B. dry
803 season and at the landscape scale in the C. wet season and D. dry season.
804
805

27

806
807 Figure 4. Response of clutter foraging guild bats at A. wet season, B. dry season and at the
808 landscape scale in the C. wet season and D. dry season.
809