

Highlights:

- Malagasy bats select rice producing agricultural areas for foraging, potentially acting as important pest suppressors.
- Open space and edge space bats benefit the most by the conversion of forest to rice fields.
- Several economically important agricultural pests and disease vectors were detected in bat faecal samples.
- Promoting and conserving bat populations in agricultural landscapes might increase agricultural yields.

1 **Bats as potential suppressors of multiple agricultural pests: a case study from**
2 **Madagascar**

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24 **Abstract**

25 The conversion of natural habitats to agriculture is one of the main drivers of biotic change.
26 Madagascar is no exception and land-use change, mostly driven by slash-and-burn
27 agriculture, is impacting the island's exceptional biodiversity. Although most species are
28 negatively affected by agricultural expansion, some, such as synanthropic bats, are capable of
29 exploring newly available resources and benefit from man-made agricultural ecosystems. As
30 bats are known predators of agricultural pests it seems possible that Malagasy bats may be
31 preferentially foraging within agricultural areas and therefore provide important pest
32 suppression services. To investigate the potential role of bats as pest suppressors, we
33 conducted acoustic surveys of insectivorous bats in and around Ranomafana National Park,
34 Madagascar, during November and December 2015. We surveyed five landcover types:
35 irrigated rice, hillside rice, secondary vegetation, forest fragment and continuous forest. 9,569
36 bat passes from a regional assemblage of 19 species were recorded. In parallel, we collected
37 faeces from the six most common bat species to detect insect pest species in their diet using
38 DNA metabarcoding. Total bat activity was higher over rice fields when compared to forest
39 and bats belonging to the open space and edge space sonotypes were the most benefited by
40 the conversion of forest to hillside and irrigated rice. Two economically important rice pests
41 were detected in the faecal samples collected - the paddy swarming armyworm *Spodoptera*
42 *mauritica* was detected in *Mops leucogaster* samples while the grass webworm
43 *Herpetogramma licarsisalis* was detected from *Mormopterus jugularis* and *Miniopterus*
44 *majori* samples. Other crops pests detected included the sugarcane cicada *Yanga guttulata*,
45 the macadamia nut-borer *Thaumatotibia batrachopa* and the sober tabby *Ericeia inangulata*
46 (a pest of citrus fruits). Samples from all bat species also contained reads from important
47 insect disease vectors. In light of our results we argue that Malagasy insectivorous bats have
48 the potential to suppress agricultural pests. It is important to retain and maximise Malagasy

49 bat populations as they may contribute to higher agricultural yields and promote sustainable
50 livelihoods.

51 **1. Introduction**

52 The pervasive conversion of forests for food production is a conspicuous symbol of the
53 Anthropocene (Malhi, 2017). Large swaths of forest have already been cleared for agriculture
54 and the encroachment of natural ecosystems is due to continue as human populations and
55 food demand continue to rise (Giam, 2017). Madagascar holds a unique ensemble of
56 ecosystems and wildlife that is almost unmatched in its biological uniqueness (Goodman and
57 Benstead, 2005). However, despite its high level of endemism and species diversity,
58 Madagascar's forests continue to face one of the highest rates of conversion in the world with
59 approximately 1% of the island's forest cover being cleared each year (Rasolofoson *et al.*,
60 2015; Eklund *et al.*, 2016; Vieilledent *et al.*, 2018). While most Malagasy biodiversity is
61 adversely affected by agriculture-driven habitat modification, some 'winner' species benefit
62 from habitat modification and increase their abundance in agricultural areas. Several of these
63 are insectivorous birds (Martin *et al.*, 2012; Rocha *et al.*, 2015) and bats (López-Baucells *et*
64 *al.*, 2017b) that through the suppression of agricultural pests can provide valuable ecosystem
65 services to local populations (Karp and Daily 2014; Maas *et al.* 2015).

66 Rice (*Oryza* spp.) is one of the most important staple food crops worldwide (Muthayya *et al.*,
67 2014). It is the main crop cultivated by Malagasy subsistence farmers (Kari and Korhonen-
68 Kurki, 2013) throughout the island, and as in numerous other high-biodiversity regions across
69 the tropics, much of the ongoing deforestation is due to agricultural expansion for rice
70 production (McConnell *et al.*, 2004; Neudert *et al.*, 2017). Such a high dependency on rice
71 creates problems when yields are affected by climatic events or pest outbreaks (Harvey *et al.*,
72 2014). Insect rice pests are known to cause severe damage to rice crop yields (Oerke, 2006).

73 Rice crop losses are predominantly caused by Lepidopteran stem borers found across several
74 families such as the Noctuidae, Pyralidae, Tortricidae or Geometridae (Nwilene *et al.*, 2013).
75 Modern day farming techniques incorporate Integrated Pest Management (IPM) to control
76 pest populations (Stenberg, 2017). However, many small-holder farmers in sub-Saharan
77 Africa are unable to access IPM techniques due to lack of financial capital or expertise (Parsa
78 *et al.*, 2014). A sustainable and low cost method to aid pest control and reduce crop losses is
79 through biological control (Bommarco *et al.*, 2013; Naranjo *et al.*, 2015). Biological control,
80 as part of a wider application of integrated pest management practices, can involve
81 insectivorous bats, and has already been proven effective for pecan and rice farms in the USA
82 and Catalonia (Brown *et al.*, 2015; Puig-Montserrat *et al.*, 2015). Multiple lines of evidence
83 support that aerial hawking insectivorous bats provide valuable agricultural pest control
84 services in both temperate and tropical regions (Boyles *et al.*, 2011; Karp and Daily, 2014;
85 Wanger *et al.*, 2014; Brown *et al.*, 2015; Russo *et al.*, 2018). For instance, in the
86 Mediterranean the soprano pipistrelle *Pipistrellus pygmaeus* was found to suppress rice borer
87 moth *Chilo suppressalis* populations through opportunistic foraging (Puig-Montserrat *et al.*,
88 2015). However, to date most research on tropical bat predation services has focussed on
89 coffee and cacao agroecosystems (Maas *et al.*, 2016), with limited research targeting rice
90 (Wanger *et al.*, 2014). One notable exception comes from Thailand where it was estimated
91 that predation of white backed planthoppers *Sogatella furcifera* by wrinkle-lipped bats
92 *Tadarida plicata* prevents rice crop losses valued at >1.2 million USD (or >26,000 rice
93 meals) each year (Wanger *et al.*, 2014).

94 Numerous bat species (particularly of the Molossidae and Vespertilionidae families) are
95 known to coexist synanthropically by exploring newly available resources. These bat families
96 have been shown to feed on pests (Brown *et al.*, 2015) and to select crops as preferred
97 foraging areas especially during insect pest outbreaks (Lehmkuhl Noer *et al.*, 2012; Taylor *et*

98 *al.*, 2013a; Davidai *et al.*, 2015). In fact, bats tend to select foraging areas based upon the
99 resources available (Ancillotto *et al.*, 2017), which makes them excellent pest suppressors
100 during seasonal insect pest outbreaks.

101 Large colonies of molossid bats roost in buildings across Madagascar (Razafindrakoto *et al.*,
102 2010; López-Baucells *et al.*, 2017b). However, any potential predation services provided by
103 these colonies are yet to be explored. Forty-two species of insectivorous bats occur in
104 Madagascar, with several species occurring more frequently in anthropogenic landscapes as
105 opposed to forest habitats (Randrianandrianina *et al.*, 2006; Rakotoarivelo *et al.*, 2007). In
106 general, most studies have focused on the dry western region (Goodman *et al.*, 2005; Kofoky
107 *et al.*, 2006; Bambini *et al.*, 2010; Racey *et al.*, 2010; Fernández-Llamazares *et al.*, 2018) as
108 opposed to the humid eastern zone (Randrianandrianina *et al.*, 2006) and only a few studies
109 have tackled habitat selection while none have addressed the potential pest suppressor role in
110 agricultural areas.

111 The DNA metabarcoding of bat faecal pellets can offer valuable insights into the dietary
112 preferences of bats and their potential role as pest suppressors (Bohmann *et al.*, 2014; Swift
113 *et al.*, 2018). Recent diet analyses of multiple bat species have detected a wide range of
114 arthropods in bat populations (Galan *et al.*, 2017) including several economically important
115 pest species (Taylor *et al.*, 2017).

116 Here, we combine bioacoustics and DNA metabarcoding to investigate if Malagasy
117 insectivorous bats are foraging within the island's agricultural matrix and if they are
118 consuming important pest species. Specifically, we address the following questions:

- 119 i) How does total bat activity, species (or species-group) activity and assemblage
120 composition change across a rice-dominated agroecosystem landscape? We
121 hypothesise that due to higher insect availability some bats will be more active

122 over rice fields compared to forested sites. We also predict a clear shift in
123 assemblage composition from open to closed landcover types.

124 ii) Which species (or species-groups) are more common within the agricultural
125 matrix? We predict that synanthropic molossids will be particularly abundant in
126 rice fields but we still anticipate some forest associated species to forage outside
127 the forest border.

128 iii) Are bats roosting within the agricultural matrix preying on agricultural insect
129 pests? We expect bats to predate mainly on moths and beetles and we predict that
130 several of these will be agricultural pests of rice and other crops.

131 **2. Methods**

132 **2.1 Study area**

133 Fieldwork was conducted primarily in the peripheral zone surrounding the Ranomafana
134 National Park (RNP) (21°16'S, 47°20'E). The peripheral zone comprises over 160 villages
135 with a population in excess of 50,000 in an area of approximately 500 km² (Kari and
136 Korhonen-Kurki, 2013). Agricultural communities in the region, like many throughout
137 Madagascar, cultivate rice through slash-and-burn agriculture (*tavy*) and irrigated paddies
138 (Peters, 1998; Brooks *et al.*, 2009). The RNP is located between the central highlands and the
139 eastern lowlands and is of particular ecological and economic interest due to its high
140 biodiversity and watershed protection role.

141 **2.2 Bat surveys**

142 Bats were surveyed from November to December 2015 in 54 sites in and around RNP (Fig.
143 1). Sites were clustered around seven villages (Kelilalina, Tsaratanana, Mangevo,
144 Andriamamovoka, Amboasary, Mandriandry and Tolongoina) and were classified into five
145 landcover categories: irrigated rice fields ($n = 12$), hillside rice fields ($n = 8$), secondary

146 vegetation i.e. fallow agricultural land of mixed successional vegetation ($n = 11$), forest
147 fragment ($n = 9$) and continuous forest in RNP ($n = 15$) (for landcover images and description
148 see supplementary materials Fig. A.1.). Bat activity was recorded using SongMeter
149 SM2BAT+ and SM3 autonomous bat detectors (Wildlife Acoustics, Concord, MA, USA).
150 Detectors were secured to a tree at approximately 1.5 m with external SMX-II omni-
151 directional microphones (Wildlife Acoustics, Concord, MA, USA). Detectors were set to
152 record calls continuously from 18:00 until 06:00 for three consecutive nights at each locality.
153 Bat activity was sampled for 1,956 hours across a total of 147 detector-nights of sampling
154 effort. Detectors were set with a 384 kHz sample rate, 12 kHz digital high pass filter, 18 dB
155 trigger level, microphone bias off, and 36 dB gain. We used a 1.0 s trigger window minimum
156 to capture calls prior to the initial trigger.

157 #Figure 1 approximately here#

158 **2.3 Bioacoustic analysis**

159 Recordings were manually classified using Kaleidoscope software version 3.1.7 (Wildlife
160 Acoustics, Concord, MA, USA). We defined a bat pass as a recording of five seconds
161 maximum with at least two pulses with more than 20 dB of difference between the
162 background noise and bat call (Appel *et al.*, 2017) Call sequences were manually identified to
163 species level or left as mixed species groups, or sonotypes, where it was not possible to
164 clearly assign a call to a particular species (Torrent *et al.*, 2018). Call sequences were also
165 identified as feeding buzzes (specific echolocation sequence that a bat uses as it pursues and
166 subsequently catches its prey). We used the frequency of maximum energy or peak frequency
167 (kHz), the start and ending frequencies (kHz), the duration (ms) and the call shape to identify
168 or group species from the existing literature and our own release calls (Fenton *et al.*, 1980;
169 Russ and Bennett, 2001; Kofoky *et al.*, 2009; Goodman *et al.*, 2011; Goodman *et al.*, 2015).
170 Our analysis included a total of 11 sonotypes from the families Emballonuridae,

171 Hipposideridae, Molossidae, Miniopteridae, Myzopodidae and Vespertilionidae. Five
172 sonotypes were classified to species level and the remaining six into sonotype groups (Table
173 1).

174 #Table 1 approximately here#

175 **2.4 Faecal sample collection**

176 Mist-nets were used to capture bats at roosts in five villages in the RNP area (for sampling
177 details see López-Baucells *et al.*, 2017). Three caves were inspected and surveyed with mist-
178 netting outside of the emergence point (for *Miniopterus* spp. and *Myotis goudoti*). Bats were
179 measured, weighed and identified using keys (Russ and Bennett, 2001; Goodman, 2011). Bat
180 capture and handling was conducted following guidelines approved by the American Society
181 of Mammalogists (Sikes *et al.*, 2011). We kept the bats in cloth bags for an hour until
182 defecation occurred. Faecal pellets were labelled and stored in 2 ml tubes in 95% ethanol and
183 stored in a cool dry space. Of the 322 bats caught, we collected faecal samples from 150 bats.
184 Fifty-eight faecal samples from six species (*Chaerephon atsinanana*, *Mops leucostigma*,
185 *Mormopterus jugularis*, *Myotis goudoti*, *Miniopterus manavi*, *Miniopterus majori*) were used
186 for the diet analysis.

187 **2.5 DNA extraction and PCR amplification**

188 The DNA was extracted from the faecal samples using the Norgen Stool Kit following
189 instructions provided by the manufacturers (Norgen Biotek Corp.). Amplification of DNA
190 from the faeces was achieved using the Leray-XT PCR primer set (Wangensteen *et al.*,
191 2018b), a highly degenerated primer set targeting a 313-bp fragment of the mitochondrial
192 cytochrome c. oxidase subunit I (COI) region. The mlCOIintF-XT primer (5'-
193 GGWACWRGWTGRACWITITAYCCYCC-3') was used as forward primer. This modified
194 version (Wangensteen *et al.*, 2018b) of the mlCOIintF primer (Leray *et al.*, 2013) included

195 two extra degenerate bases (equimolar mixtures of two different bases at a given position)
196 and two inosine nucleotides to enhance its eukaryotic universality. The reverse primer was
197 jgHCO2198 (5'-TAIACYTCIGGRTGICCRAARAAYCA-3';(Geller *et al.*, 2013)). The Leray
198 fragment has already been successfully applied to the characterisation of both marine fish gut
199 contents (Leray *et al.*, 2013), marine invertebrates (Siegenthaler *et al.*, 2018) and terrestrial
200 arthropods (Macías-Hernández *et al.*, 2018). A single-PCR step using primers with attached
201 eight-base oligo-tags (Coissac *et al.*, 2012) was used to label different samples in a
202 multiplexed library; moreover a variable number (2, 3 or 4) of fully degenerate positions (Ns)
203 was added at the beginning of each primer, in order to increase variability of the amplicon
204 sequences (Guardiola *et al.*, 2015) .The PCR mix recipe included 10 µl AmpliTaq gold 360
205 master mix (Applied Biosystems), 3.2 µg Bovine Serum Albumin (Thermo-Scientific), 1 µl
206 of each of the 5 µM forward and reverse tagged-primers, 5.84 µl water and 2 µl extracted
207 DNA template (~ 5 ng µl⁻¹). The PCR profile included an initial denaturing step of 95 °C for
208 10 min, 35 cycles of 94 °C for 1 min, 45 °C for 1 min and 72 °C for 1 min and a final
209 extension step of 72 °C for 5 minutes. After a quality check of all amplicons by
210 electrophoresis, the tagged PCR products (including a negative control) were pooled into a
211 multiplexed sample pool and purified using MinElute columns (Qiagen). An Illumina library
212 was subsequently built from these pools, using the NextFlex PCR-free library preparation kit
213 (BIOO Scientific). The library was sequenced on an Illumina MiSeq platform using v3
214 chemistry (2x250 bp paired-ends), as part of a multiplexed run including ten other unrelated
215 libraries.

216 **2.7 Bioinformatic analyses**

217 Bioinformatic analyses were performed using the OBITools metabarcoding software suite
218 (Boyer *et al.*, 2016). Read quality assessment was performed with FastQC and only paired-
219 end reads with phred quality score > 40 was retained. Demultiplexing and primer removal

220 were achieved using ngsfilter. Obigrep was applied to select all aligned reads with a length
221 between 303-323 bp and without ambiguous bases. Obiuniq was used to dereplicate the reads
222 and the uchime-denovo algorithm (Edgar *et al.*, 2011) implemented in VSEARCH (Rognes *et*
223 *al.*, 2016) was used to remove chimeric sequences. Amplicon clustering was performed using
224 the SWARM 2.0 algorithm (Mahé *et al.*, 2015) with a distance value of $d=13$, which offers a
225 conservative solution to the high variability of the COI gene (Siegenthaler *et al.*, 2018).
226 Taxonomic assignment of the representative sequences for each molecular operational
227 taxonomic unit (MOTU) was performed using the ecotag algorithm (Boyer *et al.*, 2016),
228 using a local reference database (Wangensteen *et al.*, 2018b) containing filtered COI
229 sequences retrieved from the BOLD database (Ratnasingham and Hebert, 2007) and the
230 EMBL repository (Kulikova *et al.*, 2004). This algorithm uses a phylogenetic approach to
231 assign sequences to the most reliable monophyletic unit, so that sequences are assigned to
232 different taxonomic ranks, depending on the density of the reference database. The data was
233 refined by removing contaminations of marine origin (originated by tag-switching from other
234 multiplexed libraries in the sequencing run). A minimum abundance filter of 5 total reads was
235 used to avoid false positives and low frequency noise (De Barba *et al.*, 2014; Wangensteen
236 and Turon, 2017). This pipeline, with little variations, has been previously used for analysing
237 metabarcoding data for the same COI marker in a variety of systems (e.g. Wangensteen and
238 Turon, 2017; Macías-Hernández *et al.*, 2018; Siegenthaler *et al.*, 2018; Wangensteen *et al.*,
239 2018a; Wangensteen *et al.*, 2018b). The resulting data has been deposited on Mendeley Data
240 ([dataset] Kemp *et al.*, 2018)

241 **2.8 Statistical analysis**

242 Bat activity was defined as the total number of bat passes per night from all species as well as
243 for each sonotype (Torrent *et al.*, 2018). As appropriate for count data, negative binomial or
244 Poisson generalized linear mixed models (GLMMs) with a log link function were used to

245 model the relationship between bat activity and landcover type (continuous forest, forest
246 fragments, secondary vegetation, hillside rice and irrigated rice) (Burnham and Anderson,
247 2003). Species with less than 300 recordings were not used in the analysis due to a lack of
248 model convergence. Since preliminary analyses suggested that the count data were
249 overdispersed, we accounted for this overdispersion by using a Poisson or negative binomial
250 regression in *glmer* or *glmmADMB* and adding a random intercept of “Site” nested within
251 “Location” (Bates, 2010).

252 Numbers of bat passes were positively correlated with feeding buzzes (Table A.1). We
253 therefore only used the larger bat passes dataset for modelling as a proxy for feeding activity
254 (Torrent *et al.*, 2018). Moran’s *I* test showed that there is no residual spatial autocorrelation
255 between sites (Table A.2). The difference in assemblage structure between landcover types
256 was analysed using the analysis of dissimilarity test *adonis*. It was visualised through a non-
257 metric multidimensional scaling (NMDS), based on a Bray-Curtis dissimilarity matrix, using
258 sonotype activity data per site. We analysed and presented the data using R statistical
259 software 3.4.1 (R Development Core Team, 2017) with the packages: tidyverse (Wickham,
260 2016), lme4 (Bates *et al.*, 2014), glmmADMB (Skaug *et al.*, 2015) and vegan (Oksanen *et*
261 *al.*, 2013).

262 The relative abundance of MOTU reads for prey items (excluding predator reads and
263 normalized to 10,000 total prey reads per sample) was calculated for all prey MOTUs. The
264 relative abundances per faecal sample for all prey MOTUs were then averaged per bat
265 species. We then grouped the MOTU sequences by arthropod orders and highlighted the pest
266 and disease transmitting insect species, alongside any species or genera that we suspected to
267 have a potential pest status.

268 3. Results

269 3.1 Bat activity

270 We recorded a total of 9,569 bat passes, of which 1,643 (17 %) were identified to species
271 level (*Hipposideros commersoni*, *M. manavi*, *M. goudoti*, *Myzopoda aurita*,
272 *Paraemballonura atrata*), 2,261 (24 %) were identified to sonotypes of two species
273 (*Miniopterus gleni*/*M. majori*, *Scotophilus robustus*/*M. gleni*, *S. robustus*/*M. jugularis*,
274 *Otomops madagascariensis*/*Tadarida fulminans*), and 5,665 (60 %) were attributed to
275 sonotypes Molossidae 1 (Mo1: *C. atsinanana*, *M. leucostigma*, *M. jugularis*, *Taphozous*
276 *mauritanus*) and Vespertilionidae/Miniopteridae 1 (VMi1: *M. gleni*, *M. majori*, *M. manavi*,
277 *Miniopterus soroculus*, *Neoromicia matroka*, *Pipistrellus hesperidus*, *Pipistrellus raceyi*). In
278 total 1,013 feeding buzzes were recorded, with Mo1 accounting for 389 (38 %) of feeding
279 buzzes, VMi1 for 334 (33 %) and *P. atrata* for 102 (10 %).

280 Bat activity was highest in hillside rice with a mean of 197 passes/night and more than double
281 that of the next landcover type with more bat activity - irrigated rice at 89 passes/night (Table
282 2). Overall bat activity in both types of rice field, hillside and irrigated, was higher than
283 activity levels in continuous forest (Table A.3). According to pairwise comparisons (Table
284 A.4), total bat activity over hillside rice was higher than in continuous forest ($p < 0.01$) and
285 forest fragments ($p < 0.05$) whereas activity in irrigated rice was only higher than continuous
286 forest ($p < 0.01$).

287 In hillside and irrigated rice, Mo1, VMi1, *M. goudoti* and *M. gleni*/*M. majori*, had
288 significantly higher activity compared to continuous forest while *O. madagascariensis*/*T.*
289 *fulminans* was higher in hillside rice compared to continuous forest. In continuous forest and
290 forest fragments, *P. atrata* and *M. goudoti* had the highest mean bat passes/night, respectively
291 (Fig. 2).

292 #Table 2 approximately here#

293 #Figure 2 approximately here#

294 **3.2 Assemblage composition**

295 Assemblage composition varied between landcover type (adonis: $r^2 = 0.253$; $p = 0.001$). This
296 was corroborated by the NMDS ordination which revealed distinct patterns of dissimilarities
297 in assemblage composition between the five landcover classes (Fig. 3). The NMDS had a
298 final stress value of 0.12 conveying a good representation of the data along the represented
299 dimensions.

300 #Figure 3 approximately here#

301 **3.3 Presence of insect pests in faecal samples (DNA metabarcoding)**

302 We obtained a total number of 655,205 MOTU reads from all samples. 43.5% (285,978) of
303 the reads were attributed to bats while 5.3% (34,599) of the reads were assigned to
304 arthropods. Overall, when looking at the insect orders found in the faecal samples, the highest
305 average relative abundance of MOTU reads found were of Coleoptera, Lepidoptera,
306 Ephemeroptera, Diptera and Hemiptera (Table 3). All the bats species sampled fed on, at
307 least, 11-13 orders of arthropods.

308 #Table 3 approximately here#

309 In 58 bat faecal samples we found six known pest species, seven insect vectors of human
310 diseases and 17 potential pest taxa (Table A.5). Of the known agricultural pests found in the
311 faecal samples, two economically important rice pest species were found – the paddy
312 swarming caterpillar *Spodoptera mauritia* in *M. leucogaster* and the grass webworm
313 *Herpetogramma licarsisalis* in *M. jugularis* and *M. majori*. Other crops pests detected were:
314 the black twig borer *Xyleborus ferrugineus* a pest of coffee; the sugarcane cicada *Yanga*
315 *guttulata*; the macadamia nut-borer *Thaumatotibia batrachopa* and the sober tabby *Ericeia*
316 *inangulata* a pest of citrus fruits. Potential pest species and genera, from the order

317 Lepidoptera, were found in all bat species. In particular: *Mythimna* sp. – a genus containing
318 the rice armyworm *Mythimna unipuncta*; *Emmalocera* sp. – a genus containing a sugarcane
319 root borer *Emmalocera depressella*; and *Cydia choleropa* – a sister species of the codling
320 moth *Cydia pomonella* a pest of apples and pears.

321 **Discussion**

322 Large colonies of, predominantly, molossid, vespertilionid and miniopterid bats, were found
323 to be preferentially selecting the rice fields surrounding the RNP. Six species of bats were
324 shown to have fed upon economically important insect pests such as the paddy swarming
325 caterpillar (*Spodoptera mauritia*) and the Grass webworm (*Herpetogramma licarsisalis*). In
326 agreement with Puig-montserrat *et al.* (2011) and Wanger *et al.* (2014) insectivorous bats,
327 particularly molossids, are likely to be preferentially selecting rice fields for foraging and
328 feeding upon rice crops pests and other economically important insects.

329 *Bat activity across landcover types.*

330 The highest overall mean activity was found in hillside rice followed by irrigated rice and
331 secondary vegetation (Table 2). Hillside rice has markedly lower yields compared to lowland
332 irrigated rice. Water and nutrient run-off impact the growth of upland rice. A lack of water
333 and nutrient retention in the rice crop makes it more susceptible to insect pest infestations.
334 This may be one reason why we recorded the highest activity in hillside rice. However, it is
335 also possible that there was an altitudinal detection bias as hillside rice and secondary
336 vegetation sites were on open hillsides with little vegetation and facing large valleys (Collins
337 and Jones, 2009). Both sites, however, were found at similar altitudes and had markedly
338 different results (Table 2, Table A.3). Irrigated rice sites, on the other hand, are found at the
339 bottom of valleys. Despite the possible altitudinal bias, activity within irrigated rice was the
340 second highest of the landcover types (Table 2, Table A.3). Intensive rice agriculture
341 harbours high densities of insect pests which provide an excellent resource for insectivorous

342 bats. Insects form swarms, especially tympanic moths (Noctuidae, Crambidae and Pyralidae),
343 during mating and emergence, which bats are able to opportunistically prey upon
344 (McCracken *et al.*, 2012; Malmqvist *et al.*, 2018).

345 The open space group, Mo1, was the most active overall and over hillside rice (Figure 2,
346 Table 2). This suggests that open-space aerial hawkers are important agents of pest
347 suppression in the rice-dominated landscape surrounding the RNP and potentially throughout
348 much of Madagascar's agroecosystems. Further research and action is required to improve
349 the knowledge of bats dietary preferences, both temporally and spatially. The reputation of
350 these bats among local communities needs to be improved, especially as they form large
351 colonies in public buildings (López-Baucells *et al.*, 2017b).

352 The results conform to the notion that molossids (in addition to *Taphozous mauritanus*),
353 which are open-space aerial hawkers, commute and forage at higher altitudes than other
354 families (Lee and McCracken, 2002; McCracken *et al.*, 2008; Taylor *et al.*, 2013b). Open
355 space foragers have a high wing loading ratio (fast flight; low manoeuvrability) which
356 suggests that they do not use cluttered sites and this explains their low detection in forested
357 areas (Schnitzler and Kalko, 2001).

358 The sonotype VMi1, comprised of three vespertilionids and three miniopterids, was found to
359 be the most active in irrigated rice fields and the second most active overall (Figure 2, Table
360 2). The species in this sonotype forage as edge-space aerial-hawkers (Verboom and Huitema,
361 1997; Taylor *et al.*, 2013b). The mosaic of vegetation and fruit trees, rivers and streams,
362 paths, terraces and anthropomorphic structures within the vicinity of the rice fields may
363 provide this group with the required heterogeneity or "edge" habitat to forage (Monck-Whipp
364 *et al.*, 2018). This is important for the contextualization of our results as edge-space foragers

365 are known to predate upon insect pests within agroecosystems (Taylor *et al.*, 2013a; Taylor *et*
366 *al.*, 2013b; Brown *et al.*, 2015; Puig-Montserrat *et al.*, 2015)

367 The edge-clutter species, *Myotis goudoti* and *Paraemballonura atrata*, were previously
368 captured in forest in the same region as our study (Goodman *et al.*, 2014). We recorded both
369 species at relatively high levels in irrigated rice, forest fragments and continuous forest sites.
370 Although post hoc tests showed no significant differences, this activity shows that these
371 species are selecting lowland irrigated rice and forest for foraging. The NMDS plots show
372 that both species are strongly associated with forest sites (Fig. 3). NMDS axis 2 shows *P.*
373 *atrata* is more associated with rice fields than *M. goudoti*. The fact that these edge-clutter
374 species, *P. atrata* and *M. goudoti*, switch between open and closed sites highlights the
375 importance of retaining forest nearby for roost provision and maintaining bat populations.
376 The paucity of available roosts for bats in rice dominated landscapes is certainly an issue and
377 one that requires addressing as a sustainable solution to crop losses. Installing bat houses and
378 improving landscape heterogeneity are ways to address the lack of suitable roosts available
379 (Flaquer *et al.*, 2006; Lindell *et al.*, 2018; Monck-Whipp *et al.*, 2018).

380 Additionally, we recorded two charismatic, endemic and difficult to catch species -
381 *Myzopoda aurita* and *Hipposideros commersoni*. The eastern sucker-footed bat *Myzopoda*
382 *aurita* was recorded in hillside and irrigated rice and in secondary vegetation (Table 2). This
383 species roosts in the furled-up leaves of the traveller's palm *Ravenala*
384 *madagascariensis* which can grow in open areas of vegetation or forest. Commersoni's
385 horseshoe bat *Hipposideros commersoni* is the largest insectivorous bat in Madagascar, listed
386 as Near Threatened (Andriafidison, 2008), and it was mainly recorded in hillside rice (Table
387 2). The echolocation of *Hipposideros commersoni* (high duty cycle echolocation) is
388 extremely efficient for hunting in cluttered spaces. The bat may be roosting in the remnant
389 forests and foraging in the adjacent hillside rice. The rarity of both species might limit their

390 predation services but their high association with forest habitat qualifies them as good
391 indicator taxa for the evaluation of habitat disturbance.

392 As expected, from the NMDS plots, the assemblage composition in the landscape shows that
393 there was a turnover of species and sonotypes (Fig. 3). One can see a gradient from irrigated
394 rice to continuous forest, from left to right. The open space foragers (*Mo1* and *O.*
395 *madagascariensis/T. fulminans*) occupy the left side of NMDS axis 1 while the clutter and
396 edge-space foragers (*M. goudoti* and *P. atrata*) occupy the right side of the plot, illustrating
397 the foraging preferences of the aforementioned guilds (Schnitzler and Kalko, 2001). Hillside
398 rice and secondary vegetation almost entirely overlap which illustrates the similarity of these
399 sites in terms of species assemblage.

400 *Diet analysis and implications of bat foraging behaviour*

401 The DNA metabarcoding results illustrate that insectivorous bats feed on a wide range of
402 prey including a number of economically important insect pest species that affect a range of
403 crops in addition to insect disease vectors (see supplementary materials Table A.5.). The
404 results of this study, therefore, show the potential role of insectivorous bats in suppressing
405 economically important insects in agricultural landscapes.

406 We found that the sonotypes that were preferentially selecting rice fields were also the most
407 important contributors to pest suppression in rice fields. For example, *M. leucogaster* and *M.*
408 *jugularis* from the *Mo1* sonotype were found to have fed upon the rice pests *Spodoptera*
409 *mauritia* and *Herpetogramma licarsisalis*, respectively (Table A.5). Greater pest suppression
410 leads to greater yields and less reliance upon slash and burn agriculture, or *tavy* (Styger *et al.*,
411 2007). This form of agriculture is environmentally damaging and encroaches upon forests
412 when fallow lands are no longer fertile. Forest fragments still offer valuable refuges for
413 certain species, yet insectivorous bats generally prefer rice fields for foraging. By identifying

414 the most active sonotypes and how they change across different land-uses we can begin to
415 understand the level of pest suppression that bats provide to agricultural landscapes.

416 It is important to note that the fieldwork only spanned a short amount of time (approximately
417 three days per locality). The research therefore does not reflect the seasonal and spatial
418 variation of bat diets nor do the results intentionally follow peaks in insect populations.
419 Additionally, although we have identified bat predation on predatory arthropods that can
420 potentially contribute to the suppression of agricultural pests (e.g. spiders - order Araneae -
421 were identified in the diet of *M. goudoti*; Table 3) we did not explore the effects of intra-guild
422 predation on herbivorous arthropods. Since most Malagasy bats are predominantly aerial
423 feeders we anticipated that bat predation on non-flying arthropods would be limited. We
424 suggest that future research should try to investigate the effects of intra-guild predation and
425 any potential cascading effects on the abundance of agricultural pests and on rice yield.
426 Furthermore, despite the fact that our study focussed on a rice-dominated agroecosystem, it is
427 important to note that the pests of other crops found in bat faeces illustrates the global
428 potential of bats as pest suppressors. Further research quantifying the role of bats as pest
429 suppressors in Madagascar is urgently needed as they: receive little protection from Malagasy
430 legislation; fall under game species regulations i.e. they are not actively protected; many are
431 data deficient; and there is little appreciation of their role in ecosystem services (Racey *et al.*,
432 2010).

433 **Conclusions**

434 Deforestation and habitat loss due to agricultural expansion are the primary driver of
435 biodiversity loss in Madagascar. The need for agricultural expansion to compensate for crop
436 losses is exacerbated by climatic extremes and insect pest outbreaks. We found that Malagasy
437 insectivorous bats have the potential to suppress these outbreaks as they predate upon insect

438 pests. Therefore, retaining and maximising bat populations across the island’s agricultural
439 landscapes can contribute to higher agricultural yields and help promote sustainable
440 livelihoods. Provision of artificial roosts such as bat-boxes (Puig-Montserrat *et al.*, 2015;
441 López-Baucells *et al.*, 2017a) and increased landscape heterogeneity is an important
442 consideration for agricultural and conservation planning, specifically for open and edge-
443 foragers. Since some cave-dwelling bat species (i.e. *Miniopterus manavi*, *Miniopterus majori*,
444 and *Myotis goudoti*) were also predated on insect pests, appropriate conservation legislation
445 and cave protection initiatives (i.e. regulation of the harvesting of guano and cave tourism)
446 are essential to keep their populations stable. Further research and action is required to
447 improve the knowledge of bat dietary preferences, following pest outbreaks both temporally
448 and spatially, while improving the reputation of bats among local communities.

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460 **Figure and table captions**

461 Figure 1. Map of sampling sites within and surrounding the Ranomafana National Park,
462 Madagascar.

463 Figure 2. Mean bat activity per night per sonotype (>300 passes) for each landcover type,
464 with standard errors. See Table 1 for sonotype abbreviations.

465 Figure 3. NMDS plot showing community assemblage of sonotypes (in text) relative to
466 sampling sites (coloured dots – corresponding to landcover type). See Table 1 for sonotype
467 abbreviations.

468 Table 1. List of species known to occur in the region incorporating Ranomafana National
469 Park with sonotypes created from mean peak frequency ranges from the existing literature.

470 Table 2. Mean bat passes (\pm SD) per night per sonotype across each landcover type.
471 Significant differences to continuous forest from generalised linear mixed models highlighted
472 in bold.

473 Table 3. Average relative abundance of MOTU reads per 10,000 reads for six bat species
474 (number of samples in brackets) grouped by arthropod order. See Table A.5 for insect pest
475 and disease vector species and genera.

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Table 1 - List of species and acoustics

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Table 1. List of species known to occur in the region incorporating Ranomafana National Park with sonotypes created from mean peak frequency ranges from the existing literature.

Sonotype	Family	Species	Mean peak frequency ranges (kHz)	Call shape	IUCN category
<i>H.commersoni</i>	Hipposideridae	<i>Hipposideros commersoni</i> ¹	61.6-76.5	FM-CF-FM	NT
<i>M.goudoti</i>	Vespertilionidae	<i>Myotis goudoti</i> ¹	55.3-72.1	FM	LC
<i>M.gle/maj</i>	Miniopteridae	<i>Miniopterus gleni</i> ^{1,2} , <i>Miniopterus majori</i> ^{1,2}	42.9-50.3	FM-QCF	LC; LC
<i>M.manavi</i>	Miniopteridae	<i>Miniopterus manavi</i> ^{1,2}	58.3-61.5	FM-QCF	LC
<i>M.aurita</i>	Myzopodidae	<i>Myzopoda aurita</i> ³	14	FM-CF	LC
<i>O.mad/T.ful</i>	Molossidae	<i>Otomops madagascariensis</i> ³ <i>Tadarida fulminans</i> ³	13.0-20.0	CF	LC; LC
<i>P.atrata</i>	Emballonuridae	<i>Paraemballonura atrata</i> ¹	50.0-54.3	FM-CF	LC
<i>S.rob/M.gle</i>	Vespertilionidae/Miniopteridae	<i>Miniopterus gleni</i> ^{1,2} , <i>Scotophilus robustus</i> ¹	38.4-42.8	FM-QCF	LC; LC
VMi1	Vespertilionidae/Miniopteridae	<i>Miniopterus gleni</i> ^{1,2} , <i>Miniopterus manavi</i> ^{1,2} , <i>Miniopterus majori</i> ^{1,2} , <i>Miniopterus soroculus</i> ² , <i>Neoromicia matroka</i> ⁴ , <i>Pipistrellus hesperidus</i> ⁴ , <i>Pipistrellus raceyi</i> ⁴	50.4-58.2	FM-QCF	LC; LC; LC; LC; LC; LC; DD
<i>S.rob/M.jug</i>	Molossidae; Vespertilionidae	<i>Mormopterus jugularis</i> ⁵ , <i>Scotophilus robustus</i> ¹	30.6-38.3	FM-QCF	LC; LC
Mo1	Molossidae; Emballonuridae	<i>Chaerephon atsinanana</i> ⁵ , <i>Mops leucostigma</i> ⁵ , <i>Mormopterus jugularis</i> ⁵ , <i>Taphozous mauritanus</i> ⁶	21.0-30.5	FM-QCF/CF	NA; LC; LC; LC

Sources: Kofoky *et al.* 2009, 2. Ramasindrazana *et al.* , 2011, 3. Russ and Bennett, 2001, 4. Goodman *et al.* , 2015, 5. Release calls, 6. Fenton *et al.* , 1980

Table 2 - Mean bat activity[Click here to download Tables: Table 2 - Mean bat activity.xlsx](#)Table 2. Mean bat passes (\pm SD) per night per sonotype across each landcover type. Significant differences to continuous forest from generalised linear mixed models highlighted in bold.

Sonotype	Landcover type					
	Continuous forest	Forest fragment	Secondary vegetation	Irrigated rice	Hillside rice	Total
<i>Hipposideros commersoni</i>	0	0.04 (\pm 0.2)	0	0.03 (\pm 0.2)	1.09 (\pm 3)	0.18 (\pm 1)
<i>Myzopoda aurita</i>	0	0	0.04 (\pm 0.2)	0.13 (\pm 0.6)	0.22 (\pm 0.5)	0.07 (\pm 0.3)
<i>Myotis goudoti</i>	4.21 (\pm 10)	14.65 (\pm 30)	2.16 (\pm 4)	9 (\pm23)	4.22 (\pm4)	6.69 (\pm 18)
<i>Miniopterus gleni/M.majori</i>	0.05 (\pm 0.2)	0.58 (\pm1)	2.56 (\pm4)	7.8 (\pm11)	15.65 (\pm15)	4.59 (\pm 10)
<i>Miniopterus manavi</i>	0	2.85 (\pm 8)	0.04 (\pm 0.2)	0	0.04 (\pm 0.2)	0.52 (\pm 3)
Mo1	0.12 (\pm 0.5)	5.5 (\pm11)	20.08 (\pm38)	10.67 (\pm15)	98.7 (\pm131)	22.04 (\pm 64)
<i>Otomops madagascariensis/Tadarida fulminans</i>	0.07 (\pm 0.5)	0.92 (\pm 2)	0.52 (\pm 1)	0.17 (\pm 1)	23.61 (\pm100)	4 (\pm 40)
<i>Paraemballonura atrata</i>	5.4 (\pm 29)	0.04 (\pm 0.2)	1.96 (\pm 7)	6.87 (\pm 22)	2.48 (\pm 6)	3.71 (\pm 19)
<i>Scotophilus robustus/Miniopterus gleni</i>	0	0	5.08 (\pm 8)	3.00 (\pm 5)	23.74 (\pm 26)	5.19 (\pm 14)
<i>Scotophilus robustus/Mormopterus jugularis</i>	0	0	1.52 (\pm 3)	1.93 (\pm 3)	6.04 (\pm 8)	1.60 (\pm 4)
VMi1	2.84 (\pm 7)	7.69 (\pm 15)	5.84 (\pm 8)	48.9 (\pm100)	21.3 (\pm17)	16.50 (\pm 49)
Total	12.72 (\pm 36)	32.27 (\pm 55)	39.80 (\pm 53)	88.50 (\pm127)	197.09 (\pm228)	65.1 (\pm 128)

Table 3 - Metabarcoding results per arthropod order
[Click here to download Tables: Table 3 - Metabarcoding results per arthropod order.xlsx](#)

Table 3. Average relative abundance of MOTU reads per 10,000 reads for six bat species (number of samples in brackets) grouped by arthropod order. See Table A.5. for insect pest and disease vector species and genera.

Order name	<i>C. atsinanana</i> (12)	<i>M. leucogaster</i> (10)	<i>M. jugularis</i> (9)	<i>M. goudoti</i> (9)	<i>M. majori</i> (6)	<i>M. manavi</i> (12)	Average
Araneae	0	0	0	27.34	0	0	4.56
Astigmata	0	0	0.3	0	1.68	2.54	0.76
Blattodea	2.7	33.16	134.95	19.62	307.45	325.05	137.15
Coleoptera	1095.78	1708.65	1845.63	891.49	112.43	672.35	1054.39
Dermaptera	0	0	19.36	0	0	0	3.23
Diptera	64.56	94.34	834.68	163.94	137.09	208.7	250.55
Ephemeroptera	625.26	17.09	1053.68	67.67	76.4	44.52	314.1
Hemiptera	1.42	17.23	18.86	30.32	1933.65	661.81	443.88
Hymenoptera	0.05	1.3	0.1	352.68	104.67	708.29	194.51
Lepidoptera	138.94	63.06	414.78	324.2	2351.33	846.68	689.83
Mesostigmata	0	0.8	0	1.28	0	26.12	4.7
Neuroptera	0	0	3.96	0	0	0.69	0.78
Odonata	0.32	0	0	0	0	0	0.05
Orthoptera	3.23	2.68	3.35	0	0	0	1.54
Sarcoptiformes	0.66	14.46	2.57	72.57	1.8	8.05	16.69
Siphonaptera	0.31	0	0	0	0	0	0.05
Symphyleona	0	0	0	1.74	0	0	0.29
Trichoptera	3.05	0.02	0	3.51	10.22	0	2.8
Trombidiformes	0.5	0.33	0	0.2	185.73	2.67	31.57
Total	1936.78	1953.11	4332.25	1956.53	5222.45	3507.48	

Figure 1 - Map
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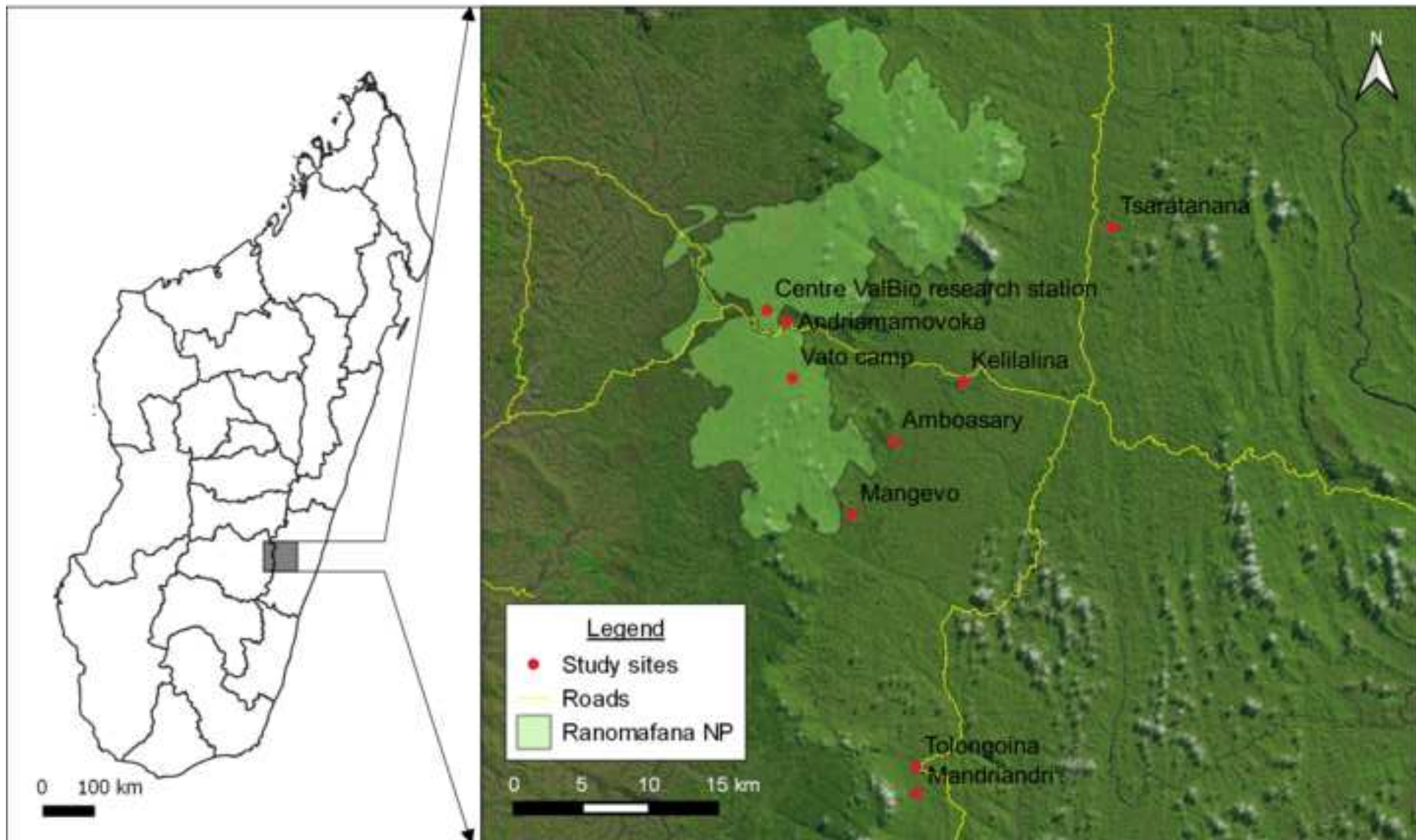


Figure 2 - Mean bat activity
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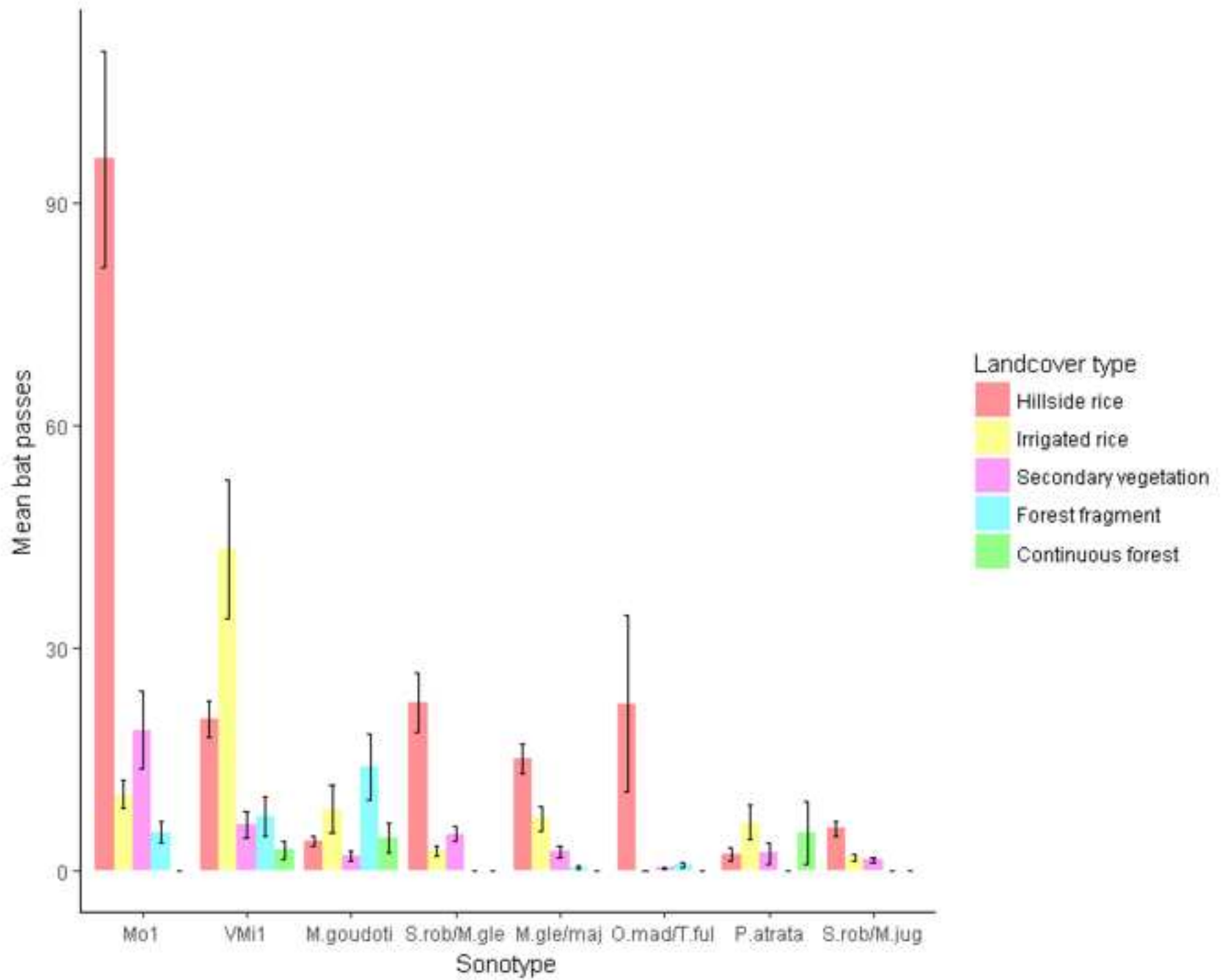
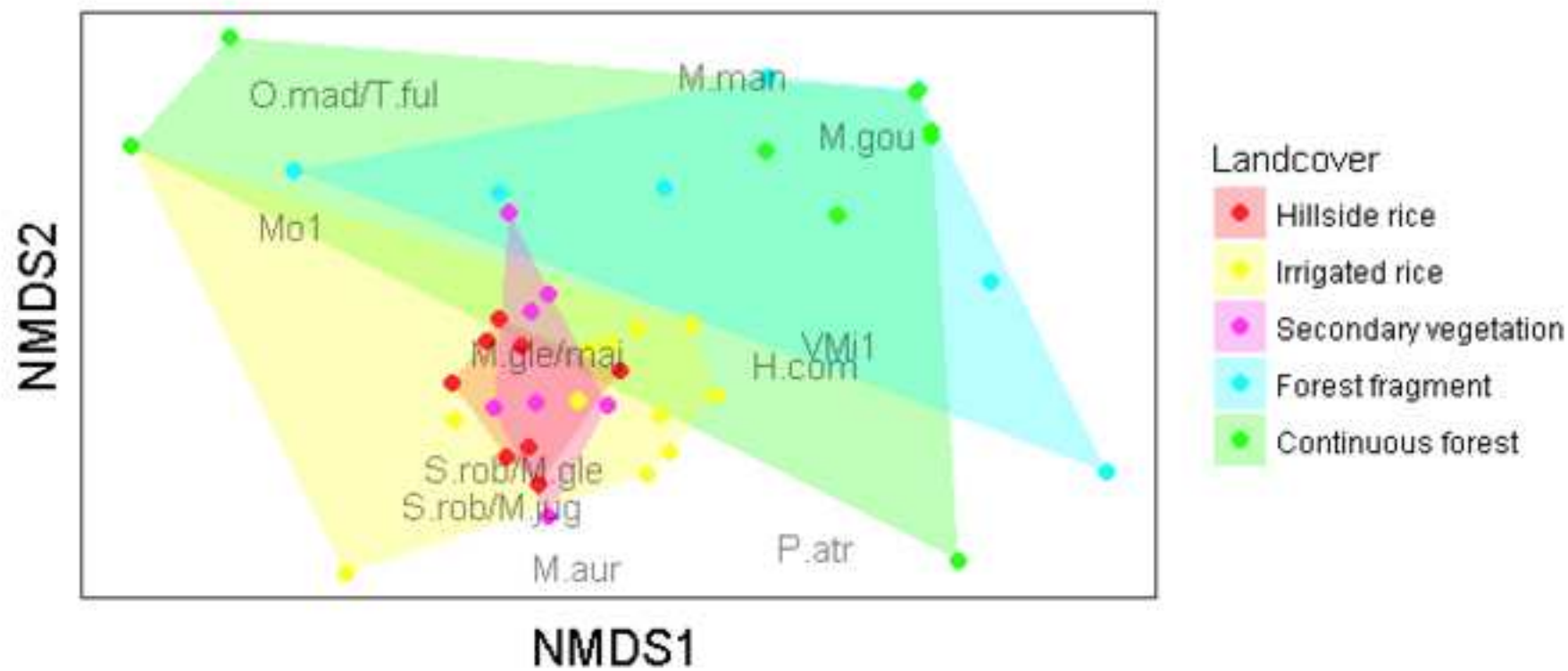


Figure 3 - NMDS

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