

1 **Title**

2 **Conservation planning with spatially explicit models: A case for horseshoe bats in**  
3 **complex mountain landscapes**

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18

**Short title**

19

20 Operational spatially explicit modelling for conservation planning

21

22 **Abstract**

23 Context Bats are considered as an ecological indicator of habitat quality due to their  
24 sensitivity to human-induced ecosystem changes. Hence, we will focus the study on two  
25 indicator species of bats as a proxy to evaluate structure and composition of the landscape to  
26 analyze anthropic pressures driving changes in patterns

27 Objectives. This study develops a spatially-explicit model to highlight key habitat nodes and  
28 corridors which are integral for maintaining functional landscape connectivity for bat  
29 movement. We focus on a complex mountain landscape and two bat species: greater  
30 (*Rhinolophus ferrumequinum*) and lesser (*Rhinolophus hipposideros*) horseshoe bats which  
31 are known to be sensitive to landscape composition and configuration.

32 Methods. Species distribution models are used to delineate high-quality foraging habitat for  
33 each species using opportunistic ultrasonic bat data. We then performed connectivity analysis  
34 combining (modelled) suitable foraging habitat and (known) roost sites. We use graph-theory  
35 and the deviation in the probability of connectivity (dPC) to quantify resilience of the  
36 landscape connectivity to perturbations.

37 Results. Both species were confined to lowlands (< 1000m elevation) and avoided areas with  
38 high road densities. Greater horseshoe bats were more generalist than lesser horseshoe bats  
39 which tended to be associated with broadleaved and mixed forests.

40 Conclusions. The spatially-explicit models obtained were proven crucial for prioritizing  
41 foraging habitats, roost sites and key corridors for conservation. Hence, our results are being  
42 used by key stakeholders to help integrate conservation measures into forest management and  
43 conservation planning at the regional level. The approach used can be integrated into  
44 conservation initiatives elsewhere.

45 **Keywords**

- 46 Species distribution modelling, ensemble modelling, expert based knowledge, landscape
- 47 connectivity, landscape structure, complex mountain landscapes, greater horseshoe bat, lesser
- 48 horseshoe bat
- 49

## 50 **1. Introduction**

51 Many bat populations are endangered at the regional, national and even continental levels  
52 (Mickleburgh et al. 2002; O'Shea et al. 2003; Vincent and Letscher 2008; Ingersoll et al.  
53 2013). As a result, international conservation agreements have placed specific designations  
54 for the conservation of bats such as the Program for the Conservation of Migratory Bats of  
55 Mexico and the United States and the Agreement on the Conservation of Bats in Europe  
56 (under the Bonn Convention). Many non-governmental organizations (NGOs) also target bat  
57 protection and conservation (Racey 2009). In Britain, for example, all bat species and their  
58 roosts are legally protected by domestic and international legislation. In France, the law for  
59 the protection of nature passed in 1976 represented an important step forward to protect bats  
60 but it proved insufficient. As an example, almost half of the bat species in the Rhône-Alpes  
61 region of France are listed as endangered in the regional red list (UICN 2003). To reverse this  
62 trend, national and regional action plans have been recently set up.

63 Bat decline is primarily due to anthropogenic pressures impacting both their roosting and  
64 foraging habitats (Mickleburgh et al. 2002; Wordley et al. 2015). In particular, many forest bats  
65 are threatened by land use/land cover changes and intensive forestry activity (Chaverri and  
66 Kunz 2011). Despite clear differences in habitat preferences among bat species that forage and  
67 roost in forests, many bat species forage predominantly in mature forests and are sensitive to  
68 changes in forest structure. In particular, forest practices that lead to younger and more  
69 homogenous forest mosaics have negative effects on bats populations (Jaberg et al 2001;  
70 Kaňuch et al. 2008; Archaux et al. 2013). Additionally, forest loss and fragmentation have been  
71 linked to the decline of bat species since the 1960s ( Kokurewicz 1990; Motte and Libois 2002;  
72 Flanders and Jones 2009; Tournant et al. 2013; Razgour et al. 2016). Forest fragmentation  
73 results in lower habitat connectivity; which can reduce the number of maternal colonies in a

74 meta-population and subsequently lead to increased inbreeding and greater extinction risk  
75 (Ransome and Hutson 2000; Rossiter et al. 2002).

76 Current knowledge on the ecology, behavior, requirements and distribution of many bat  
77 species are constraining the development of beneficial management measures for bats that  
78 could be implemented in a spatial context. Innovative tools are therefore needed to improve  
79 the efficiency of conservation planning based on expert knowledge. In particular, there is a  
80 clear need to improve our understanding of the important habitat features associated with bat  
81 roosting and foraging, as well as landscape features allowing bats to move between roosting  
82 and foraging sites.

83 In this study we take a landscape-based approach to study the spatial distribution and  
84 connectivity of foraging habitat for the greater and lesser horseshoe bats in the Rhône-Alpes  
85 region of France. These species were selected for their high sensitivity to habitat  
86 fragmentation due to their inability to detect distant objects with their high frequency calls.  
87 Thus, greater and lesser horseshoe bats rely heavily on linear features, such as hedgerows or  
88 tree lines, to commute between roosts and foraging habitat (Downs et al. 2016). The study site  
89 is presented as an example where an indicator species is used to support spatial planning for  
90 conservation purposes. The spatially-explicit approach aims to facilitate and support decisions  
91 by different stakeholders in terms of where and how to implement management and  
92 conservation activities. Stakeholders were involved from the very beginning in all phases of  
93 the study. To do this, we first developed species distribution models (SDM) to locate the  
94 most suitable foraging and commuting habitats used by greater and lesser horseshoe bats  
95 within the region and submitted the models for validation to a group of stakeholders. . Then  
96 we used spatially explicit habitat connectivity analysis to map corridors connecting important  
97 habitat patches. In all, SDMs in combination with explicit habitat connectivity analysis to map  
98 corridors connecting important habitat patches offer an effective tool for identifying species

99 conservation requirements and provide valuable inputs for forecasting how global  
100 environmental changes will affect species diversity and distribution (Correa et al 2016). This  
101 approach is particularly relevant for bats because their nocturnal behaviour hinders  
102 detectability and identification in flight (Razgour et al. 2016). Despite their important  
103 contribution to global biodiversity and wide geographical ranges, bats have been under-  
104 represented in early SDM studies, and only in the last few years has this approach become  
105 more widely used in bat research (Razgour et al. 2016). This work is the first attempt in this  
106 mountain region of the French Alps to provide landscape-based mapping specifically for bat  
107 conservation

108 The novelty of the study lies in the combination of statistical and expert-knowledge  
109 approaches to model selection, the pairing of SDM and connectivity analysis, and the  
110 integration of multiple data sources associated with foraging habitat or roosting sites (see  
111 Decout et al. 2012 for a comparable approach).

112 Through our analysis, we identify important habitat regions and corridors vital to maintaining  
113 functional landscape connectivity for greater and lesser horseshoe bats. Our results are being  
114 utilized by local stakeholders to identify potential areas where bat conservation goals could be  
115 integrated into multi-function forest management planning.

116

## 117 **2. Materials and methods**

### 118 **2.1 Study site**

119 The study site encompasses 1,760 km<sup>2</sup> of a complex mountainous landscape at the eastern  
120 border of the French Alps within the Natural Regional Park of Vercors (NRPV) (Auvergne  
121 Rhône-Alpes region, Figure 1). The study site is at the border between the northern and the  
122 southern French Alps and is part of the network of Long Term Ecological Research (LTER)  
123 sites (<https://www.lternet.edu/>). The area constitutes an important network for nature

124 conservation and biodiversity, including different protection levels, such as Natura 2000 areas  
125 and Integral Biological Reserves. Forest represents the dominant ecosystem (62%) within this  
126 complex landscape mosaic of natural open fields (29%, including grasslands, bare soil and  
127 cliffs), crop land (5%), urban land (3%) and wetlands (1%). Three environmental gradients  
128 strongly influence habitat composition and environmental conditions of the study area:  
129 elevation, aspect and latitude (see Table 1). Mixed broadleaved forests occur at low elevations  
130 and include beech (*Fagus sylvatica*), maple (*Acer sp.*), linden (*Tilia sp.*) and ash (*Fraxinus*  
131 *excelsior*). At higher elevations, mixed beech-silver fir (*Abies alba*), pure silver fir and  
132 Norway spruce forests (*Picea abies*) dominate. Alpine areas are mainly covered with  
133 calcareous bare soil, grasslands or pastures with sporadic mountain pine forests (*Pinus mugo*).  
134 A north-south mountain ridge runs through the center of the study site and makes a natural  
135 barrier from East to West. In the southern parts of the NRPV, more moderate temperatures  
136 facilitate the development of oak forests (*Quercus pubescens*). Wetlands and rivers are  
137 present on the piedmont of the mountain range. Human activities also concentrate in these  
138 areas, resulting in a dense road network, villages with an incipient urban sprawl and pressures  
139 from tourism and related activities (Gonzalez-Redin et al., 2016; Tenerelli et al., 2016). The  
140 population density in Vercors is 22 inhabitants/km<sup>2</sup>. The southern part of the NRPV is less  
141 populated (ca 9-14 inhabitants/km<sup>2</sup>) compared to the northern part (30-44 inhabitants/km<sup>2</sup>).  
142 The largest town, Villard-de-Lans, has a population of roughly 4,100 inhabitants.

143

144 < Figure 1 here >

145

## 146 **2.2 Bat data**

147 Our analysis used bat occurrence data taken from an existing database collected by experts  
148 from two local NGOs: the League for the Protection of Birds (LPO, Drôme and Isère

149 sections) and Chiroptera group (ChiroRA). Point locations were recorded with GPS (Garmin  
150 60x) with a location accuracy of 10 m (<http://www.garmin.com/>). Locations included 310  
151 point counts where ultrasonic detectors were used to record bat activity and 60 roost site  
152 locations. We used the ultrasonic data for habitat modelling and combined the resulting  
153 habitat maps with roost site locations for connectivity analysis (see supplementary material  
154 for further details on ultrasonic detector data and data sampling). In fact, in order to model the  
155 spatial distribution of suitable habitat for the night activity of bats we first needed acoustic  
156 data only. Then, we added roost site locations for the connectivity analysis aiming at showing  
157 potential corridors between roost sites and suitable habitats for their night activity.

158

### 159 **Ultrasonic data**

160 Bat ultrasonic sampling was conducted from 16 March (2000) to 22 October (2003) but ca 95%  
161 of the censuses (295/310) were performed from May to September with a monthly average of  
162 59 censuses (Supplementary material, Fig. SM1); the whole study area was relatively equally  
163 sampled in all months (Fig. SM2). From May to September, *Rhinolophus* bats were recorded  
164 in 17% of the censuses on average, this proportion being slightly higher in May (27.5%), June  
165 (20.6%) and September (25.6%) than in July (9.2%) and August (13.1%). 82.4% of the sites  
166 were sampled only one night, 11.8% two nights and 4.4% three nights. Only three sites were  
167 sampled more than three nights (respectively 4, 12 and 21 nights).

168 The ultrasonic detector data encompassed 81 passive records collected with SM2 bat+ detectors  
169 (<http://www.nhbs.com/>) as well as 229 active records obtained with Pettersson ultrasonic  
170 detectors D 240x and D 980 (<http://www.batsound.com/>). Full spectrum automatic SM2 bat+  
171 detectors recorded any bat nearby all night long. They were located in potentially favorable  
172 habitats, such as open areas and coniferous forests hedges. Each record lasted one night (about

173 8 hours), totalizing ca 648 hours of recordings. Analysis of calls were carried out *ex-situ* with  
174 the software SonoChiro® (<http://www.biotope.fr/fr/accueil-innovation/sonochiro>). In the case  
175 of active records, point counts covered all semi-natural habitats such as clearings, riparian  
176 forests, oak and hornbeam forests, scots pine forests, open areas, coniferous, broadleaved and  
177 mixed forests hedges (i.e. potential hunting areas) as well as caves, cliffs, bridges and buildings  
178 (i.e. potential roosting sites) in the study area. The detectors were used in the time expansion or  
179 in the heterodyne mode. As the two species can be easily separated from each other and from  
180 other bats by their call characteristics (Walters et al., 2012), they were generally identified in  
181 the field. When identification was doubtful, it was checked *ex situ* with BatSound® software  
182 (<http://www.batsound.com/>). Count duration for active records varied between 15 min to 3  
183 hours and the number of repetitions varied among point counts. Unfortunately, count duration  
184 was available for a very limited number of cases, so that this variable could not be considered  
185 in the modelling to avoid biases. Assuming a mean duration of 30 min, active recordings  
186 represented ca 114.5 hours of recordings.

187 There was a clear geographical bias between active and passive recordings, the latter being  
188 restricted in the south-western part of the study area (Fig. SM3). As a result, environmental  
189 conditions on active recording plots significantly differed from passive recordings, e.g.  
190 elevation or NDVI values were significantly lower for passive recordings. This geographical  
191 bias in sampling methodology may have overemphasized the role of some of the environmental  
192 variables. However, the most influential variables in analyses were coherent with the existing  
193 literature and the output maps were coherent with extra-knowledge of bat experts, so that we  
194 are rather confident that this bias does not strongly impact our conclusions.

195 The combined set of ultrasonic detection data was reported in a geographic information system  
196 (GIS; ArcGIS version 10, <http://www.esri.com/>) and coded in terms of presence-absence.  
197 Presences included the locations with at least one acoustic signal of the study species and

198 absences the locations with no contact whatever the type of record. For lesser horseshoe bat,  
199 the final data consisted of 24 presence points (16 by automatic recording and 5 by ultrasonic  
200 detector) and 286 absence points. For greater horseshoe bat, the final data comprised 14  
201 presences (10 by automatic recording and 4 by ultrasonic detector) and 296 absences.

202 Neither active, nor passive recordings differentiated foraging from commuting bat signals, so  
203 that data analysis should be broadly interpreted in terms of bat activity. It is very likely that a  
204 significant proportion of absences in our data set corresponded to false absences (overlooking  
205 errors). We performed both presence-absence models and presence-only models; presence-  
206 absence models were preferred based on both model fit criteria and expert judgment of the  
207 output maps. As a result, modelled probability of presence should be interpreted more as a  
208 relative probability (e.g. between two locations) rather than as an absolute probability of  
209 presence.

210

## 211 **Roost sites**

212 Roost sites were located by experts from March (2001) to November (2012) using active  
213 search of potentially favorable sites (e.g. building attics, caves, barns, tunnels) according to  
214 their knowledge of the region. Roost sites were identified with different techniques: calls  
215 identified by Pettersson ultrasonic detectors D 240x and D 980 used in the time expansion  
216 mode, net and hand capture with identification *in situ*, droppings and visual observation at  
217 roost exit. The number of bats observed was counted each time a colony was found. The  
218 presence of lactating females and young individuals was reported when observed in order to  
219 attest for colony reproduction. The total number of roost sites was 34 roosts for the greater  
220 horseshoe and 26 for the lesser horseshoe bat. The number of individuals recorded at roost  
221 sites varied between only one and 213 bats. For the greater horseshoe bat, reproduction clues

222 were observed in 9 roosts. For this species, roost sites were predominantly (69%) found in  
223 artificial structures, such as houses, churches, tunnels and stone-pits. The remaining greater  
224 horseshoe bat roost sites (31%) were found in natural cavities, such as caves. Roost sites for  
225 lesser horseshoe bat were only found in natural cavities and reproduction clues were observed  
226 in four roosts.

227

### 228 **2.3 Environmental data**

229 In order to model the distribution and connectivity of foraging habitat for greater and lesser  
230 horseshoe bats, we considered 12 environmental variables based on previous studies  
231 investigating the influence of habitat and landscape complexity on bats in France (Tournant et  
232 al. 2013) and elsewhere in Europe (Warren and Witter 2002; Rebelo and Jones 2010; Bellamy  
233 et al. 2011; Bellamy et al. 2013; Razgour et al. 2014; Bellamy and Altringham 2015). Data for  
234 the environmental variables were obtained from available national databases, or directly  
235 computed. The data collection effort meant we were able to obtain or derive environmental  
236 variables with a higher spatial resolution than if they had been taken from large-scale  
237 bioclimatic databases. The final selection of the variables included topography, hydrology, soil,  
238 and land cover composition of the study region (Table 1). In order to avoid edge effects in  
239 calculations involving distance-to measurements, we used a buffer area surrounding the study  
240 region.

241 The spatial resolution of the environmental layers was set to 25 m in all analysis. The resolution  
242 was selected on the basis that the navigational calls of greater and lesser horseshoe bats extend  
243 to approximately 5-10 m (Barataud, 2012), thus a 25 m pixel resolution broadly captures the  
244 immediate area influencing bat navigation. Based on a series of exchanges with experts, such a  
245 fine spatial resolution was also desirable for local stakeholders working with these species.

246 Correlation between environmental layers was examined using Spearman rank tests and all  
247 correlation coefficients were under 0.6, suggesting that our variables were not strongly  
248 correlated. Additionally, we compared environmental variables associated with bat sampling  
249 locations (whether bats were present or not) to that of a set of 7000 randomly selected locations  
250 across the study area. There was no significant difference between the environmental gradients  
251 of the observed vs random locations which suggests there was no bias in environmental  
252 conditions associated with the bat sampling.

253

254 <Table 1 here >

255

## 256 **2.4 Modelling approach**

257 A two-stage modelling approach was adopted to i) delineate foraging habitat for greater and  
258 lesser horseshoe bats, and ii) investigate factors influencing foraging habitat connectivity  
259 across the landscape (Figure 2). In the first stage, species distribution modelling (SDM) was  
260 applied to the ultrasonic data to delineate suitable foraging habitat areas. In the second stage,  
261 connectivity analysis was applied to the suitable foraging areas and roost site data to identify  
262 corridors between foraging habitat areas and/or known roost sites. We then analysed the  
263 relative importance of different habitat nodes (i.e., roost sites and foraging habitat patches).  
264 The approach combines habitat suitability modelling (Guisan and Thuiller 2005) with graph  
265 theory (used to quantify habitat connectivity; (Urban and Keitt 2001; Saura and Torné 2009)  
266 where a graph represents a landscape as a set of nodes (e.g., habitat patches) connected by  
267 edges that join pairs of nodes functionally (e.g., via dispersal or corridors). Such a coupled  
268 modelling approach (see Figure 2) facilitates a comprehensive assessment of the geographic  
269 distribution and connectivity of greater and lesser horseshoe bat foraging habitat using  
270 modern spatial analysis methods.

271

272 < Figure 2 here >

273

## 274 **2.5 Species Distribution Modelling**

275 Species distribution modelling was implemented using the ultrasonic detector data (but not  
276 roost sites) and related environment variables. We assumed here that all roost sites were  
277 known. To find the best performing SDM, we implemented ensemble modelling using the  
278 Biomod2 package in R (Thuiller et al. 2009; Thuiller et al. 2016). Six potential algorithms  
279 were tested: classification tree analysis (CTA) (Breiman et al. 1984), flexible discriminant  
280 analysis (FDA) (Hastie et al. 1994; Manel et al. 1999), generalized additive models (GAM)  
281 (Guisan et al. 2002; Pearce and Ferrier 2000), generalized boosting model (GBM) (Friedman  
282 1991; Elith et al. 2008), generalized linear models (GLM) (Vincent and Haworth, 1983) and  
283 maximum entropy (Maxent) (Elith et al. 2011). Maxent is a presence-background method and  
284 only provides estimates of *relative* suitability approach whereas GAM, GLM, GBM and FDA  
285 require presence-absence data. The CTA algorithm can be used with presence-only data or  
286 presence-absence data. All algorithms were therefore implemented using true presence and  
287 true absence defined as per the ultrasonic data collection procedures noted above. Only  
288 Maxent models were based on true presence data and automatically generated pseudo-absence  
289 data. Default Biomod2 parameters were used for all algorithms, except for Maxent for which  
290 we increased the number of iterations (to 500 instead of 200). Model selection was based on  
291 the true skill statistic (TSS) (Allouche et al. 2006), Cohen's kappa (Monserud and Leemans  
292 1992) and AUC (Area Under the receiver operating Curve) (Pearce and Ferrier 2000; Baldwin  
293 2009).

294 Two experts (one from each local NGO that provided bat data) were then asked to rank the 12  
295 models per species (six algorithms with presence-only or presence-absence data) by comparing

296 the model outputs (habitat suitability maps, response curves) to their knowledge of the study  
297 area and of the species ecology in the area (Figure 2). We ended up with a smaller selection of  
298 variables and models and produced a new set of models. Finally, we organized a workshop  
299 inviting a wide range of institutional stakeholders in order to present the method and results of  
300 the different model outputs. Twenty experts participated in the exercise and evaluated the  
301 models output, highlighting and ranking the outputs. Overall, we used different evaluation  
302 approaches combining statistical analysis and expert knowledge to choose a model for  
303 producing the map of habitat suitability for each bat species. The use of expert opinion was  
304 proven useful to tailor the project objectives to match the interests and understanding the  
305 motivations and expectations from experts at different levels. Thus final decision were based  
306 not just on statistical analysis but also on knowledge of the species from experts working on the  
307 ground (Roy et al. 2012).

308 To test for potential spatial autocorrelation in model residuals, we calculated the parametric  
309 test Moran's I using R library ape (Paradis et al., v.3.5). The tests indicated significant spatial  
310 autocorrelation in the residuals for the two species (*Rhinolophus ferrumequinum*: Moran's I =  
311 0.036,  $p= 0.007$ ; *R. hipposideros*: Moran's I = 0.082,  $p < 0.001$ ). Yet, while the test is  
312 significant, the actual Moran's I values are very low  $\sim 0$ , which suggests spatial  
313 autocorrelation is not likely a significant problem.

314

## 315 **2.6 Connectivity and Node Importance Analysis**

316

317 We assessed landscape connectivity by identifying and ranking those foraging habitat patches  
318 which are functionally more important to the connectivity of the entire landscape for greater  
319 and lesser horseshoe bats. A graph theory approach was used to evaluate landscape  
320 connectivity of foraging habitat and roost sites. We assumed that all roost sites were known

321 and thus captured by the roost site data, while potential foraging habitat was unknown and  
322 thus captured by the SDM. Graph theory represents the landscape as a graph network  
323 comprised of nodes (i.e., foraging habitat patches and roost sites) and movement links  
324 between nodes (i.e., corridors) (Urban and Keitt 2001; Saura and Torné 2009). Here we are  
325 interested in the functional connectivity between roost sites and suitable habitat areas. Thus,  
326 we considered both roost sites, identified from observational data, and high-quality foraging  
327 habitat patches, obtained from SDM output maps, jointly as nodes, maintaining their  
328 distinction for later interpretation. Roost site nodes were simply taken from the roost site data,  
329 while high-quality foraging habitat nodes were delineated as contiguous regions of high-  
330 quality habitat from SDM model (where high-quality habitat was defined as having a  
331 predicted probability of occurrence  $\geq 0.75$  for both species).

332

333 The links between nodes were evaluated by least-cost corridor analysis (Fall et al. 2007).  
334 Least-cost corridor analysis uses a resistance surface to generate a map providing the  
335 weighted distance (real distance multiplied by resistance score) from each pixel on the map to  
336 the nearest node. From this weighted distance map, the least-cost corridor can be identified  
337 between any pair of nodes. Here the resistance surface represents the perceived permeability  
338 of the landscape to greater and lesser horseshoe bat movement. To compute the resistance  
339 surface, it was assumed that high-quality foraging habitat (taken from the SDM output) was  
340 more permeable to movement than lower quality habitats. A linear function was used to  
341 transform SDM predicted probability of occurrence scores directly into resistance surfaces  
342 following (Trainor et al. 2013) using the equation:  $r_i = 50 - 49 \times \text{SDM}_i$ , where  $r_i$  is the resistivity  
343 and  $\text{SDM}_i$  the SDM probability score in cell  $i$ . Crops and bare soil, urban lands and main  
344 roads are not potential foraging habitat for bats (Rebelo and Jones 2010; Kunz et al. 2011).  
345 Thus we considered these land cover classes as highly resistant to bat movement and gave

346 them an arbitrarily high resistance score of 100 (Tournant et al. 2013). Least-cost corridors  
347 between roost and habitat nodes were then calculated using the software Linkage Mapper  
348 from Circuitscape (McRae et al. 2008).

349 The probability of connectivity index (PC; see Saura and Pascual-Hortal 2007) was used to  
350 determine the overall level of connectivity of the landscape for greater and lesser horseshoe  
351 bat movement. The PC index is an overall measure of landscape connectivity that sums the  
352 probability of an animal going between any two patches in the landscape and divides by the  
353 overall area of the landscape. PC increases with landscape connectivity and is bounded from 0  
354 to 1. PC is 0 when there are no habitat patches in the area and is 1 when the entire landscape  
355 is represented by a single habitat patch. Each node and link was ranked according to its  
356 importance in maintaining the current level of connectivity using the deviation in the  
357 probability of connectivity (dPC; Saura and Rubio 2010), which measures the change in  
358 overall connectivity when a given node or link is removed from the network. The calculation  
359 of the mean dPC for all nodes and links in the landscape provides information on the global  
360 connectivity of the landscape and also the resiliency of the system to change (Decout et al.  
361 2012). The calculation of PC and dPC scores was conducted using the software Conefor 2.6  
362 (Saura and Torné, 2009).

363 Finally, the dispersal distance used to perform the calculation of the connectivity indices were  
364 taken from radio-tracking surveys conducted by LPO (Drôme section). The mean dispersal  
365 distance recorded on the first survey was of 2.0+-0.85km. The second radio tracking survey  
366 also on four lactating females of greater horseshoe bat presented a mean dispersal distance of  
367 4.0+-1.6km. Dispersal distances recorded by radiotracking surveys on Vercors were in  
368 accordance to dispersal distance from other studies in Europe. Mean dispersal distance for  
369 lesser horseshoe bat was recorded between 1.3 to 2.5km (e.g. Bontadina et al. 2002;  
370 Holzhaider et al. 2002; Motte and Libois 2002; Zahn et al. 2008; Arthur and Lemaire 2009;

371 Reiter et al. 2013). For greater horseshoe bat mean dispersal distances recorded were between  
372 3-5km (e.g. Ransome and Hutson 2000; Arthur and Lemaire 2009)

373

### 374 **3. Results**

#### 375 **3.1 Species Distribution Modelling**

376 Among the six algorithms implemented, Maxent, GBM and GLM models performed best,  
377 both in terms of statistical performance (Table 2) and through qualitative verification of the  
378 output maps and response curves by experts. For greater horseshoe bat, the Maxent model  
379 performed best according to the three chosen evaluation statistics (TSS, Cohen's K, and  
380 ROC), while for lesser horseshoe bat, three models performed similarly well (Maxent, GBM,  
381 and GLM) in terms of statistical evaluation and response curves (Table 2). The evaluation of  
382 models by the two experts from the two local NGOs confirmed that Maxent model performed  
383 very well for the greater horseshoe bat. Concerning the lesser horseshoe bat, Maxent and  
384 GBM models appeared similarly good in terms of spatial results and variable selection.

385

386 < Table 2 here >

387

388 To facilitate straightforward comparisons between both species, we decided to base all  
389 subsequent analyses on the SDM obtained using Maxent approach for both greater and lesser  
390 horseshoe bats (see supplementary material for details on Maxent parameters). This choice  
391 was validated during the workshop with twenty experts as aforementioned. The  
392 environmental variables selected in the SDM's were similarly ranked for both bat species  
393 (Figure SM4).

394

395 The most important variable was elevation. Both greater and lesser horseshoe bats were  
396 modelled to preferentially choose habitats below elevations of 1000 m (Figure SM5). The  
397 second most influential variable was road density, with areas having high road densities being  
398 avoided. In line with this result, optimal foraging habitats for both species were found away  
399 from urban areas (Figure 3). The SDM for lesser horseshoe bat suggests a preference for  
400 deciduous forests over other habitats, while the SDM for greater horseshoe bat suggests more  
401 flexible habitat use. In the end, the geographical distribution of the two bat species was  
402 relatively similar, mostly found on the western part of the study area (Figure 3). However, one  
403 key difference is that greater horseshoe bat was uncommon in the North (Figure 3a).

404

405 < Figure 3 here >

406

### 407 **3.2 Connectivity and Node Importance Analysis**

408 Unsurprisingly, corridors were frequent in areas where the network of roost and foraging  
409 habitat nodes were very dense. In such areas, bats can reach multiple habitat nodes from  
410 almost every roost node. However, in areas with few roosts and few foraging habitat patches,  
411 we found only a limited number of movement corridors. For instance, the roost sites of the  
412 greater horseshoe bat in the central northern part of the study site appear isolated alongside  
413 several highly favorable habitat patches with relatively small patch sizes (Figure 3c). The  
414 most important roost nodes were spread along the main western valleys for the lesser  
415 horseshoe bat, while they concentrated in the south-western part of the study area for the  
416 greater horseshoe bat (Figure 3b). The most important foraging habitat nodes were logically  
417 located close to the most important roost site nodes for both bats. For the greater horseshoe  
418 bat, the main regions important for connectivity are located at low elevations along the border  
419 of the study site. For lesser horseshoe bat, the most important nodes are located along main

420 valleys of the eastern part of the study area. The mean dPC of all nodes is greater for lesser  
421 horseshoe bat (mean  $dPC_{all\ nodes}=2.58\%$ ) than for greater horseshoe bat (mean  $dPC_{all}$   
422  $nodes=1.85\%$ ). Observed dPC were low for both species, which may be explained by the high  
423 density of habitat nodes which implies a high connectivity between all nodes of the landscape.  
424 Consequently in this study site, the landscape is seemingly favorable for species dispersion at  
425 night.

426

## 427 **4. Discussion**

### 428 **4.1 Environmental niches of horseshoe bats**

429 Foraging habitat, for both species, was primarily located in the piedmont of Vercors massif  
430 (Figure 3a) where low elevation forests are denser and dominated by broadleaved species, and  
431 in the south where the Mediterranean climatic influence is stronger (Blanchard, 1918). The  
432 greater horseshoe bat is a Mediterranean species that needs warm microclimates in the  
433 northern part of its range. The models highlighted that greater and lesser horseshoe bats have  
434 very low occurrence probabilities above 1,000 m, such as in the reserve of the Hauts plateaux  
435 du Vercors where elevation ranges from 1,050 to 2,341 m. (Figures 1 and 3a). Related to this  
436 elevational gradient, this area land cover classes in this area are not suitable for horseshoe  
437 bats, as it is mainly covered with grasslands and bare soil. This may also act as a barrier to  
438 bats that need a network of vertical structures in the landscape to navigate (Bontadina et al.  
439 2002; Holzhaider et al. 2002; Motte and Libois 2002; Reiter 2004).

440 The results suggest a niche overlap between the two species; confirming the importance of  
441 forested areas for foraging, especially broadleaved and mixed forests characterized by a dense  
442 canopy and mature trees (Ransome and Hutson 2000; Bontadina et al. 2002; Zahn et al.  
443 2008). Lesser horseshoe bats showed a stronger preference for broadleaved forests, while  
444 greater horseshoe bat appeared less specialized, foraging in a higher diversity of habitats. This

445 latter result is consistent with previous studies showing greater horseshoe bats prefer mixed  
446 landscapes with pastures interlaced with deciduous woodlands (Ransome and Hutson 2000;  
447 Flanders and Jones 2009).

448 Both species avoided areas with a high road density, which is coherent with the existing  
449 literature on bat behavior (Siemers and Schaub 2011; Berthinussen and Altringham 2012;  
450 Bennett et al., 2013; Reiter et al., 2013). Roads can affect bats in three main ways: i) wildlife  
451 vehicle collisions, ii) degradation to roost sites and foraging habitat, and iii) reduced  
452 connectivity of patches (Berthinussen and Altringham 2012). Roads are known to have a  
453 strong influence on bat activity in other species and regions (Russell et al. 2009; Berthinussen  
454 and Altringham 2012; Bennett et al. 2013). In many cases, collisions with traffic are a major  
455 cause of mortality and thus avoiding roads is a necessary adaptation for horseshoe bats  
456 (Medinas et al. 2012). The fact that horseshoe bats avoided areas with a dense road network  
457 lends weight to the decision to implement a high resistance cost for roads in the connectivity  
458 analysis. Yet this hypothesis requires further investigation using methods which are able to  
459 collect data on actual movement trajectories (e.g., radio-tracking).

460

#### 461 **4.2 Conservation implications for the Natural Regional Park of Vercors**

462 Maintaining and restoring landscape connectivity is currently a central concern in the  
463 conservation policy arena, resulting in direct implications for regional planning (Correa et al  
464 2016). Vercors massif is still a very rural region (ca 20 versus 139 inhabitants/km<sup>2</sup> at the  
465 regional level) (Lebrun and Coudène 2011) with areas of low anthropic disturbance that could  
466 serve to enhance mechanisms for natural resource governance combined with recognition of the  
467 economic and social value of ecosystem services provided by natural habitats (Nelson et al 2009). At  
468 the same time, the population is rapidly growing and the number of houses in the region has  
469 doubled since the 1960s (Lebrun and Coudène 2011). Parts of the region are characterized by  
470 incipient urban sprawl in addition to tourism and related activities impacting the natural

471 landscape (Tenerelli et al. 2016). These changes are affecting landscape structure and  
472 consequently having a direct impact on the functional landscape connectivity that is vital for  
473 the survival of these two bat species. There is increasing demand for user-driven tools to  
474 integrate landscape connectivity in spatial planning and decision making. In order to focus  
475 conservation efforts on key landscape features and achieve conservation goals, information is  
476 needed about how species perceive and use the landscape. A critical outcome of this research  
477 is the importance of prioritizing parcels of foraging habitat for conservation to help the local  
478 populations of greater and lesser horseshoe bats.

479 Our approach emphasized the importance of areas with low road density. Our connectivity  
480 approach gave the same weight to foraging habitats and roost sites but priority should be  
481 given to existing roost sites given their importance to bat populations and as key nodes in  
482 maintaining a functionally connected landscape (Dixon et al., 2013; Entwistle, 2001). The  
483 corridors identified here can be prioritized for conservation to minimize the impact of  
484 increasing anthropogenic pressures (including roadways) acting as barriers to bat movement  
485 and consequently fragmenting current populations. In the same way, it will be important to  
486 focus conservation of movement corridors that allow bats to access roost sites.

487 Future analysis would benefit in particular from integrating radio-tracking data of the two  
488 species (although this is more costly and requires greater expertise) along with studies of  
489 landscape genetics (e.g., Razgour et al. 2014), to better understand individual and genetic  
490 mobility across the region. Compared to bat counts with ultrasonic recorders, radio-tracking  
491 delivers detailed data on fine-scale individual movements (Jaberg and Guisan 2001). Radio-  
492 tracking also provides additional information about dispersal distance and foraging habitat  
493 (Willis and Brigham 2004) along with landscape features facilitating bat movement.

494

## 495 **5. Conclusion**

496 The challenge for conservation is to provide operational methods that can support conservation  
497 plans at regional level to identify the spatial scale(s) and key landscape elements needed to  
498 maintain or restore connectivity and the ecological processes that are promoted by it. To meet  
499 the final objective of favoring species viability and ecosystem diversity, landscape ecologists  
500 should be able to deliver conservation guidelines and indicators at the spatial scale at which the  
501 impacts of landscape change are most prominently affecting the abundance and persistence of  
502 the focal species (Luque et al . 2012). In this study, we take a landscape-based approach using  
503 SDMs in combination with explicit habitat connectivity analysis to develop an operational  
504 method oriented to conservation planning. The spatially-explicit models obtained were proven  
505 useful for prioritizing foraging habitats, roost sites and key corridors to help guide conservation  
506 activities. Here greater and lesser horseshoe bats are the focal species, but conservation of other  
507 key species will benefit from the same spatially-explicit approach. The landscape-based  
508 approach presented provides an example of key decision-making tools useful for local experts  
509 and stakeholders. Conservation planners and experts require detailed information (i.e., in the  
510 form of a map) to decide where to implement a conservation strategy. In ecology everything  
511 happens somewhere; still the *where* question in biological conservation is one that is often  
512 overlooked in an effort to understand *why* conservation is needed. In reality, managers and  
513 stakeholders often have a clear understanding of why conservation is needed at the local and  
514 regional scale, but need operational support tools to assist in implementing solutions; and  
515 specifically those that can assist in spatial prioritization to guide decisions and planning. Our  
516 aim here was to work together with practitioners to develop tools for making the theoretical and  
517 methodological developments on landscape connectivity available for (and usable by) them.  
518 The approach developed in this study can also provide key information for woodland managers  
519 to balance conservation interests according to the Habitats Directive while still targeting a  
520 sustainable forest management. Along with this manuscript, a guide and two related articles

521 were produced in French to support local and national level decision makers and different  
522 stakeholders providing specific recommendations with detailed maps and an explanation of the  
523 methods (Le Roux et al. 2014; Le Roux et al. 2016). These outputs are currently being used to  
524 improve sampling efforts and to plan and target conservation measures in the region.

525

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543

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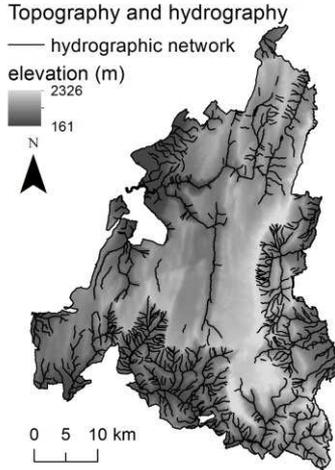
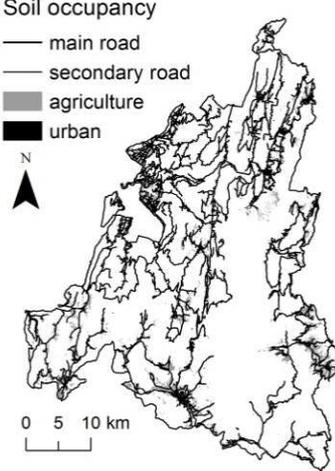
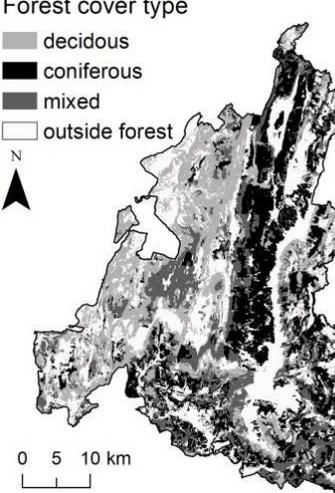
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767 Table 1: Environmental variables used for foraging habitats distribution modeling (resolution

768 25m)

Category	Variable	Range	Data source	Relation with greater and lesser horseshoe bat habitat	
<b>Topography and water</b>  <p>Topography and hydrography — hydrographic network elevation (m) 2326 161 N 0 5 10 km</p>	Elevation (m)	184 - 1860	IRSTEA, 2014 (calculated from sources: National Geographic Institute (IGN), 2009)	For both bats, temperature is determinant for roost site and foraging territories selection. For example, greater horseshoe bat is originally a Mediterranean species. Therefore elevation is a limiting factor.	
	Topographic index	4 classes: valleys, slopes, ridges, plains		Euclidean distance calculation in GIS (data source: IGN, 2009)	Both bats are sensitive to air moisture for roost selection and foraging activity. Insect abundance is dependent on climatic and atmospheric conditions. In mountain regions, topographic variables complement elevation data by giving more information about warm/cold and dry/moist conditions.
	East-West aspect	-1 (West) to 1 (East)			
	North-South aspect	-1 (South) to 1 (North)			
Distance to water (km)	0 – 3.5		Water habitats impact bat distributions because they offer open areas, rich with insects and give a structural diversity to the landscape. Conversely, they provide no vertical structures to navigate.		
<b>Anthropisation</b>  <p>Soil occupancy — main road — secondary road ■ agriculture ■ urban N 0 5 10 km</p>	Road density (km/km <sup>2</sup> )	0. 4 – 15.2	IRSTEA, 2014 (data sources: IGN, 2009; National Forest Office)	Low flying bats (such as greater and lesser horseshoe) are more susceptible to road mortality by car collision. However, roads also structure the landscape and offer edges within forest stands.	
	Distance to urban areas (km)	0 - 4.4	Euclidean distance calculation in GIS (IRSTEA, 2014, data source: National Alpine Botanical Conservatory (CBNA), 2012)	Urban areas are associated with roost selection for some species, but also represent unsuitable habitat in terms of light pollution, car collisions and other related anthropogenic disturbances.	
	Distance to agricultural areas (km)	0 - 6.6		Agricultural areas are not usually used as foraging areas by horseshoe bats. However, edges around those habitats often provide structured habitats for movement.	
<b>Natural habitats</b>  <p>Forest cover type ■ deciduous ■ coniferous ■ mixed □ outside forest N 0 5 10 km</p>	Type of forest cover	4 classes : Broadleaved, coniferous, mixed, outside forest	CBNA, 2012	Greater and lesser horseshoe bats hunt in foliage, their foraging habitat is highly dependent on forest type and tree species.	
	NDVI	-0.2 – 0.5	IRSTEA (2010)	Normalized Difference Vegetation Index NDVI, can add general information on bare soil and forest structure and composition. Greater and lesser horseshoe bats can hunt in very dense forest because they have a very fine scale navigational system.	
	Distance to forest edges (km)	0 - 1.2	Euclidean distance calculation in GIS (IRSTEA, 2014, sources: National Forest Institute, 2009 ; CBNA, 2012)	Forest edges are used as landmarks for movement.	
	Distance to open areas (km)	0 - 1.4		In a heterogeneous landscape, open areas mixed with forests facilitate food accessibility for bats and provide a structural element for bat movement.	

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771 Table 2: Evaluation of the six models tested in Biomod2 using receiver operating curve  
 772 (ROC), Cohen’s Kappa and true skill statistic (TSS) for greater horseshoe bat and lesser  
 773 horseshoe bat

		MAXENT	GBM	GLM	CTA	FDA	GAM
greater horseshoe	ROC	0.791	0.701	0.705	0.605	0.715	0.644
	Kappa	0.461	0.376	0.376	0.202	0.315	0.244
	TSS	0.610	0.429	0.497	0.294	0.497	0.356
lesser horseshoe	ROC	0.726	0.753	0.717	0.620	0.675	0.706
	Kappa	0.254	0.270	0.302	0.203	0.204	0.270
	TSS	0.502	0.484	0.512	0.295	0.389	0.464

774

775 **Figure captions**

776 Figure 1: Study area showing the location of Natural Regional Park of Vercors (NRPV) and  
 777 the natural reserve of “Hauts plateaux du Vercors” (Auvergne-Rhône-Alpes region), France  
 778 and the different types of observation data.

779 Figure 2: Flow diagram showing bat ultrasonic data and environmental data integration into  
 780 the species distribution model and then, alongside with roost data, into the connectivity  
 781 model.

782 Figure 3: a) Habitat quality map and b) landscape connectivity analysis of greater horseshoe  
 783 bat and lesser horseshoe bat. The inset in c) shows a small area of the greater horseshoe bat  
 784 range.

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