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1 **The role of complex vegetation structures in determining hawking bat activity in**
2 **temperate forests**

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16 **Abstract**

17 Forests constitute one of the most important feeding and foraging habitats for bats. Because bat populations are
18 declining, most likely due to habitat loss or fragmentation, it is imperative to understand the issues concerned with
19 timber exploitation on bat conservation. We investigated the foraging activity of edge- and open-space foragers in
20 relation to stand and vegetation structure, characteristics that are commonly affected by forestry. Acoustic surveys,
21 culminating to 713 point count sites were undertaken covering 46 different forest massifs across mainland France
22 over 6 years. We used generalized linear mixed models to analyse the activity of ten species; 6 edge-habitat and 4
23 open-habitat foragers. *Pipistrellus pipistrellus* was the most detected edge-habitat forager, while *Nyctalus leisleri*
24 was the most recorded of the open-habitat foragers. *Eptesicus serotinus* and *P. pipistrellus* responded positively to
25 heterogeneous vertical vegetation volume. In addition, *P. kuhlii* and *P. nathusii* responded negatively to tree basal
26 area. *Barbastella barbastellus*, *Hypsugo savii*, and *P. nathusii* were associated with either ground deadwood and/or
27 logging tracks and minor-traffic roads, confirming the importance of edge space. Finally, *B. barbastellus*, *E.*
28 *serotinus*, and *P. nathusii* were positively linked to the presence of tree microhabitats. This study demonstrates
29 that bat use in forests is complex and multifaceted. Maintaining ground deadwood and heterogeneity of vegetation,
30 at the forest plot scale, should ensure the ecological functioning of exploited forest systems and the conservation
31 of edge- and open-habitat foraging bats.

32 **Keywords:** *Chiroptera*; Activity; Vegetation volume; Tree basal area; Deadwood; Silviculture; Conservation
33 implications.

34 1. Introduction

35 Europe's landscape has been heavily influenced by man for the last several thousand years (Peterken, 1996;
36 Svenning, 2002). As a result, European forests resembling a true virgin state have been largely replaced by
37 production forest systems (Saunders et al., 1991; Jung et al., 2012) surrounded by a matrix of other land uses as
38 overexploitation and inappropriate agricultural practices have progressively fragmented the landscape over time
39 (Saunders et al., 1991). Indeed, this conversion of natural habitats has negative effects on biodiversity (Saunders et
40 al., 1991; Law et al., 1999; Cruz et al., 2016) and is threatening the long-term conservation and sustainability of a
41 number of vertebrate (Jones et al., 2009; Cruz et al., 2016), invertebrate (Connor et al., 2002), and plant species
42 (Hanski, 2011; Xiao et al., 2016). Forests are relatively important habitats for the abundance of bats (Kerbirou et
43 al., 2018), as they provide excellent potential for roosting and foraging (Tillon, 2015a, 2015b; Russo et al., 2016).
44 As a consequence, bats are progressively being included in conservation management plans across Europe and
45 elsewhere (Russo et al., 2016; Tillon et al., 2018). This means that forest managers are being confronted with the
46 challenges of accommodating for biodiversity, in particular for bats, by adapting silvicultural approaches in
47 exploited forests.

48 Silvicultural practices make products suitable for human consumption, but indirectly manipulate supplies of
49 water, nutrients and solar radiation with the removal of undesired trees (Guldin et al., 2007). Over time, changes
50 to the composition, structure and stratification i.e. the arrangement of vegetation in layers of a forest, occur as the
51 stand is manipulated towards the desired future condition (Guldin et al., 2007). Changes to the composition and
52 structure can, at least in the following decades and sometimes definitively, alter the habitat quality of a given site
53 (Russo et al., 2010), because they directly affect the availability of roosting sites and feeding opportunities for bats
54 (Graves et al., 2000; Hayes and Loeb, 2007; Russo et al., 2010). Also, in forests exploited for timber production,
55 the number of available trees with cavities that can be used by bats is generally low, as young vigorous trees are
56 favoured for wood production (Russo et al., 2010; Ruczyński et al., 2010; Tillon et al., 2018). Less than 1% of
57 *Quercus robur* trees of 100 years old or less were shown to form a cavity, compared to 50% of trees aged between
58 200 and 300 years old (Ranius et al., 2009). The majority of European forests are subject to timber harvesting,
59 which presents a considerable constraint to the biodiversity associated with tree microhabitats as many species
60 directly depend on tree cavities during their life cycles, notably for food, shelter, and reproduction (Entwistle,
61 2001; Kunz and Lumsden, 2003; Larrieu et al., 2013). Furthermore, forestry changes the spatial arrangement of
62 vegetation (Guldin et al., 2007; Jung et al., 2012; Willcox et al., 2017). This can have a profound impact on animal
63 movement, important for small mammals e.g. red squirrel (Laguet, 2012), but especially for flying animals that

64 must navigate through foliage from the ground to the canopy (Arlettaz et al., 2001; Jung et al., 2012; Müller et al.,
65 2013). In contrast to silviculture-based clearcutting, intermediate treatments such as successive thinning to
66 gradually reduce competition of plants in a stand may temporarily decrease density and favour flying animals such
67 as bats (Graves et al., 2000; Patriquin and Barclay, 2003; Guldin et al., 2007). However, such actions may
68 negatively influence the availability of foliage-dependent insects by reducing vegetation, which would be
69 problematic as they constitute a major food source for bats (Kaňuch et al., 2005a, 2005b; Müller et al., 2012). As
70 bats provide fundamental ecosystem services such as predation (Jones et al., 2009; Jung et al., 2012; Barataud,
71 2015; Russo et al., 2016) by contributing to the control of leaf-eating insects in temperate forests (Jones et al.,
72 2009; Kunz et al., 2011; Müller et al., 2012) their conservation is of important interest to sustainable forest
73 management. Unsurprisingly, bat species richness and abundance is noticeably higher in forests that resemble a
74 natural state (Russo et al., 2010; Law et al., 2016), perhaps in direct response to a greater presence of certain forest
75 environments, linked to the abandonment of logging practices, such as deadwood and tree cavities (Hayes and
76 Loeb, 2007; Law et al., 2016; Russo et al., 2016; Tillon et al., 2018).

77 While the responses of birds to different forest environments have been well documented in Europe and
78 elsewhere (e.g. Bradbury et al., 2005; Morante-Filho et al., 2015; Terraube et al., 2016), bat responses to forest
79 parameters remain comparatively under studied. In addition, studies on bats and forests are, more often than not,
80 based on a limited number of selected forest massifs (e.g. Russo and Jones, 2003; Willcox et al., 2017), and few
81 studies have attempted a nationwide approach. However, it is very likely that the complex three-dimensional
82 arrangement of vegetation in managed stands affects bats differently to birds and leads to a separation of bat
83 assemblages as species-specific morphology and echolocation call structure pose maneuverability and foraging
84 challenges (Schnitzler & Kalko 2001, Adams, et al., 2009, Müller et., 2012, Jung et al., 2012).

85 Small hawkers (bats that forage close to or at the edge of vegetation hawk insects in the air) (e.g. *Pipistrellus*
86 spp.) have a higher wing aspect ratio and faster flights than their gleaning counterparts (bats that forage within
87 dense vegetation and glean insects from the substrate such as leaves, branches and the ground) (Schnitzler and
88 Kalko, 2001; Denzinger and Schnitzler, 2013). They thus require open spaces, such as forest gaps, paths, corridors,
89 and edges even if they still hunt foliage-dependent insects (Norberg and Rayner, 1987; Denzinger and Schnitzler,
90 2013; Bouvet et al., 2016; Caras and Korine, 2009). Contrary to small bats, large hawkers (e.g. *Nyctalus* spp.,
91 *Eptesicus* spp., *Tadarida* spp.) are more adapted to a long-range pursuit of aerial insects above the vegetation (Jung
92 et al., 2012; Denzinger and Schnitzler, 2013), notably due to the fact that this group emits low frequency
93 echolocation calls which are better adapted to open habitats as echoes from background vegetation reach the bat

94 later and do not disturb their detection of prey (Brigham et al., 1997). Consequently, the differences in forest
95 structure and stratification should affect hawking bat activity.

96 Here, with the use of Barataud's identification tools (Barataud, 2015) and the accumulation of six years of data,
97 culminating to 713 point count sites across 46 different forest massifs in metropolitan France, we present data
98 linking forest environments in managed stands to bats. We expected edge- and open-habitat foraging bat activity
99 to increase in forest zones of high vegetation heterogeneity, as this is known to positively influence insect richness
100 (Haddad et al., 2009) and should provide free-space within forests (Müller, et al., 2013). Equally, we expected
101 these two bat guilds to use edge-space features such as logging tracks and minor-traffic roads as they may allow
102 clutter intolerant species to navigate in and around a given forest stand (Kirkpatrick et al., 2017).

103 Hence, the specific aims of our study were; 1) to assess how the activity of identified hawking bat species (i.e.
104 not analysing bat calls only determined to bat genus) responds to stand structure and vegetation stratification, while
105 also taking into account the influence of deadwood and the presence of tree cavities; 2) To use the findings to
106 highlight appropriate conservation measures in a sustainable forestry context.

107 **2. Materials and Methods**

108 *2.1 Study area*

109 We carried out acoustic surveys covering 46 different forests in mainland France. Each biogeographical region
110 was represented. In all, data from 18 forests in the Continental region, 13 forests in the Atlantic region, 7 from
111 Alpine and 8 from the Mediterranean were included in a national scale analysis. Across the 46 forests, a total of
112 713 point counts were undertaken. At the forest plot scale, a number of point counts were conducted in order to
113 account for various forest environments, such as different age/growth stages, edge-space, different compositions
114 (i.e. dominant tree species), and areas of varying presence of tree cavities, all across a range of even- and uneven-
115 aged stands (with and without understory) from lowland to alpine regions.

116 *2.2 Bat acoustic surveys*

117 Ultrasound detection is an indirect, effective and non-invasive technique which provides "access" to bats across
118 all forest habitat types. It is one of the most commonly used methods (Jennings et al., 1997; Brigham et al., 2004;
119 Barataud, 2015; Tillon et al., 2016). Accordingly, in order to assess bat activity in relation to forest stand predictors,
120 bat acoustic surveys were carried out in forest plots at least 200 meters apart, across France in from 2011 to 2016.

121 All lowland forest stands were surveyed by a pair of trained chiropterologists applying a protocol which
122 included two 30 minute surveys (hereafter referred to as MCD30), one in summer and one in autumn. Similarly,

123 all alpine and Mediterranean forest stands were surveyed by a pair of chiropterologists carrying out two 45 minute
124 point counts, in summer and in autumn (hereafter referred to as MCD45). Note, it was not possible to survey in
125 spring in mountainous terrain due to the sometimes extreme metrological conditions (i.e. too much snow) which
126 impedes access to the forest, and significantly reduces bat activity. It is assumed that bat hibernation endures longer
127 in alpine regions with reduced activity in spring (Kaňuch and Krištín, 2006; Widerin and Reiter, 2017). Thus,
128 spring surveys in lowland forests were not analysed.

129 All survey start times were between 30 minutes and 3 hours after time of sunset. Bat activity was quantified
130 using bat detectors: Petterson D980, Petterson D240x with numeric recorder Marantz PMD620MKII, or HP tablet
131 with Soundchaser & Dodotronic microphone positioned at 0.5-1m above ground, at a vertical angle of 45 degrees.
132 At each point count site, two observers continually listened for all possible *Chiroptera* calls using the detector's
133 heterodyne mode, which required each chiropterologist to scan the entire 10-120 kHz frequency band. When a bat
134 echolocation call was detected, the sequence was manually recorded for post-identification using the software
135 Batsound 3.3 (Pettersson Elektronik™), and following the methods of Barataud (2012). The method allows the
136 user to identify the species (or bat genus) by comparing the recorded echolocation call with Barataud's referent
137 frequency ranges. Additionally, at each point count location, we recorded temperature (°C) as this is known to
138 influence bat activity (Kerbirou et al., 2018a) and time elapsed after sunset was calculated in order to account for
139 the variability of species detection in relation to time of emergence (Russo et al. 2007). This was achieved with
140 the aid of the website <https://promenade.imcce.fr/en/pages5/51.html>. GPS location and date were needed to
141 retrieve official sunset times. Having recorded all point count start times we were able to compute minutes after
142 sunset.

143 2.3 Analysing bat calls

144 All ultrasounds were recorded in time expansion (x10) for identification. The bat calls were manually identified
145 to species level, verified by referents, or to genus level if it proved impossible to distinguish bat calls. In this study,
146 we only analysed bat signals identified and confirmed to species level, eliminating ambiguity but reducing amount
147 of data analysed. In accordance with a number of studies (e.g. Zupal and Řehák, 2006; Bartonička and Řehák,
148 2007; Müller et al., 2013) bat activity was formatted as minute counts minimising possible observer effects that
149 may occur when classifying bat passes using smaller time scales and when several bats are present at the same
150 time and at the same point. This interval length has also been shown to be a superior choice to longer intervals
151 when measuring bat activity in forest habitats (Müller et al., 2013). Since we only analysed bat calls confirmed to
152 species level and not to the genus level such as previous studies (e.g. Jung et al., 2012; Kirkpatrick et al., 2017;

153 Willcox et al., 2017), we were unable to model the activity of *Nyctalus lasiopterus* and *Eptesicus nilssonii* alone
154 due to the difficulty of assigning ultrasound calls to the species, likewise for *Vestertilio murinus*.

155 2.4 Forest Habitat Description

156 All forest habitat characteristics were measured and recorded by teams of experienced forest technicians during
157 the months of July and August. To collect data in the forest, a circular basal area plot measurement (25m radius)
158 was centered on the bat detector location.

159 2.4.1 Assessment of stratification

160 To describe the arrangement of vegetation across the vertical profile of the forest, the vegetation clutter from
161 the ground to the canopy was initially visually recorded as a percentage of the “closure of vegetation” i.e. all
162 vegetation and obstacles impeding the flight of a bat (trees, leaves, twigs, branches...) to the nearest 10%. The
163 observer at ground level estimated this percentage for 8 forest strata (<0.5m; 0.5-1; 1-2; 2-4; 4-8; 8-16; 16-32; >32).
164 After which we converted this percentage to a volume (m³). This was viewed as the most appropriate method so
165 as to account for potential observer effects, and to model activity in relation to a quantitative variable. We defined
166 volume as:

$$\text{volume by layer} = \pi \times r^2 \times h \times \frac{\text{clutter (\%)}}{100} \quad (1)$$

167 where r is the radius of forest survey site (i.e. 25m), h is the height of the stratum described and clutter is the
168 “closure of vegetation”. In order to fully answer the question of stratification: vegetation volume at three principal
169 strata was calculated. 1) 0-4m representing the shrub layer, 2) 4-16m, representing the understory, and 3) 16->32m,
170 the canopy tree layer. A Shannon index (Peet, 1974; Hill, 1973; Heip et al., 1998) was applied in order to quantify
171 the heterogeneity of vegetation volume across the three different forest layers. We defined heterogeneity as:

$$H' = - \sum_{i=1}^n p_i \log_2 p_i \quad (2)$$

172 where H' is the Shannon-wiener index and p_i is the proportion of vegetation at each height interval.

173 2.4.2. Assessment of stand structure

174 Total basal area (TBA) was the chosen explanatory variable for measuring stand structure in relation to bat
175 activity. TBA is the cross-sectional area at diameter breast height (DBH) (1.3m above the ground) measured in
176 m². Total BA of each plot was achieved with the use of a Relascope set to a basal area factor of 1 (Edwards, 1983;

177 Bitterlich, 1984). In parallel, four different size classes for living trees were identified: small trees ($\geq 17.5\text{cm}$ –
178 27.5cm at DBH), medium trees (27.5cm – 47.5), large trees (47.5cm – 67.5) and very large trees ($> 67.5\text{cm}$).

179 2.4.3 Assessment of associated deadwood and tree-microhabitats

180 We included two variables describing presence of deadwood. 1) ground-lying deadwood was recorded, in
181 steres (st), a unit of volume from the original metric system equal to one cubic meter of stacked wood (Rehnus et
182 al., 2013). We identified two parameters from our dataset: i) less than 3steres, ii) more than 3steres. 2) A Standing
183 deadwood variable was described as a score, calculated by applying a weighted coefficient to the size of snags
184 (only taking into account snags larger than 17.5cm in diameter and a height of 1.3m) present at the forest plot. The
185 same diameter classes used for living trees were applied to standing deadwood. The highest coefficient was applied
186 to *Very Large Snags* (i.e. $>67.5\text{cm}$) as greater volumes of standing deadwood are associated with insect abundance
187 (Dajoz, 2007), and tree related microhabitat diversity and abundance (Ruczyński et al., 2010; Larrieu et al., 2013;
188 Tillon and Aulagnier, 2014). Thus, small snags were assigned a coefficient of one, medium-sized snags a
189 coefficient of two, large snags a coefficient of three, and very large snags a coefficient of four.

190 In addition, we assessed the influence of tree microhabitats independently; a binary predictor
191 (presence/absence) and a discrete variable (number of different microhabitat types present per site) were modeled,
192 as the positive relationship between bats and tree cavities is already known (e.g. Regnery et al., 2013a, Paillet et
193 al., 2018). All microhabitats were searched and recorded at the plot scale by The French National Forest Office
194 staff. A maximum of five different tree microhabitats, potentially usable as bat roosts, were observed: *woodpecker*
195 *hollows, crevices, peeling bark, decay cavities, and other natural holes.*

196 2.4.4 Assessment of edge effects

197 Finally, we observed the presence (or absence) of three edge-space features common in production forest
198 systems, 1) logging tracks, 2) low-traffic roads, and 3) forest limit/edges. Forestry tracks are common in production
199 forest systems as access by truck to logging sites is necessary. Also, low-traffic minor B-roads may commonly
200 traverse forest massifs between rural villages. We decided not to analyse these habitat elements separately. Thus,
201 we modelled ‘positive edge effects’ against bat activity as a single binary variable (i.e. if only one or all three
202 features were present at the same time) at the local scale (recording their presence when within 200m from point
203 count location), because such linear forms may be advantageous for bats, either as flight paths or feeding sites
204 (Verboom and Spoelstra, 1999; Kirkpatrick et al., 2017).

205 2.5 Statistical analyses

206 All statistical analyses were carried out in RStudio 1.1.463 with R 3.5.2 (see Supplemental Materials 1-10).
207 We used packages *glmmTMB* for performing generalized linear mixed models (GLMM: Bolker et al., 2009) and
208 *ncf* for detecting spatial auto-correlation. In addition, *emmeans* and *Plot* packages were used in order to compute
209 least-square means for comparison of categorical factors and for producing graphs.

210 In order to respect the assumptions of GLMM, analysis included the following stages:

211 Firstly, all predictors selected for inclusion in the models were tested for collinearity, avoiding those correlated
212 with a person's coefficient greater than 0.27 in the same maximal model. Additionally, we performed variance-
213 inflation factors (VIF) for the continuous and categorical explanatory variables to further check for
214 multicollinearity (Seavy et al., 2005; Zuur et al., 2009; Crawley, 2009). If inflation factors were >2, the variable
215 in question was not included in the maximal model (Zuur et al., 2009). Biogeographical regions, forest
216 composition, and sampling method were systematically collinear over the years, indicating unequal sampling of
217 forest types within biogeographical regions over time. These variables were therefore included as random
218 intercepts in the GLMMs in order to cope with the variance heterogeneity arising from such sampling bias.
219 Secondly, because analyzing data which include geographical locations, it is statistically likely that point counts
220 close in space and/or time will have similar bat activity therefore implying spatial and temporal autocorrelation
221 (Zuur et al., 2009; Kerbiriou et al., 2018). We thus performed correlograms for verification (Zuur et al., 2009). We
222 did not detect spatial autocorrelation for points within 5km (steps by 250m; see Supplemental Materials 1-10)
223 when Forest site was added as a random intercept (in order to correct for spatial autocorrelation). Adding a year
224 random intercept also improved variance modeling. Thus, our models were structured as follows:

225 [Activity] ~ Method + Season + Temperature + Time from sunset + Vegetation volume heterogeneity + Tree
226 basal area + Microhabitats + Ground deadwood + Standing deadwood + Positive edge effect + (1|Forest massif) +
227 (1|Year) + (1|Biogeographical region) + (1|Forest composition).

228 Furthermore, in order to account for false zeros (Zuur et al., 2009), we systematically eliminated point count
229 data from forests where the species in question is known to be absent. For example, *Hypsugo savii* and *Tadarida*
230 *teniotis* are not present in much of northern France and the Atlantic coast (*cf.* "INPN - National Inventory of The
231 Natural Heritage Program"), subsequently surveys carried out in these regions were not included in the analysis of
232 these species (Table 2). Very few records of *P. pygmaeus* were found in all the forests investigated within Alpine
233 and Atlantic regions (Table 2), which were therefore also discarded from its analysis.

234 All continuous predictor variables entered into the maximal model were centred around a mean of zero
235 (Burnham and Anderson, 2002; Zuur et al., 2009). Furthermore, bat 'activity' was expressed as minute counts (or

236 positive minutes) rather representing a relative activity index. Subsequently, we treated relative activity as number
237 of minutes in which a bat species signal was recorded over the total number of minutes spent at the survey site
238 (i.e., 30 or 45 depending on sampling method). Thus, due to the nature of the response variable and potential
239 overdispersion we chose the best error distribution among Poisson, a negative binomial distribution with a logit
240 link (in similar fashion to Kerbiriou et al., 2018). All model dispersion parameters ranged from 0.90 to 1.28
241 demonstrating good model fits (Table 3).

242 3. Results

243 During 49980 minutes from surveys, we detected a total of 13 hawking bat species during summer and
244 autumn acoustic surveys. Around 70% of total bat activity of studied hawkers was allocated to *P. pipistrellus*.
245 This species was detected in all regions and forest types with a mean activity ranging from 3.65 ± 1.83 to 8.63 ± 2.92
246 (Table 2). Of the large hawkers, *N. leisleri* was the most detected (and in all regions and forest types), mean activity
247 was highest in dominant conifer stands in Mediterranean regions. *N. noctula* had the lowest mean activity levels,
248 zero minute counts were assigned to the species in Alpine and Mediterranean regions.

249 3.1 Responses to Survey Method and Season

250 Only one open-habitat forager species responded to survey method (*Nyctalus noctula*), its activity being greater
251 in lowland forest surveys (i.e. MCD30 method) when compared to the alpine survey protocol ($p = 0.005$; Table
252 3). All large hawkers except *Nyctalus leisleri*, which showed no effect, appeared more active in summer than in
253 autumn. Concerning edge-space foraging bats, all species' activity seemed evenly distributed across survey
254 methods. Although, *H. savii* ($p = 0.036$; Table 3) and *P. kuhlii* ($p = 0.003$; Table 3) both appeared more active in
255 summer than in autumn, respectively, while *P. nathusii* was more active in autumn ($p = <0.001$; Table 3). However,
256 *B. barbastellus*, *P. pipistrellus*, and *P. pygmaeus* did not show any temporal differences.

257 3.2 Responses to Temperature and Time after sunset

258 *Eptesicus serotinus* was the only open-habitat forager to respond positively and strongly to temperature ($p =$
259 0.002 ; Table 3). *N. leisleri*, *N. noctula* and *T. teniotis* showed no response (Table 3). *E. serotinus* and *N. noctula*
260 both responded negatively and significantly ($p < 0.001$; Table 3), respectively, to time elapsed after sunset. Equally,
261 only one small hawker responded to temperature, *P. nathusii* activity being positively influenced ($p = <0.001$;
262 Table 3). In addition, three species of small hawkers responded negatively to time elapsed after sunset (*B.*
263 *barbastellus*, $p = <0.001$; *H. savii*, $p = <0.001$; *P. kuhlii*, $p = <0.001$; Table 3).

264 3.3 Responses to Vegetation volume heterogeneity and Basal area

265 *Eptesicus serotinus* was the only large hawkler to respond positively to the Shannon diversity index on
266 vegetation volume across the vertical forest profile ($p = 0.005$; Table 3; Fig. 1). All other large hawklers were
267 unaffected. Concerning tree basal area, no open-habitat forager responded to this forest variable. Regarding small
268 hawklers, *Pipistrellus pipistrellus* was positively associated with vegetation volume diversity across the vertical
269 forest profile ($p = <0.001$; Table 3; Fig. 2). However, no other edge-habitat forager responded to vegetation volume
270 diversity. Both *P. nathusii* ($p = 0.010$; Table 3; Fig. 2) and *P. kuhlii* ($p = 0.027$; Table 3; Fig. 2) demonstrated
271 negative responses to tree basal area, respectively. No other small hawkler responded to this forest variable.

272 3.4 Responses to Tree microhabitats

273 Here we tested different hypotheses as not all species target the same tree cavity type (see Table 1 for *à priori*
274 hypotheses). Regarding large hawklers, *Eptesicus serotinus* responded positively and significantly to the presence
275 of woodpecker hollows and/or crevices ($p = 0.035$; Table 3; Fig. 1). However, the activity of *N. leisleri*, *N. noctula*
276 and *T. teniotis* did not appear affected by tree cavity presence. Only two bats from the edge-habitat foraging guild
277 responded to the presence of tree microhabitats; the activity of *B. barbastellus* ($p = 0.001$; Table 3; Fig. 2) and *P.*
278 *nathusii* ($p = 0.036$; Table 3; Fig. 2) was positively associated with the presence of crevices and/or peeling bark.

279 3.5 Responses to Deadwood environments

280 No open-habitat forager responded to the presence of ground deadwood. However one species, that of *Nyctalus*
281 *noctula*, appeared negatively associated with standing deadwood at the forest plot scale ($p = 0.041$; Table 3; Fig.
282 1). Equally, *Eptesicus serotinus* demonstrated a negative trend in relation to standing deadwood but no significance
283 was confirmed ($p = 0.067$; Table 3). With regards to small hawklers, *P. nathusii* responded positively to forest
284 zones where ground deadwood exceeded a quantity of three steres ($p = <0.001$; Table 3; Fig. 2), while no other
285 small hawkler appeared associated with ground deadwood volume. Lastly, only *P. pipistrellus* appeared affected
286 by standing deadwood, its activity was weakly negatively associated ($p = 0.044$; Table 3).

287 3.6 Responses to Positive edge effects

288 Interestingly, no large hawkler appeared positively linked to such linear features. In fact *T. teniotis* even
289 demonstrated a negative response ($p = 0.021$; Table 3; Fig 1.). Contrary to large hawklers, three edge-habitat
290 foraging bats seem more active where logging tracks, minor-traffic roads and/or forest edges are present; *B.*
291 *barbastellus* ($p = 0.043$; Table 3; Fig. 2), *P. nathusii* ($p = <0.001$; Table 3; Fig. 2) and *H. savii* ($p = 0.033$; Table
292 3; Fig. 2) all showed a positive response, respectively. Moreover, *P. pipistrellus* demonstrated a weak positive
293 trend to such linear forms ($p = 0.065$; Table 3).

294 4. Discussion

295 The findings demonstrate that hawking bats do not all respond to forest habitats in the same manner and that
296 detection rates vary. Indeed, the results for large hawkers may need to be interpreted with caution as these open-
297 habitat foragers predominantly use the zone above the canopy (Müller et al., 2013). Therefore, monitoring these
298 species from within forest stands (and without of a microphone positioned at canopy level) will likely fail to
299 accurately measure their flight behaviour (Collins and Jones, 2009; Müller et al., 2013), even if they project their
300 echolocations signals far and are capable of detecting prey over long distances (Denzinger and Schnitzler, 2013).
301 This could explain the observed underestimation of activity. Equally, Müller et al. (2013) and Rydell et al. (2010)
302 demonstrate that *P. pipistrellus* activity increases with stand height, therefore a microphone at ground level may
303 not be sufficient despite the species being common across all stand types. Furthermore, our method of both
304 assessing bat calls uniquely confirmed to species level (i.e. to the lowest taxonomic rank) and partitioning records
305 at the minute timestamp may have reduced explanatory power. A more robust method may be to format bat calls
306 as “total activity” assigning each echolocation signal to a 5 second interval (e.g. Tillon et al., 2016). In addition,
307 caution should prevail when extrapolating weak trends due to our method bias of using multiple bat detectors.

308 4.1 Effects of vegetation volume heterogeneity

309 Of the open-space hawkers, *E. serotinus* responded strongly and positively to the Shannon diversity index of
310 vertical stratification. It is unsurprising that *Tadarida teniotis* did not respond to this variable as the species is
311 known to fly particularly higher above trees and at greater speeds than the other bats in this guild (Marques et al.,
312 2004). Although *E. serotinus* has been predominantly described as an open-space forager, the growing literature
313 would make it seem that the species may be able to adapt and exploit forest interiors if there is sufficient
314 heterogeneity in vegetation volume allowing for manoeuvrability. Plank et al. (2012) revealed that *E. serotinus*
315 was more active at ground level than at canopy level in broadleaved stands, which would confirm its ability to
316 forage at lower forest levels suggesting a certain capacity to use the full forest profile if empty space is available.
317 Additionally, Collins and Jones (2009) found that *ca. 7%* of bats at ground level were *Nyctalus/Eptesicus*.
318 However, this increased heterogeneity of the vegetation structure may also promote greater insect abundance
319 (Haddad et al. 2009; Jung et al., 2012) and subsequently increase bat activity due to higher prey availability (Jung
320 et al., 2012). Furthermore, in our study, one edge-habitat forager; *P. pipistrellus* also revealed a positive association
321 with the Shannon diversity index (H'). Since the index represents heterogeneity of vegetation volume between the
322 three measured strata, it implies several scenarios. For instance, if there is little clutter in one layer (e.g. 4-16m)
323 and a varied amount of clutter in the canopy or shrub stratum, a high value of H' is the result due to the difference
324 in vegetation volume between the three principal forest layers. Thus, should a lack of vegetation exist at one of the

325 height intervals or if a vegetation layer is entirely missing, then this may allow edge-space or open-space bats,
326 which possess greater wing loading (Schnitzler and Kalko, 2001; Denzinger and Schnitzler, 2013), to forage in the
327 interior of the forest. In the case of even-aged managed plots, when trees reach a mature age, vegetation volume
328 is largely concentrated in the canopy stratum resulting in a comparatively clear understory and subsequently
329 heterogeneity between vegetation layers. Further research is required in order to conclude if large hawkers target
330 even-age stands. Conversely, the index illustrates that if vegetation volume is similar in each vegetation layer then
331 homogeneity exists across the vertical forest profile and a lower value of H' is calculated. This is often the case in
332 uneven-aged stands (like in traditionally managed French mountain stands) as the canopy, understory and shrub
333 layer can exist simultaneously as different tree ages are desired. Our findings are in contrast to Froidevaux et
334 al.(2016) who found that heterogeneity in 'vegetation scatter' reduced the detection of 'medium-range
335 echolocaters' such as *Pipistrellus* spp. In our study, the only species to show a negative relationship, albeit weak,
336 was that of *N. noctula*.

337 4.2 Effects of stand structure

338 Two species responded negatively and significantly to tree basal area (m²/ha). In line with our predictions
339 (Table 1), *P. nathusii*, and *P. kuhlii* which commonly use the edges of forests, appear to avoid dense zones. Their
340 morphology i.e. high wing ratios (Norberg and Rayner, 1987; Schnitzler and Kalko, 2001; Jung et al., 2012) and
341 quicker flight (Denzinger and Schnitzler, 2013) are clearly two attributes that hinder navigation in dense space
342 (Rainho et al., 2010). Generally, this bat group do not have the echolocation call structures adapted to zones that
343 require signal recognition where high background vegetation interference prevails (Arlettaz et al., 2001; Schnitzler
344 and Kalko, 2001; Hiryu et al., 2008; Denzinger and Schnitzler, 2013). Even though a high tree basal area in
345 exploited forests systems is typically associated with mature stands, therefore a greater proportion of large to very
346 large diameter trees leading to a greater quantity of vegetation located at canopy level, it may also correspond to
347 young dense (regrowth) forests when several small diameter stems are desired. Subsequently a high BA of living
348 trees should also be linked to greater vegetation clutter. Vegetation would therefore limit access to a site for edge
349 foraging species (*Pipistrellus* spp.) (Hayes and Loeb, 2007; Tillon et al., 2016). Contrary to our initial hypotheses,
350 there was a lack of ecological responses by bats to basal area. We suggest that total BA as a variable may not be
351 adapted to explaining the ecology of bats, and that a true measure of density i.e. number of stems at the plot scale
352 would be more conclusive (e.g. Kirkpatrick et al., 2017).

353 4.3 The presence of tree cavities

354 Indeed, an increased presence of tree microhabitats is associated with higher bat activity most likely due to a
355 greater availability of potential bat roosts (Russo et al., 2004; Tillon and Aulagnier, 2014; Tillon et al., 2015). In
356 our study we confirmed that *P. pygmaeus* showed higher activity where a greater diversity of microhabitats were
357 present, albeit a weak trend ($p = 0.050$; Table 3). While *B. barbastellus* and *P. nathusii* both appear positively
358 associated to the presence of crevices and/or peeling bark. In addition, a positive link between the presence of
359 woodpecker hollows or crevices and *E. serotinus* activity was confirmed. Although loose bark provides a less
360 stable microclimate than woodpecker holes, especially during unfavourable weather (Greenaway, 2001; Russo et
361 al, 2004), *B. barbastellus* and *P. nathusii* may take advantage of such microhabitats so as to avoid competition
362 from birds and other mammals (even bats) for more stable cavities (Russo et al., 2004). Indeed bat species that
363 seek out less stable roosts often have a more pronounced roost-switching behaviour (Barclay and Kurta, 2007;
364 Hillen et al., 2010). Concerning *B. barbastellus*, non-lactating females can change roosts as regularly as every
365 2.0 ± 1.8 days (Hillen et al., 2010). Thus, it may not be imperative to compete for more stable roosts if such a
366 quick turnover is feasible. Equally, for many small tree-dwelling European bat species, colonies do not exceed a
367 few dozen individuals per roost thus allowing for the selection of temporary roosts such as exfoliating bark (Tillon
368 et al., 2018). On the contrary, larger bat species such as *E. serotinus* prefer more durable cavities such as
369 woodpecker hollows or crevices, which are commonly selected at the tree crown height (Tillon, 2015). *E. serotinus*
370 are known to accommodate greater numbers of individuals per roost (Catto et al., 1995). Thus, woodpecker holes
371 might be the most appropriate cavity type (Catto et al., 1995; Russo et al., 2004).

372 4.4 The presence of deadwood

373 Only *P. nathusii* was positively associated to forest zones where the presence of ground deadwood was in excess
374 of three steres, independent of other variables. Such quantities may represent fallen branches or tree crowns thus
375 resulting in temporary gaps or clearings in the canopy and understory, amplifying edge effects (Kirby et al.,
376 1998; Tillon et al., 2016; Bouvet et al., 2016). Therefore, these zones may be particularly favourable to edge-
377 space foraging bats because space previously occupied by healthy tree now remains empty. Tillon et al. (2016)
378 revealed that bat occurrences significantly increased after a threshold of $110\text{m}^3/\text{ha}$ of ground deadwood. Ground
379 deadwood should also provide a food source of saproxylic insects or deadwood dependent *Lepidoptera* for
380 opportunistic hawkers (Tillon, 2015; Bouvet et al., 2016). Furthermore, large quantities of ground deadwood
381 could encourage an indirect ecological phenomenon, that of allowing sunlight to arrive to the forest floor and
382 increase local temperatures during the first hours after sunset, providing an interesting microhabitat for many
383 flying insects which are consequently preyed upon by bats (Rydell, et al., 1996; Dajoz, 2007; Müller et al., 2012;

384 Tillon et al., 2016). The activity of *P. nathusii* and *E. serotnius* both seem to increase in relation to temperature,
385 with the latter also appearing crepuscular, which may support our hypothesis. Curiously, we did not find a
386 positive relationship to standing deadwood which was against our initial hypothesis (see Table 1), as such
387 features are often associated with cavity roosting bats and bat prey (Dajoz, 2007; Russo et al., 2004; Ruczyński
388 et al., 2010; Tillon et al., 2015). Contrary to the findings of Tillon et al. (2016), *N. noctula* appears negatively
389 affected by greater standing deadwood. This must in certain circumstances suggest a concentration of dead
390 branches, which constitute obstacles for fast flying species, and present potential collision risks, as a result such
391 zones might be avoided. Equally, a greater presence of snags may indirectly represent a proxy for an open
392 canopy. Given *Nyctalus* sp. prefer closed canopy structures (Müller et al., 2013), this may explain the reason for
393 its negative response. Similarly, *P. pipistrellus* was less active in the vicinity of standing deadwood. This
394 negative association may be linked to a lack of prey source, as snags no longer provide the foliage needed for the
395 development of insects (such as *Diptera* or phytophagous *Lepidoptera*) which also constitute part of its diet
396 (Swift, et al., 1985; Tillon, 2015).

397 4.5 Use of forest edges

398 We were unable to demonstrate any associations at a local scale between open-habitat foragers and positive
399 edge effects. In this study, given that a positive edge effect denoted the presence of three possible features; logging
400 tracks, low-traffic roads and/or edge of forest massif (either one feature alone or all at the same time) appears to
401 suggest that this bat group, which target more regularly the space above the trees, is not particularly affected by
402 the presence of such features. Large Hawkets are able to perceive echoes from features that resemble forest edges
403 from over 30m away (Denzinger and Schnitzler, 2013). It is thus possible that the scale perceived, or indeed the
404 method used (lack of microphone at height) does not allow for this type a relationship to be confirmed. It is likely
405 that the distances (and heights, and great speeds especially for *T. teniotis*) (Marques et al., 2004; Roemer et al.,
406 2017) covered by these species from their diurnal roosts, of several kilometers, prevents any statistical link being
407 established.

408 On the other hand, small hawkets that tend to exploit edge-space appear positively affected. The relative
409 activity levels of three species *B. barbastellus*, *P. nathusii*, and *H. savii* highly and significantly increased when
410 these features were present within a 200m radius, moreover *P. pipistrellus* also demonstrated a positive trend
411 towards such linear features. Edges of this nature may provide the opportunity for clutter-intolerant species to
412 navigate more easily from one feeding site to another (Kirby et al., 1998; Law and Chidel, 2002; Hein et al., 2009;
413 Morris et al., 2009; Heer et al., 2015). Likewise, with a greater foliage surface available from the ground to the

414 canopy, the edge could offer a better three-dimensional foraging terrain. Trajectory and image technologies
415 should help to confirm this hypothesis. At the same time, forest edges may provide protection from wind for weak
416 flying insects such as *Diptera*, among other taxa, causing an aggregation of prey blown in from adjacent less
417 cluttered zones (Verboom and Spoelstra, 1999; Kirkpatrick et al., 2017). Additionally, for small bat species
418 commuting to different foraging sites, logging tracks and low-traffic roads, in particular, could provide protection
419 from predators (Verboom and Spoelstra, 1999; Kirkpatrick et al., 2017). Thus, higher activity levels close to
420 logging tracks support the hypothesis that linear landscape features can facilitate the flight of bats, especially for
421 edge-habitat foragers (Verboom and Spoelstra, 1999; Adams et al., 2009). However, while tracks appear to be
422 important flight paths for bats, caution must prevail because an increase of activity in the vicinity of tracks does
423 not necessarily represent an amelioration of the forest habitat quality (Adams et al., 2009), as bats are renowned
424 opportunistic hunters (Müller et al., 2012).

425 **5. Conclusion**

426 Our study demonstrates that even bats from similar ecological guilds vary in the way they use forests. Vertical
427 structure, vegetation volume, presence of deadwood and microhabitats all play a role in determining their activity
428 in woodlands. However, our results are, to an extent, ‘incomplete’ further suggesting the necessity to use
429 microphones at/or above the canopy level (Adams et al., 2009; Müller et al., 2013). The scientific literature on
430 bats has been accumulating over the last decade, however long-term studies e.g. Barlow et al., 2015, Azam et al.,
431 2016, Kerbiriou et al. 2018a, Kerbiriou et al., 2018b, still remain in the minority, which may be important in order
432 to determine temporal effects (Maron et al., 2005; Kerbiriou et al. 2018a), and bat responses in years following
433 silvicultural treatments (Patriquin and Barclay, 2003). The varying flight behaviour of hawkers observed in our
434 study could also be due to treatment practices. Even though recent studies have demonstrated the relationships
435 between management, tree microhabitats and vegetation (e.g. Regenry et al. 2013a, Paillet et al. 2017), in future
436 studies we highly recommend testing management practices directly. Because lowland forests treated as even-aged
437 or coppice with standards should demonstrate varying vegetation clutter given that typically a single dominant
438 stratum exists whereas the reverse would be expected for uneven-aged stands in French mountain sites. A
439 categorical variable of such may further shed light on these cryptic animals.

440 *5.1 Management recommendations for the studied hawkers*

441 Given that there are differences in the ecological functioning of forests, i.e. different compositions,
442 stratification and structure, combined with various silvicultural approaches that indirectly manipulate growth

443 conditions (Guldin et al., 2007), proposing relevant management strategies rapidly becomes arduous for the
444 conservation biologist (Law et al., 2016; Russo et al., 2016; Tillon, 2015). Here, we attempt to propose a selection
445 of appropriate management strategies for these edge- and open-habitat foragers:

446 First, our results illustrate the need to maintain tree cavities. *B. barbastellus*, *Eptesicus serotinus*, and *P. nathusii*
447 were strongly and positively influenced by their presence. Also, *P. pygmaeus* showed a weak positive trend.
448 Indeed, it will be necessary to conserve a diversity of cavity types because large hawkers e.g. *Eptesicus* sp. and
449 *Nyctalus* sp. target woodpecker hollows (Ruczyński and Bogdanowicz, 2008), whereas *B. barbastellus* is known
450 to target peeling bark (Russo et al., 2004; Tillon, 2015), which we were able to confirm. Also, it is common to
451 observe appropriate roosting cavities for bats on large diameter trees (Larrieu et al., 2013; Tillon and Aulagnier,
452 2014). We recommend systematically protecting *a minima* three microhabitat-bearing trees per hectare in
453 production forests as a realistic target without jeopardizing economic interests (Tillon et al., 2018).

454 Second, the presence of bats in production forest systems is likely due to prey availability (Morris et al., 2009;
455 Müller et al., 2012; Kirkpatrick et al., 2017). Müller et al. (2013) considers the maintenance of favourable habitats
456 for the production of insects allowing to continually provide an indispensable prey source for bats. Suitable feeding
457 habitats often correlate to forests that resemble a natural state (Cruz et al., 2016; Hayes and Loeb, 2007; Law et
458 al., 2016; Saunders et al., 1991). Therefore, one way of providing favourable habitats for bats in forests would be
459 to take a naturalness approach by setting aside a number of small sites or “harvest exclusion areas” of no more
460 than a few hectares in size (Law et al., 2016; Tillon et al., 2018). By doing so, this would ensure the presence of
461 tree cavities, deadwood, and vegetation heterogeneity to naturally occur across an entire forest mosaic (Law et al.,
462 2016; Tillon et al., 2018). This would equally support a wider diversity of invertebrates (Dodd et al., 2012).
463 Provided the necessary attention is paid to “harvest exclusion areas”, accompanying such zones with corridors will
464 prove vital for flying animals such as bats to navigate across the forested landscape (Patriquin and Barclay, 2003).
465 We found that the presence of ground deadwood superior to three *steres* in quantity positively affected the activity
466 *P. nathusii*. Maintaining such quantities should be easier in exclusion areas (Patriquin and Barclay, 2003; Law et
467 al., 2016). Indeed, in plots strictly managed for timber, a volume greater than 3 *steres* could be more challenging
468 for the forest manager (Tillon et al., 2018). In cases where exploitable stems are removed, it is however
469 recommended to maintain the non-dismembered crown. Such measures should still favour the production of
470 potential prey and forest environments favourable to hawkers (Tillon et al., 2016).

471 Third, in agreement with Adams et al. (2009) we suggest promoting the presence of forest aisles especially when
472 young dense forest is the desired stand structure, in years following harvesting. Allowing for a patchwork-like

473 mosaic of re-growth stands should, at least, enable edge-habitat foraging bats access to a vertical vegetation surface
474 even though the interior would remain inaccessible (Adams et al., 2009; Jung et al., 2011). Thus, enhancing
475 heterogeneity at the landscape scale will be advantageous for bats (Kirkpatrick et al., 2017). Since forests cover
476 great distances, maintaining natural-resembling zones (Russo et al., 2016), logging tracks (Law and Chidel, 2002),
477 dense growth (Müller et al., 2013), and thin growth conditions, will allow hawking species that regularly select
478 forest edges (Law and Chidel, 2002; Morris et al., 2009), the chance to continue using managed forests.

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486 **Ethics.** No injuring experiment involved the animals in our study. Thus, no ethics agreement was required.

487 **Data accessibility.** Data shall be made available on request.

488 **Authors' contributions.** LT and SL designed the study and carried out acoustic surveys. JL, BP and FA
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754 **Table 1:** *A priori* hypotheses regarding effects of forest parameters on bat activity in managed forest stands. (+)
 755 indicates positive association expected, (-) negative association, while (0) indicates no relationship expected.

Forest parameter	Predicted effect for LARGE HAWKERS	Based on example references
Vegetation volume heterogeneity	<i>Eptesicus serotinus</i> (+)	(Collins and Jones, 2009) (Plank et al., 2012) (Zukal and Gajdošík, 2012)
	<i>Nyctalus leisleri</i> (+)	(Russo and Jones, 2003) (Collins and Jones, 2009)
	<i>Nyctalus noctula</i> (+)	
	<i>Tadarida teniotis</i> (0)	(Russo and Jones, 2003)
Tree basal area	<i>E. serotinus</i> (-)	(Tillon, 2015) (Tillon et al., 2016)
	<i>N. leisleri</i> (-)	(Tillon, 2015) (Tillon et al., 2016)
	<i>N. noctula</i> (-)	(Tillon, 2015)
	<i>T. teniotis</i> (0)	(Russo and Jones, 2003)
Tree microhabitats	<i>E. serotinus</i> : woodpecker holes + crevices (+)	-
	<i>N. leisleri</i> : woodpecker holes + decay cavities (+)	(Spada et al., 2008)
	<i>N. noctula</i> : woodpecker holes only (+)	(Ruczynski and Bogdanowicz, 2005)
	<i>T. teniotis</i> : no. of different microhabitat types (0)	(Pejic et al., 2017) (Marques et al., 2004)
Ground deadwood	<i>E. serotinus</i> (+)	(Tillon, 2015)
	<i>N. leisleri</i> (+)	(Tillon, 2015) (Tillon et al., 2016)
	<i>N. noctula</i> (0)	(Tillon et al., 2016)
	<i>T. teniotis</i> (+)	-
Standing deadwood	<i>E. serotinus</i> (+)	(Tillon, 2015) (Tillon et al., 2016)
	<i>N. leisleri</i> (+)	(Tillon et al., 2016)
	<i>N. noctula</i> (0)	(Tillon et al., 2016)
	<i>T. teniotis</i> (0)	-
Positive Edge effect	<i>E. serotinus</i> (+)	(Froidevaux et al., 2016) (Archaux et al., 2013)
	<i>N. leisleri</i> (+)	(Froidevaux et al., 2016) (Archaux et al., 2013)
	<i>N. noctula</i> (+)	(Froidevaux et al., 2016) (Archaux et al., 2013)
	<i>T. teniotis</i> (0)	-
Predicted effect for SMALL HAWKERS		
Vegetation volume heterogeneity	<i>Barbastella barbastellus</i> (0)	-
	<i>Hypsugo savii</i> (+)	-
	<i>Pipistrellus kuhlii</i> (+)	-
	<i>Pipistrellus nathusii</i> (+)	-
	<i>Pipistrellus pipistrellus</i> (+)	(Jung et al., 2012)
	<i>Pipistrellus pygmaeus</i> (+)	-
Tree basal area (-)	<i>B. barbastellus</i> (+)	(Tillon, 2015) (Tillon et al., 2016)
	<i>H. savii</i> (-)	-
	<i>P. kuhlii</i> (0)	(Tillon et al., 2016)
	<i>P. nathusii</i> (-)	-
	<i>P. pipistrellus</i> (-)	-
	<i>P. pygmaeus</i> (-)	(Kirkpatrick et al., 2017)
Tree microhabitats	<i>B. barbastellus</i> : crevices + peeling bark (+)	(Russo et al., 2004)
	<i>H. savii</i> : no. of different microhabitat types (0)	(Regnery et al., 2013a)
	<i>P. kuhlii</i> : no. of different microhabitat types (0)	(Regnery et al., 2013a)
	<i>P. nathusii</i> : crevices + peeling bark (+)	(Regnery et al., 2013a)
	<i>P. pipistrellus</i> : crevices + peeling bark (+)	(Regnery et al., 2013a)
	<i>P. pygmaeus</i> : no. of different microhabitat types (0)	(Lourenço and Palmeirim, 2004)
Ground deadwood (+)	<i>B. barbastellus</i> (+)	(Bouvet et al., 2016)(Tillon et al., 2016)
	<i>H. savii</i> (+)	(Bouvet et al., 2016)(Tillon et al., 2016)
	<i>P. nathusii</i> (+)	-
	<i>P. kuhlii</i> (+)	(Bouvet et al., 2016) (Tillon et al., 2016)
	<i>P. pipistrellus</i> (+)	(Bouvet et al., 2016) (Tillon et al., 2016)
	<i>P. pygmaeus</i> (+)	(Bouvet et al., 2016) (Tillon et al., 2016)
Standing deadwood (0)	<i>B. barbastellus</i> (+)	(Russo et al., 2004)
	<i>H. savii</i> (0)	-
	<i>P. kuhlii</i> (+)	-
	<i>P. nathusii</i> (0)	-
	<i>P. pipistrellus</i> (0)	-
	<i>P. pygmaeus</i> (+)	(Bouvet et al., 2016)
Positive Edge effect (+)	<i>B. barbastellus</i> (+)	-
	<i>H. savii</i> (+)	-
	<i>P. kuhlii</i> (+)	(Müller et al., 2013)
	<i>P. nathusii</i> (+)	(Müller et al., 2013) (Froidevaux et al., 2016)
	<i>P. pipistrellus</i> (+)	(Müller et al., 2013) (Froidevaux et al., 2016)
	<i>P. pygmaeus</i> (+)	(Müller et al., 2013) (Bartonička and Reháč, 2007)

756

757 **Table 2:** Mean (\pm SE) number of positive minutes recorded for bat species during summer and autumn inventories
758 by forest type and biogeographical region. DBL = dominant broadleaf, DC = dominant conifer, MF = mixed forest.
759 n represents the number of points counts. n varies in accordance to the species' natural distribution. E.g. *E.*
760 *Serotinus* and *P. pipistrellus* are theoretically present across the entire french mainland territory. However, the
761 presence of some species is missing from certain regions. E.g. *T. teniotis* is not present in the north and west coast
762 of mainland France, thus data from forest inventories carried out in the corresponding regions were not included
763 in its analysis.

764

Biogeography Composition	Alpine			Atlantic			Continental			Mediterranean		
	DBL	DC	MF	DBL	DC	MF	DBL	DC	MF	DBL	DC	MF
N. Forest n	5 34	5 79	5 35	11 490	8 80	8 47	16 206	5 190	9 44	5 84	6 164	4 10
<i>E. serotinus</i> N. Forest n	0.09 \pm 0.06 5 34	0.03 \pm 0.02 5 79	0.20 \pm 0.11 5 35	0.34 \pm 0.07 10 474	0.29 \pm 0.11 8 80	0.30 \pm 0.16 7 43	0.22 \pm 0.05 16 206	0.17 \pm 0.07 5 190	0.09 \pm 0.04 9 44	0.07 \pm 0.04 5 84	1.73 \pm 0.41 6 164	0.30 \pm 0.15 4 10
<i>N. leisleri</i> N. Forest n	0.24 \pm 0.13 3 4	0.20 \pm 0.07 1 59	0.49 \pm 0.35 2 15	0.24 \pm 0.05 10 474	0.16 \pm 0.07 8 80	0.35 \pm 0.17 7 43	0.26 \pm 0.06 15 204	0.19 \pm 0.04 8 164	0.27 \pm 0.15 4 42	0.24 \pm 0.08 2 18	2.23 \pm 0.47 2 22	1.00 \pm 0.49 1 4
<i>N. noctula</i> N. Forest n	0 5 34	0 5 79	0 5 35	0.03 \pm 0.06 - -	0.05 \pm 0.08 - -	0.19 \pm 0.18 - -	0 3 16	0.01 \pm 0.03 4 85	0 3 19	0 5 84	0 6 164	0 4 10
<i>T. teniotis</i> N. Forest n	0.24 \pm 0.31 5 34	0.01 \pm 0.04 5 79	0.20 \pm 0.28 5 35	- 11 490	- 8 80	- 8 47	0 15 204	0.01 \pm 0.04 8 182	0 4 40	0.32 \pm 0.61 4 52	1.91 \pm 1.42 5 154	0.80 \pm 0.58 4 10
<i>B. barbastellus</i> N. Forest n	0.06 \pm 0.07 3 24	0 4 71	0 3 25	0.17 \pm 0.25 11 490	0.12 \pm 0.15 8 80	0.11 \pm 0.12 8 47	0.22 \pm 0.25 14 198	0.13 \pm 0.14 7 154	0.05 \pm 0.06 4 42	0.04 \pm 0.06 5 84	0 6 164	0.68 \pm 0.49 4 10
<i>P. nathusii</i> N. Forest n	0 5 34	0 5 79	0 5 35	0.02 \pm 0.04 11 490	0.01 \pm 0.03 8 80	0.02 \pm 0.04 8 47	0.36 \pm 0.48 16 206	0.03 \pm 0.05 5 190	0.02 \pm 0.04 9 44	0.05 \pm 0.06 5 84	0.01 \pm 0.02 6 164	0.10 \pm 0.09 4 10
<i>P. pipistrellus</i> N. Forest n	7.06 \pm 3.09 5 34	3.65 \pm 1.83 5 79	6.60 \pm 3.28 5 35	6.22 \pm 2.37 - -	4.64 \pm 1.71 - -	4.23 \pm 1.70 - -	4.58 \pm 2.11 4 26	7.68 \pm 2.92 5 99	5.89 \pm 2.68 2 15	1.19 \pm 0.74 5 84	8.63 \pm 2.92 4 148	4.00 \pm 2.75 5 10
<i>H. savii</i> N. Forest n	0.24 \pm 0.13 5 34	0.20 \pm 0.07 5 79	0.49 \pm 0.35 5 35	- 11 490	- 8 80	- 8 47	0.08 \pm 0.09 14 198	0.39 \pm 0.50 5 119	0 9 17	0.35 \pm 0.32 5 84	2.01 \pm 1.68 6 164	1.50 \pm 0.57 4 10
<i>P. kuhlii</i> N. Forest n	1.29 \pm 1.35 - -	0.01 \pm 0.03 - -	0 - -	0.24 \pm 0.26 - -	0.22 \pm 0.23 - -	0.53 \pm 0.76 - -	0.50 \pm 0.78 14 198	0.24 \pm 0.31 7 154	0.06 \pm 0.07 4 42	1.49 \pm 1.64 5 84	1.09 \pm 0.95 6 164	9.40 \pm 4.11 4 10
<i>P. pygmaeus</i>	-	-	-	-	-	-	0.46 \pm 0.68	0.06 \pm 0.15	0.17 \pm 0.31	1.01 \pm 1.49	1.24 \pm 0.92	0

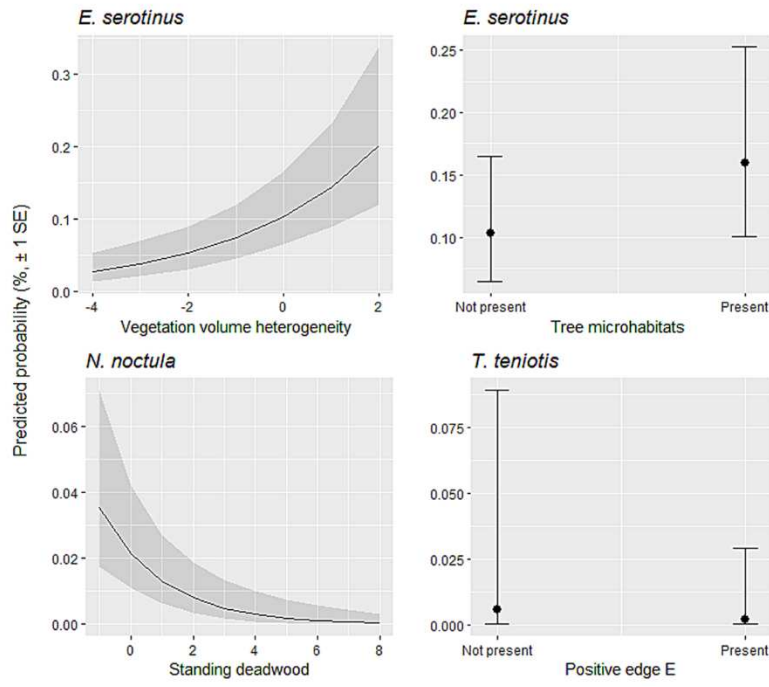
765

766 **Table 3.** Details of the GLMM analysing the variation in relative activity of the ten bat species with forest habitat features between 2011-2016 across French mainland territory.

767 Significant *p* values in bold only.

Guild	Large Hawkers						Small Hawkers													
	<i>E. serotinus</i>		<i>N. leisleri</i>		<i>N. noctula</i>		<i>T. teniotis</i>		<i>B.barbastellus</i>		<i>P. nathusii</i>		<i>P. pipistrellus</i>		<i>H. savii</i>		<i>P. kuhlii</i>		<i>P. pygmaeus</i>	
Parameters	$\beta_{LSM} \pm SE$	P	$\beta_{LSM} \pm SE$	P	$\beta_{LSM} \pm SE$	P	$\beta_{LSM} \pm SE$	P	$\beta_{LSM} \pm SE$	P	$\beta_{LSM} \pm SE$	P	$\beta_{LSM} \pm SE$	P	$\beta_{LSM} \pm SE$	P	$\beta_{LSM} \pm SE$	P	$\beta_{LSM} \pm SE$	P
DISPERSION ϕ	0.92		0.94		1.28		1.25		0.99		1.22		1.04		1.14		0.94		0.90	
<i>RANDOM EFFECTS</i>																				
σ (Forest)	1.51		1.47		1.73		1.86		2.84		2.16		0.80		1.33		2.31		2.03	
σ (Year)	<0.01		<0.01		<0.01		1.07		0.61		<0.01		0.24		0.20		<0.01		<0.01	
σ (Biogeographic_regions)	<0.01		<0.01		<0.01		1.50		0.24		0.70		0.14		<0.01		<0.01		<0.01	
σ (Forest_composition)	<0.01		<0.01		0.45		<0.01		0.17		<0.01		0.14		<0.01		<0.01		<0.01	
<i>FIXED EFFECTS</i>																				
Intercept	-2.27±0.48	<0.001	-1.65±0.46	<0.001	-3.77±0.67	<0.001	-5.07±2.77	0.067	-4.70±1.02	<0.001	-4.10±0.94	<0.001	1.46±0.37	<0.001	-2.24±0.47	<0.001	-1.95±0.64	<0.001	-2.03±0.95	<0.001
Method MCD45 vs.MCD30	-0.99±0.56	0.075	-0.40±0.53	0.458	-2.73±0.98	0.005	1.20±2.56	0.640	-0.59±1.07	0.579	-1.90±1.10	0.085	-0.07±0.42	0.870	-	-	-0.72±0.82	0.381	-0.30±1.05	0.771
Season SUMMER vs. AUTUMN	0.70±0.21	<0.001	0.25±0.17	0.143	0.80±0.24	<0.001	1.74±0.36	<0.001	0.21±0.12	0.097	-1.11±0.24	<0.001	0.04±0.07	0.649	0.47±0.23	0.036	0.60±0.20	0.003	-0.20±0.19	0.288
Temperature	0.41±0.13	0.002	0.03±0.10	0.758	0.20±0.21	0.346	-0.20±0.21	0.324	0.16±0.08	0.061	0.42±0.11	<0.001	-0.06±0.04	0.160	0.06±0.13	0.667	<0.01±0.13	0.974	0.13±0.11	0.231
Time from sunset	-0.37±0.11	<0.001	-0.03±0.09	0.756	-0.86±0.14	<0.001	0.02±0.18	0.923	-0.46±0.07	<0.001	-0.18±0.12	0.147	-0.01±0.04	0.876	-0.59±0.14	<0.001	-0.22±0.10	<0.001	0.06±0.11	0.601
Vegetation volume heterogeneity	0.34±0.12	0.005	0.16±0.11	0.134	-0.27±0.15	0.078	0.13±0.20	0.534	0.02±0.08	0.760	-0.12±0.17	0.481	0.18±0.05	<0.001	-0.13±0.12	0.307	-0.12±0.11	0.267	0.08±0.12	0.497
Tree basal area	-0.16±0.12	0.212	-0.07±0.10	0.510	0.01±0.19	0.963	0.14±0.20	0.477	0.12±0.08	0.113	-0.55±0.21	0.010	-0.03±0.05	0.552	-0.11±0.13	0.403	-0.29±0.13	0.027	0.16±0.13	0.224
Microhabitats*	0.43±0.21	0.035	-0.15±0.20	0.447	0.23±0.27	0.382	0.21±0.15	0.167	0.49±0.15	0.001	0.56±0.27	0.036	-0.14±0.08	0.083	-0.07±0.13	0.609	0.05±0.08	0.592	0.19±0.10	0.050
Ground deadwood MORE vs. LESS 3 ST	-0.17±0.22	0.452	-0.21±0.20	0.273	0.03±0.31	0.924	-0.06±0.34	0.854	-0.24±0.15	0.106	1.12±0.27	<0.001	-0.13±0.09	0.146	-0.14±0.24	0.569	-0.27±0.24	0.266	-0.15±0.19	0.421
Standing deadwood	-0.21±0.11	0.067	0.11±0.11	0.306	-0.50±0.24	0.041	-	-	-0.08±0.10	0.387	-0.14±0.17	0.415	-0.09±0.04	0.044	-	-	-0.03±0.13	0.796	-	-
Positive Edge PRESENCE vs.ABSENCE	0.16±0.23	0.500	0.23±0.23	0.313	-0.02±0.28	0.942	-1.09±0.47	0.021	0.40±0.20	0.043	1.27±0.29	<0.001	0.17±0.09	0.065	0.67±0.31	0.033	-0.09±0.23	0.706	-0.33±0.23	0.147

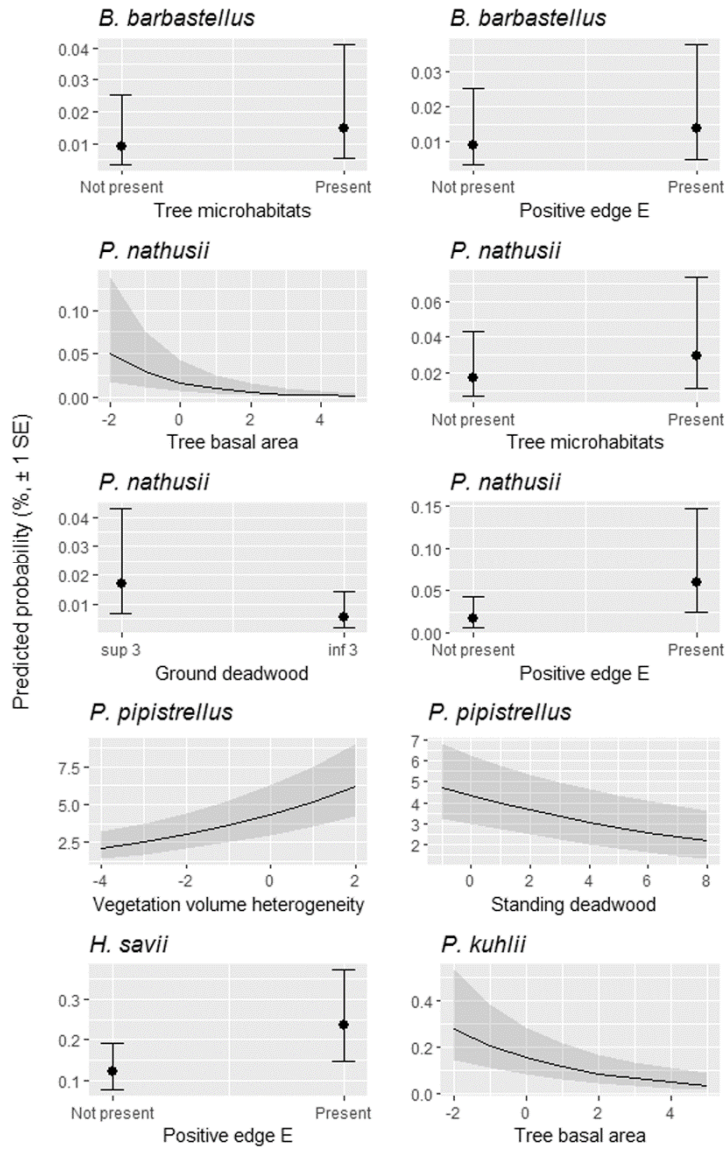
768 *Tree microhabitat variable changed according to the hypothesis of each species; for *Eptesicus serotinus* the variable was presence/non-presence of woodpecker hollows and/or crevices, for *Nyctalus leisleri* tested
769 presence/non-presence of woodpecker hollows and/or decay cavities, for *N. noctula* we tested presence/non-presence of woodpecker hollows only, for *H. savii*, *P. kuhlii*, *P. pygmaeus*, and *T. teniotis* Number of different
770 tree microhabitats present was tested as the species are not considered to target a particular microhabitat type. Finally, for *Barbastella barbastellus*, *Pipistrellus nathusii* and *P. pipistrellus* the variable was presence/non-
771 presence of crevices and/or peeling bark.



772

773 **Figure. 1.** Large hawks' estimated probability of relative activity in relation to forest variables. Only significant

774 results are shown.



775

776 **Figure 2.** Small hawkers' estimated probability of relative activity in relation to Forest variables. Only significant

777 results are shown.