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1 From field surveys to LiDAR:

2 Shining a light on how bats respond to forest structure

3  
4 Jérémy S. P. Froidevaux<sup>1,2,\*</sup>, Florian Zellweger<sup>2,3,\*†</sup>, Kurt Bollmann<sup>2</sup>, Gareth Jones<sup>1</sup>, and Martin K.  
5 Obrist<sup>2</sup>

6  
7 <sup>1</sup>University of Bristol, School of Biological Sciences, Life Sciences Building, 24 Tyndall Avenue,  
8 BS8 1TQ Bristol, United Kingdom.

9 <sup>2</sup>Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Zürcherstrasse 111, CH-  
10 8903 Birmensdorf, Switzerland.

11 <sup>3</sup>Forest Ecology, Institute of Terrestrial Ecosystems, Department of Environmental Systems Science,  
12 ETH Zürich, CH-8092 Zürich, Switzerland.

13  
14 \*These authors contributed equally to this study.

15  
16 †Corresponding author:

17 Florian Zellweger

18 Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Zürcherstrasse 111, CH-8903  
19 Birmensdorf, Switzerland

20 Tel: +41 44 7392 821

21 E-mail: [florian.zellweger@wsl.ch](mailto:florian.zellweger@wsl.ch)

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24 **ABSTRACT**

25 Detailed information about three-dimensional vegetation structure proves increasingly useful for  
26 studying species-habitat relationships in forest ecosystems. This particularly applies to species that  
27 make extensive use of the three-dimensional habitat space in forests, such as bats. Bats show  
28 considerable variation in flight morphology and echolocation traits that are shaped by habitat features,  
29 and are excellent model taxa for investigating relationships between vegetation structure and animal  
30 occurrence and movement. The aims of this study were (1) to investigate the relationship between the  
31 activity of bats and forest structure and (2) to compare the performance of airborne Light Detection  
32 and Ranging (LiDAR) and terrestrial field surveys for measuring habitat features in a representative  
33 sample of mixed and deciduous forests in the Swiss lowlands. Leaf-on and leaf-off LiDAR data were  
34 used separately, as well as in combination, to evaluate the relative strength of these datasets to  
35 describe 3D canopy architecture and vertical forest structure. Field measurements included structural  
36 variables such as leaf area index (LAI), vertical layering, snags, as well as shrub and ground  
37 vegetation cover. We recorded 145,433 echolocation call sequences from bats and assigned them into  
38 three echolocation guilds (short-, mid- and long-range echolocators; SRE, MRE, LRE, respectively)  
39 treating separately the dominant species (*Pipistrellus pipistrellus*; Pp). We used Generalized Mixed  
40 Effects Models (GLMMs) and applied an information-theoretic approach to assess relationships  
41 between guild-specific activity patterns of bats and forest structure in the forest interior, as well as in  
42 forest gaps. Standardized coefficients were used to evaluate variable effect sizes and relative  
43 importance. We found that guild-specific bat activity was clearly related to three-dimensional forest  
44 structure. The activity of SRE, MRE and Pp bats was negatively affected by foliage height diversity,  
45 indicating that a large scatter of vegetation elements along 3D forest profiles may restrict accessibility  
46 for manoeuvrable bats. Outer canopy surface ruggedness was significantly and positively related to  
47 the activity of MRE and LRE bats, as well as Pp, all of which may profit from increased canopy  
48 surface ruggedness for foraging (food abundance) and commuting (cover) purposes. The highest  
49 variable effect sizes were obtained by combining leaf-on and leaf-off LiDAR data. Leaf-off  
50 outperformed leaf-on data, particularly in describing foliage height diversity. LiDAR provided  
51 information about bat habitat structure in forests that is not readily available from field surveys.

52 LiDAR thus increases the scope of inference for future investigations of how species respond to  
53 vegetation structure, which can now readily and contiguously be assessed at relevant grain sizes and  
54 across large areas.

55

56 **KEYWORDS**

57 Airborne laser scanning; Bat guild; Chiroptera; Field survey; Habitat structure; Passive acoustic  
58 echolocation sampling.

## 59 1. INTRODUCTION

60 In forest ecosystems, vegetation structure is an important biotic factor affecting the presence  
61 and abundance of animal species at local scales (Hunter 1999; Tews et al. 2004). Forest vegetation  
62 structure and its complexity influence species behaviour and diversity through several mechanisms,  
63 e.g. by affecting the availability and diversity of resources and niches, modifying microclimatic  
64 conditions, or by providing breeding and roosting sites, shelter or concealment from predators  
65 (MacArthur and MacArthur 1961; Melin et al. 2014; Suggitt et al. 2011). The fundamental  
66 importance of vegetation and habitat structure for the understanding and maintenance of biodiversity  
67 in forests is increasingly recognised (Gustafsson et al. 2012; Noss 1990, 1999), and recent advances in  
68 remote sensing may substantially improve our knowledge about relationships between species and  
69 habitat structure (Davies and Asner 2014; Simonson et al. 2014).

70 While forest vegetation structure affects the habitat use of a wide range of taxa (e.g.  
71 Zellweger et al. 2015), it is particularly important for insectivorous bats, which use forest habitats for  
72 different purposes such as roosting (Ruczynski et al. 2010; Russo et al. 2004), foraging (Patriquin and  
73 Barclay 2003) and commuting (Schaub and Schnitzler 2007; Schnitzler et al. 2003). The influence of  
74 forest structure on bat activity and occupancy at the stand scale has been well studied in several  
75 regions (Adams et al. 2009; Dodd et al. 2012; Erickson and West 2003; Jung et al. 2012; Kalcounis et  
76 al. 1999; Müller et al. 2013; Obrist et al. 2011). These studies in general show that regardless of the  
77 stratum studied, an increase in vegetation density reduces bat activity (Adams et al. 2009; Brigham et  
78 al. 1997; Obrist et al. 2011). However, bats show different responses to vegetation structure  
79 depending on their foraging strategy, ecomorphological traits and echolocation call design (Aldridge  
80 and Rautenbach 1987; Norberg and Rayner 1987; Schnitzler and Kalko 2001). For example, bat  
81 species with low flight manoeuvrability and long echolocation range (e.g. *Nyctalus* spp.) prefer  
82 foraging in the open, whereas species with high flight manoeuvrability and short echolocation range  
83 (e.g. *Myotis* spp.) make extensive use of the vertical complexity of a forest (Adams et al. 2009;  
84 Kalcounis et al. 1999; Müller et al. 2013). These distinct relationships with structural attributes  
85 suggest that accurate information of the three-dimensional forest structure is important for better  
86 understanding habitat use by bats.

87           Until the advent of remote sensing technologies, such as Light Detection and Ranging  
88 (LiDAR), data collection on stand-scale forest structure was largely restricted to observational field  
89 surveys. Apart from being laborious, the availability of field survey data is limited to sample plots,  
90 and area-wide evaluations of structural attributes across a range of grain sizes and spatial extents are  
91 thus not feasible. Furthermore, field data to study species-habitat structure relationships and to build  
92 habitat models are usually collected across relatively small areas. This constrains the scope of  
93 inference from such data and poses limitations for many applications in ecology and conservation,  
94 which would profit from contiguous and detailed data across a range of scales (e.g. Lindenmayer et al.  
95 2008; Wiens 1989). Moreover, field observations are limited in describing important habitat  
96 properties related to the canopy. Fine-scale aspects and variation in canopy architecture and  
97 associated vegetation density and surface area, for example, influence the abundance and diversity of  
98 spiders and other arthropods (Halaj et al. 2000; Müller et al. 2014). However, such features are  
99 difficult to describe in the field and may remain largely concealed from an observer on the ground.  
100 Methods that provide objective tools to contiguously depict the entire 3D habitat space in forests and  
101 deliver ecologically interpretable variables are thus required to fully appreciate the ecological  
102 relevance of forest structure. By providing detailed and contiguous information on habitat structure  
103 across large areas, airborne LiDAR has considerably advanced our abilities to meet these  
104 requirements. Thus, novel opportunities to study species-habitat structure relationships across a range  
105 of scales have emerged and applications of LiDAR are rapidly increasing in number (Davies and  
106 Asner 2014; Simonson et al. 2014; Vierling et al. 2008). Based on structural attributes such as vertical  
107 complexity, canopy height and heterogeneity, LiDAR has frequently been applied to study bird  
108 diversity and habitat use in forests (Bradbury et al. 2005; Clawges et al. 2008; Goetz et al. 2007;  
109 Hinsley et al. 2006; Lesak et al. 2011; Zellweger et al. 2013). The diversity and activity of other  
110 taxonomic groups, such as arthropods, is related to LiDAR-derived canopy architecture and indicators  
111 of microclimatic conditions in the lower stratum of forests (Müller et al. 2014; Müller and Brandl  
112 2009; Vierling et al. 2011). Despite the strong dependence of bats on forests, studies using airborne  
113 LiDAR to investigate how bat behaviour is related to forest structure, however, are still relatively rare  
114 (Davies and Asner 2014). Jung et al. (2012) found a strong relationship between bat occurrence and

115 activity and structural heterogeneity related to canopy and edge characteristics in different managed  
116 forest types. Fabianek et al. (2015) found that a high proportion of LiDAR-derived canopy gaps  
117 within mixed and coniferous forests positively affected roost selection by male *Myotis* bats in Canada,  
118 and ground-based LiDAR has provided insights into the flight behaviour of big brown bats (*Eptesicus*  
119 *fuscus*) in a deciduous forest (Yang et al. 2013). Furthermore, the potential of LiDAR to complement  
120 field surveys by delivering unique information on structural habitat attributes, as well as potential  
121 benefits from using a combination of leaf-on and leaf-off LiDAR data to measure habitat structure  
122 remain to be explored. Given the increased canopy penetration of laser pulses during leaf-off  
123 conditions, we expect it to carry essential information about subcanopy vegetation elements  
124 potentially affecting the manoeuvrability of bats. Outer canopy and edge characteristics, however,  
125 may be more accurately represented by leaf-on data, hence a combination of leaf-on and leaf-off data  
126 provides ecologically valuable information in deciduous and mixed forests, such as the ones studied  
127 here.

128         The aim of this study was to test the assumption that forest vegetation structure strongly  
129 affects bat activity and that this relationship depends on species' eco-morphological traits such as  
130 flight manoeuvrability and echolocation call design. Such effects should thus be specific for guilds  
131 consisting of short- (SRE), mid- (MRE) and long- (LRE) range echolocators. We used a set of  
132 variables representing structural forest attributes from both field and LiDAR surveys, and investigated  
133 their effect on guild-specific activity patterns in mixed and deciduous forests. The main objectives  
134 were (i) to determine key structural variables that influence bat activity at the guild level and (ii) to  
135 compare the performance of terrestrial field and LiDAR surveys of forest structure and (iii) to  
136 investigate the relative strength of leaf-on and leaf-off LiDAR, as well as a combination thereof for  
137 providing unique information on forest structural attributes affecting bat habitat use.

## 138 2. MATERIAL AND METHODS

### 139 2.1. Study area

140 The study area was situated in Central Europe in the northern part of Switzerland, at the  
141 interface between the lowlands and the Jura Mountains (Canton of Aargau: 47°14'–47°62'N, 7°71'–  
142 8°46'E, 260-910 m a.s.l.). The average annual temperature and rainfall in this region are 9.7°C and  
143 1076 mm, respectively (www.meteosuisse.admin.ch). The landscape consists of a mosaic of  
144 fragmented habitats such as forests (37%), agricultural land (45%) and urban areas (15%). The most  
145 abundant forest tree species are *Fagus sylvatica* (32%), *Picea abies* (26%), *Abies alba* (14%),  
146 *Quercus* spp. (7%) and *Fraxinus excelsior* (7%).

147 We applied a stratified-random sampling design to select eight 1-km<sup>2</sup> cells that were  
148 characterised by more than 50% of temperate forest cover (Figure 1). Each cell contained four  
149 randomly selected forest plots. Forest plots included both forest interior habitats and forest gaps, and  
150 were located within deciduous (covered with more than 66% deciduous trees) or mixed (covered with  
151 between 33 and 66% deciduous trees) forest stands. We defined the forest gap as an open area within  
152 a forest where the canopy cover was considerably lower than in the surrounding forest areas (Runkle  
153 1992). We identified forest gaps during field investigations; the minimum size of a forest gap was 400  
154 m<sup>2</sup> (mean 1,318 m<sup>2</sup>). The distances between the recording sites in the forest gap and the forest interior  
155 ranged from 46 to 140 m (mean 81 m). To avoid biases from potential edge effects, the plots were  
156 located at least 50 m away from outer forest edges, and at least 20 m away from forest roads (for  
157 details, see Froidevaux et al. 2014).

158

### 159 2.2. Bat echolocation call recording and identification

160 Sampling took place between 4 June and 29 August 2013 (71 full nights) when weather  
161 conditions were optimal, i.e. during dry nights with a minimum temperature  $\geq 7$  °C, conditions that  
162 are suitable for insect flight and consequently for activity in aerial-feeding bats. We digitally recorded  
163 bat echolocation calls at 312.5 kHz sampling rate and 16 bits depth with 12 ultrasound detectors  
164 (BATLOGGER; Elekon AG, Lucerne, Switzerland), each protected by a Strongbox (Elekon AG,  
165 Lucerne, Switzerland). Microphones were water resistant, omnidirectional and sensitive between 10



166 and 150 kHz ( $\pm 5$  dB). We programmed detectors to automatically record bats throughout the night  
167 (from sunset to sunrise, 21:30 h – 05:30 h).

168 We allocated three detectors per forest plot, one located in the centre of the forest gap  
169 mounted on a pole at a height of 1.35 m, and two in the forest interior. There, we placed one detector  
170 on a pole at 1.35 m height, and another detector up in the canopy at a mean height of 18.9 m, using a  
171 slingshot, rope and pulley system. We developed this design to better account for the vertical habitat  
172 use of bats in forests (Adams et al. 2009; Kalcounis et al. 1999; Müller et al. 2013). In total, each  
173 forest plot was sampled between 6 and 12 nights throughout the field season. This extensive sampling  
174 effort considerably increased the accuracy and completeness of data on bat activity (Froidevaux et al.  
175 2014).

176 We identified bat echolocation calls using BATSCOPE, a semi-automatic bat identification  
177 software package (Boesch and Obrist 2013). The process consisted of extracting 23 relevant numeric  
178 variables from call spectrograms (0.31 kHz x 0.16 ms resolution) and comparing these with variable  
179 values from 19,636 reference calls from 27 European species (Obrist et al. 2004). Based on three  
180 classifiers (*Support Vector Machine*, *K Nearest Neighbours*, *Quadratic Discriminant Analysis*), calls  
181 were then classified into species with an average correct classification rate of 95.7% when all three  
182 classifiers agreed (i.e. 76.4% of the cases; predictions obtained from 10-fold cross-validation; see  
183 Boesch and Obrist 2013). We then verified bat call sequences (i.e. series of echolocation calls) to  
184 taxonomic entity using the semi-automatic processes provided by BATSCOPE, which implements  
185 multiple filter combinations to reach the taxonomic level most appropriate for identification (for  
186 details, see Froidevaux et al. 2014). According to their affiliation (i.e. species, complex of species,  
187 genus, complex of genera), we grouped bats into different guilds reflecting their echolocation range  
188 (Aldridge and Rautenbach 1987; Schnitzler and Kalko 2001; Schnitzler et al. 2003), namely short-  
189 range echolocators (SRE; *Myotis* spp. and *Plecotus* spp.), mid-range echolocators (MRE; *Pipistrellus*  
190 spp. and *Hypsugo savii*) and long-range echolocators (LRE; *Eptesicus* spp., *Nyctalus* spp. and  
191 *Vespertilio murinus*) (see Table 1 in Frey-Ehrenbold et al. 2013 for more details). As *Pipistrellus*  
192 *pipistrellus* largely dominated the MRE guild (84.1 % of sequences), we excluded this species from  
193 the guild and analysed its activity pattern separately.

194

## 195 **2.3. Assessment of forest structure**

### 196 2.3.1. Field survey

197 We conducted field measurements on forest structure in July and August 2013, when trees  
198 were in full leaf. To collect data in the forest interior, we defined a stand around each forest ground  
199 site where the bat detector was placed, measuring an area of 30 x 30 m, by using poles and a laser  
200 distance meter (LEICA, Disto D8) and aligned it parallel to the terrain's slope. Each stand was then  
201 divided into four quarters (15 x 15 m) to optimise precision during data collection (e.g. estimation of  
202 shrub cover). Similarly, forest gaps were delimited by the tree lines and divided in four equal parts  
203 with a compass. Following the methodology of the Swiss National Forest Inventory (Keller 2011), we  
204 surveyed seven forest variables for the forest interior and five for the forest gap, each representing the  
205 local vegetation structure (Table 1). To minimize any observer bias, the same person (J.S.P.  
206 Froidevaux) collected all the data.

207 The degree of understory vegetation density was measured from the centre of the forest stand  
208 with a profile board (Nudds 1977), which was placed subsequently in the four corners of the stand.  
209 The leaf area index (LAI) was used as a surrogate of the combined cover of both the canopy and the  
210 subcanopy strata. We calculated the LAI with the program Hemisfer 1.5 (Schleppi et al. 2007;  
211 Thimonier et al. 2010) from five hemispherical photographs that were taken in the centre of each 15 x  
212 15 m quadrat of the forest stand. In forest gaps, the structure of the edge was classified as either open  
213 or closed (Hamberg et al. 2009), based on visual inspection, and the gap size was calculated using  
214 ArcGIS Desktop v10.

### 215 2.3.2. LiDAR metrics

216 We used discrete multiple return airborne LiDAR data to compute a number of metrics  
217 describing forest structural properties that are ecologically relevant to bats (Table 1). Milan  
218 Geoservices GmbH acquired raw data for the study area twice in 2014, once during leaf-on and once  
219 during leaf-off conditions. The data were acquired using a RIEGL LMS-Q680i airborne laser scanner  
220 flown at an average altitude of 700 m a.s.l. and average flight speed of 110 km h<sup>-1</sup>, with a beam  
221 divergence of 0.5 mrad. The overlapping flight strips and a pulse repetition frequency of 300 kHz led

222 to an average pulse density in each dataset of 7.5 pulses/m<sup>2</sup>, resulting in an average echo density of 22  
223 pts/m<sup>2</sup> across all plots. Comparison with 30 reference points from terrestrial measurements revealed  
224 an average vertical accuracy of 3.1 cm.

225 We merged the data from both flight missions and used a suite of LAStools algorithms  
226 (Isenburg 2013) involving point classification and triangulation to calculate a terrain model, which  
227 was then used to calculate the terrain-corrected (normalized) vegetation heights. We used the  
228 normalized point clouds of the leaf-on and leaf-off data sets separately, as well as the combination  
229 thereof to investigate the relative strengths of these different LiDAR datasets and whether they  
230 provide unique and complimentary structural information compared to field vegetation surveys. For  
231 each of the three LiDAR datasets we computed nine variables describing forest vegetation structure  
232 with potential relevance to bat activity, applying a height threshold of 1.3 m to identify vegetation  
233 points (Næsset 2002) (Table 1). Canopy height was computed as follows: we gridded the vegetation  
234 heights using a cell (pixel) size of 0.5 m, retained the highest available point per cell and assigned its  
235 height to the respective cell, thus representing the upper canopy surface. None of the point clouds  
236 contained returns from infrastructure such as power lines or buildings. Canopy ruggedness was  
237 calculated using the terrain ruggedness index (TRI), algorithm (Wilson et al. 2007). Canopy  
238 ruggedness measures the local variation in canopy height by comparing a central pixel with its  
239 neighbours, taking the absolute values of the differences, and averaging the results (Wilson et al.  
240 2007). Variation in outer canopy height and associated edge characteristics may be important for bats  
241 because it affects their foraging and commuting behaviour. We derived this variable for both the  
242 forest interior and the gap, and used the same nomenclature (i.e. canopy ruggedness) for the two.  
243 However, we are aware of the fact that in forest gaps, this variable represents the ruggedness of the  
244 upper vegetation surface, which may not always be referred to as canopy. To describe the degree of  
245 scatter of vegetation elements along the vertical forest profile, we adopted the foliage height diversity  
246 (FHD) concept proposed by MacArthur and MacArthur (1961). We defined FHD as

247 
$$\text{FHD} = H' = - \sum p_i \ln p_i,$$

248 where  $H'$  is the Shannon–Wiener information index and  $p_i$  is the proportion of vegetation points in the  
249  $i^{\text{th}}$  height interval. We calculated four equal height intervals (i.e. horizontal bands) delineated by the  
250 quartile heights of the vegetation point cloud (cf. Clawges et al. 2008).

251 Each variable was calculated for the field plot dimensions, and spatial co-registration was  
252 undertaken based on the averaged coordinates from at least three GPS recordings, using a GARMIN  
253 GPS device (GPSMAP 62st). The accuracy of the GPS localization varied in average 2.7 m in the  
254 gaps and 3.7 m in the forest interior. Given that the distance at which a bat can be detected is species  
255 specific, typically in the range of 10 to 50 m, these GPS values were sufficiently accurate to  
256 subsequently describe the habitat structure relevant to bats.

257

#### 258 **2.4. Statistical analyses**

259 Bat guild activity per night was measured by counting the number of 5 min intervals where  
260 bat sequences of a given taxon were recorded. This time period limits possible bias arising from the  
261 fact that single bats may forage in the recording range of a microphone for extended times. Acoustic  
262 data from the forest ground sites were previously pooled with those from the corresponding canopy  
263 sites to get a single activity index for the forest interior. We applied the Mantel test for testing the  
264 spatial independence of the total bat activity data by using two distance matrices, namely (i) the  
265 spatial distance between the sampling sites and (ii) the distance between the bat activity indexes  
266 measured at the given sites. No spatial autocorrelation was found (Mantel statistics:  $|r| = 0.04$ ,  
267 *empirical p.value* = 0.17, with 999 permutations). To assess the relationship between guild-specific  
268 bat activity (dependent variable) and vegetation structure (independent variable), we used generalized  
269 linear mixed models (GLMMs) (function *glmer*, R package *lme4*) with the appropriate distribution:  
270 Poisson for LRE guild and negative binomial for SRE and MRE guilds, as well as for *P. pipistrellus*,  
271 due to overdispersion in the data. Mean night temperature and forest variables were considered as  
272 fixed effects whereas the number of location-replicates and nights were implemented as random  
273 effects to avoid pseudo-replication. Before integrating the forest variables into the models, we  
274 investigated any correlations among variables using Spearman's correlation test. Each variable was  
275 standardized to obtain the same unit measures and enable a comparison of variable importance based

276 on the effect sizes in the GLMMs. When correlations were found ( $|r| > 0.7$ , Table S1), we kept only the  
277 variable with the highest ecological significance to explain bat activity. Moreover, if correlated  
278 variables had equal ecological importance, we tested them independently within our models to select  
279 the variable with the most explanatory power. Finally, to identify the most parsimonious model we  
280 applied an information-theoretic approach using Akaike's Information Criterion corrected for small  
281 sample sizes ( $AICc$ ), and chose the model with the fewest parameters when models were considered  
282 equivalent ( $\Delta AICc < 2$ ) (Burnham and Anderson 2002). Statistical analyses were performed using R  
283 3.0.1 (R Core Team 2013).

### 284 3. RESULTS

285 A total of 145,433 bat sequences containing 2,064,188 bat echolocation calls were recorded  
286 over 71 nights, including 113,340 sequences belonging to *P. pipistrellus*. 112,822 sequences (99.6%)  
287 could be affiliated to a guild. We assigned 68% of them to the MRE guild, 30% to the SRE guild, and  
288 2% to the LRE guild. While nocturnal activity (i.e., number of 5 min intervals where sequences of a  
289 given taxon were recorded) of SRE was higher in the forest interior than in forest gaps, the opposite  
290 was true for MRE and LRE, in spite of the fact that we sampled both at ground and canopy level in  
291 the forest interior (Table 2). Only 5-10% of all echolocation call sequences recorded contained  
292 terminal buzzes indicative of feeding behaviour (Griffin et al. 1960). Thus, we were unable to  
293 separate feeding behaviour and commuting behaviour in our analysis.

294 The effect of vegetation structure on bat activity was guild-specific, as revealed by the  
295 different variables and effect sizes in the GLMMs (Table 3). In the forest interior, the activity of SRE  
296 increased with decreasing FHD and density of trees. However, with the leaf-off and combined LiDAR  
297 datasets we found a comparably larger negative effect of FHD for MRE and *P. pipistrellus*, both of  
298 which responded positively to increasing canopy ruggedness and negatively to the LAI. LRE activity  
299 increased with increasing mean canopy height and was positively associated with increasing  
300 temperature.

301 In gaps, the activity of SRE increased with increasing ground vegetation cover, whereas MRE  
302 and LRE activity increased with increasing mean vegetation height and canopy ruggedness,  
303 respectively. *P. pipistrellus* showed the same trend as the MRE guild.

304 Significant effects of forest structure on bat activity were revealed by four LiDAR variables  
305 (i.e. FHD, canopy ruggedness, mean canopy height, and mean vegetation height), which were more  
306 often retained than the three significant variables measured in the field (i.e. density of trees, LAI and  
307 ground vegetation cover) were retained. The combined leaf-on and leaf-off dataset performed best in  
308 describing structural variables related to bat activity. This was particularly evident for FHD and  
309 canopy ruggedness, where the variable effect sizes were generally larger compared to the results of  
310 either leaf-on or leaf-off data. Leaf-off data represented the effect of FHD on SRE, MRE and *P.*  
311 *pipistrellus* activity better than leaf-on data. Although canopy ruggedness from leaf-on data was not

312 retained for MRE and *P. pipistrellus* (Table 3), canopy ruggedness frequently occurred in the top  
313 models in the leaf-on model selection for MRE and *P. pipistrellus* (Table S2).

## 314 **4. DISCUSSION**

### 315 **4.1. Vegetation structure affects bat habitat use**

316 Our results indicate a strong effect of the three-dimensional structure of forests on bat activity  
317 at the stand scale, and that this effect depends on guild-specific traits. Bat habitat use, in addition to  
318 foraging strategy, is mainly constrained by their echolocation call design and ecomorphological  
319 characteristics (Schnitzler and Kalko 2001; Schnitzler et al. 2003). The activity of SRE, for example,  
320 was higher in the forest interior, suggesting that bats that emit short-range echolocation calls and  
321 manoeuvre well with their low wing loadings, may be better adapted to forage in the forest interior  
322 than bats with a high wing loading and corresponding high flight speed, low manoeuvrability and  
323 long-range echolocation. While the short-range echolocation calls allows the members of the SRE  
324 guild to obtain a better perception of the near surroundings and to better deal with background echoes,  
325 higher manoeuvrability helps them avoid collisions with obstacles in their flight path within  
326 vegetation. This finding is consistent with previous studies that reported guild-specific responses to  
327 vegetation structure (Jung et al. 2012) and confirmed that bats respond to habitat structure in  
328 functionally different ways.

329 Bat detection probability may be affected by vegetation density and call frequency because  
330 higher call frequencies travel shorter distances than lower ones due to greater atmospheric attenuation.  
331 This could have biased our interpretations of the relationship between bat activity and forest structural  
332 components. However, Yates and Muzika (2006) and Bender et al. (2015) showed that the probability  
333 of bat detection in forests was not related to vegetation density, although bat occupancy was.  
334 Moreover, Obrist et al. (2011) showed experimentally that foliage density only weakly ( $\approx 5\%$ )  
335 attenuates calls at frequencies between 20-60 kHz, and the bat species we studied are not known to  
336 change call frequency substantially in relation to the habitat they preferably use. Of more concern is  
337 the likelihood that bats may reduce call intensity when flying in dense vegetation, making them less  
338 likely to be detected. Indeed, bats are likely to reduce call intensity in dense foliage to avoid acoustic  
339 masking by clutter echoes (Brinklov et al. 2010). Although we acknowledge that variation in habitat-  
340 dependent call intensity may bias our results to some extent, we are encouraged that the trends we  
341 document fit with expectations from flight morphology. For example species that use short-range



342 echolocation have wing shapes adapted for flying in cluttered situations and show higher levels of  
343 activity in the forest interior, even though their call intensity may be lower there. Furthermore, any  
344 decreases in bat detection probabilities caused by decreases in call intensity in dense vegetation may  
345 be compensated by increased pulse repetition rates as bats may need more details of the acoustic  
346 scene. Finally, it is also likely that the density of vegetation may affect the quality of the echolocation  
347 calls recorded and thus their identification (O'Keefe et al. 2014), which might be more of an issue  
348 when working at the species level. In our study, while bat identification was challenging (e.g.  
349 similarity of calls between species, poor-quality calls) the clustering of species into guilds allowed us  
350 to make a nearly complete use of our dataset: we were able to affiliate 99.6% of the bat sequences  
351 recorded into guilds. Thus, we assume that the density of vegetation played only a small role in  
352 affecting bat detectability relative to estimates of occupancy.

353

#### 354 4.1.1. Bat activity in the forest interior

355 Our findings highlight an important variable, foliage height diversity (FHD), for SRE, MRE  
356 and *P. pipistrellus* species. Since FHD represents the degree of scatter of vegetation heights along the  
357 vertical forest profile, higher FHD values may negatively affect bat accessibility and manoeuvrability.  
358 Thus, the negative correlations and relatively high effect sizes of FHD on the activity of MRE as well  
359 as *P. pipistrellus* were expected. These findings corroborate several studies that show that, edge  
360 specialist bat species avoid forests with highly scattered vertical vegetation profiles when foraging or  
361 commuting (Adams et al. 2009; Brigham et al. 1997; Erickson and West 2003; Obrist et al. 2011).  
362 Similarly, increased LAI, representing more closed forests, also affects activity of both these groups  
363 negatively. However, while we hypothesized a positive relationship between FHD and activity for the  
364 SRE guild (Norberg and Rayner 1987; Schnitzler and Kalko 2001), we found a negative relationship,  
365 though with a relatively low effect size. This suggests that even bats with high flight manoeuvrability  
366 concentrate their activity in vertically less complex forests. The most plausible reason for this finding  
367 arises from the fact that all forests in the study area are managed according to principles of  
368 sustainable, multi-purpose forestry (excluding plantations and monocultures) and thus, are strongly  
369 limited in the gradient of observed FHD. Although we randomly selected the sampling sites, we

370 obtained a small gradient from moderate to high FHD values ranging from 0.84 to 1.28 (mean: 1.08;  
371 SD: 0.10). Therefore bats with high manoeuvrability and short echolocation range belonging to the  
372 SRE guild seem to show a preference for a scattered profile until a certain threshold, after which the  
373 vegetation is too dense, restricting accessibility, manoeuvrability and, ultimately, their foraging  
374 efficiency (Rainho et al. 2010; Schnitzler and Kalko 2001). There is now widespread support for this  
375 hypothesis, regardless of the forest type investigated (Adams et al. 2009; Brigham et al. 1997; Müller  
376 et al. 2013). FHD has originally been proposed to explain bird diversity and positive correlations are  
377 usually found (Clawges et al. 2008; MacArthur and MacArthur 1961), implying that higher FHD  
378 leads to greater niche diversity along the vertical gradient of the forest. Even though we are aware that  
379 we used an adjusted version of the FHD concept and that we investigated bat activity and not bat  
380 diversity, our results point out that the same forest structural attribute may have very different  
381 ecological consequences for different taxa that utilise the same three-dimensional habitat space.

382 We further found canopy ruggedness to be important for the activity of bats from the MRE  
383 guild, as well as for *P. pipistrellus*. As suggested in other studies (Jung et al. 2012; Kalcounis et al.  
384 1999; Müller et al. 2013), bats may use the external canopy surface as a surrogate of edges when  
385 commuting and foraging. Thus, for edge specialist bats such as *Pipistrellus* spp., higher heterogeneity  
386 of the canopy surface provides greater benefits such as protection from predators, shelter from wind  
387 (Verboom and Spoelstra 1999), and acoustic landmarks for commuting (Schaub and Schnitzler 2007).  
388 Moreover, an increased canopy surface ruggedness may produce particular microclimatic conditions  
389 favourable to a higher abundance of insects (Ulyshen 2011), thus indirectly affecting bat activity.

390 The height of the canopy had an effect on the activity of the LRE guild, as suggested by Dodd  
391 et al. (2012) for lasiurine bats. However, given that *Eptesicus* spp., *Nyctalus* spp. and *Vespertilio*  
392 *murinus*, which comprise the LRE guild, are known to forage or commute over the forests at high  
393 altitudes or in open spaces (Vaughan et al. 1997), detectors placed in high canopies may be more  
394 likely to record their echolocation calls (Müller et al. 2013), potentially introducing a recording bias.  
395 Open space foragers are also more exposed to lower temperatures (e.g. dropping quicker during the  
396 night in the open space than at edges or in the forest interior), which might explain their activity  
397 showing stronger temperature dependence than e.g. the SRE-guild.

#### 398 4.1.2. Bat activity in forest gaps

399           Vegetation height and canopy ruggedness were the main variables influencing LRE, MRE  
400 and *P. pipistrellus* in gaps. Only the SRE guild was influenced by the ground vegetation cover,  
401 probably reflecting the preferences of most *Myotis* species (except *Myotis myotis*; Arlettaz 1996;  
402 Audet 1990) to forage above vegetated ground, e.g. when gleaning prey from leaves. As for the forest  
403 interior, MRE and *P. pipistrellus* showed the same trend: in forest gaps these edge specialist bats  
404 seem to prefer areas with higher vegetation heights. Given that we deliberately excluded heavily  
405 overgrown gaps in our design to maximise detection of bats and to record high quality bat  
406 echolocation calls for optimising bat acoustic identification (Obrist et al. 2004), the vegetation height  
407 may be interpreted in terms of different early stages of forest regeneration. In a recent study, Müller et  
408 al. (2012) demonstrated that the abundance of insect prey eaten by bats is vegetation-dependent, with  
409 higher prey abundance in dense vegetation. This implies that gaps with rapid vegetation succession  
410 may harbour more insects that thrive on the young plants or leaves, thus attracting more bats such as  
411 LRE, MRE and *P. pipistrellus*, which forage in these open forest habitats. Higher insect abundance  
412 may also result from favourable microclimatic conditions and heterogeneity of the vegetation  
413 structure and composition, which provides a great diversity of microhabitats (Bouget and Duelli  
414 2004). The ruggedness of the external vegetation surface is a good proxy for the heterogeneity of the  
415 vegetation in the gaps and is likely associated with the availability and abundance of food.

416

#### 417 **4.2. LiDAR provides unique habitat information**

418           Our results suggest that forest structure derived from LiDAR data provides ecological  
419 information that is complementary if not superior to field vegetation survey data. Although  
420 complementary effects of LiDAR-derived habitat variables in combination with field surveys are  
421 documented for measuring forest bird habitats (Zellweger et al. 2014), the large difference in  
422 ecological relevance we found explaining bat activity was surprising. A potential reason for this may  
423 be related to how habitat is measured and how bats perceive and use forest habitats. Vegetation  
424 surveys in the field normally involve visual inspection from an observer close to the ground. Thus,  
425 several important aspects of the three-dimensional habitat space, such as upper canopy characteristics,

426 may remain concealed due to restricted visibility. LiDAR overcomes this restriction by measuring  
427 forests from a “top-down” perspective, which in many cases is more similar to how bats perceive and  
428 use forest habitats compared to the “bottom-up” view in field surveys. Thus, the high level of detail in  
429 LiDAR data representing canopy characteristics provides novel opportunities to study species-habitat  
430 relationships that were previously not readily available. Furthermore, LiDAR data gathered by the  
431 same instrumentation and survey configuration will have less of an “observer bias” that is commonly  
432 present in field data surveys where multiple people are involved. However, if LiDAR data were  
433 acquired with different settings, the accuracy and precision of the derived variables need to be tested  
434 and compared for the different settings.

435         Compared with datasets from either leaf-on or leaf-off LiDAR surveys, it appears that the  
436 combined leaf-on and leaf-off dataset carried more ecologically relevant information about canopy  
437 architecture and vertical forest structure for studying the activity of bats in mainly deciduous forests.  
438 This was particularly apparent for canopy ruggedness and FHD, and their relatively large effects on  
439 the activity of MRE and *P. pipistrellus*. Although canopy ruggedness frequently occurred in the top  
440 models in the leaf-on model selection (Table S2), it was surprising that its effect was a lot stronger  
441 when derived from combined leaf-on and leaf-off data. While such effects remain to be explored, they  
442 are potentially influenced by the abundance of coniferous trees and the fact that leaf-off data may  
443 contribute essential information about structural elements of the canopy other than foliage, such as  
444 twigs or branches. FHD was best represented in the combined dataset as well, however, its effects on  
445 bat activity were also evident when using the leaf-off data only. This suggests that leaf-off LiDAR  
446 may be superior to leaf-on LiDAR in describing habitat attributes related to the vertical structure in  
447 deciduous forests. As shown by Wasser et al. (2013), this is most likely related to the increased laser  
448 pulse penetration through the canopy during leaf-off conditions, which enhances the detection of  
449 subcanopy vegetation elements affecting the manoeuvrability of bats. As illustrated in Figure 2, the  
450 increased canopy penetration during leaf-off conditions leads to an increased detection of vegetation  
451 elements in the lowest forest strata, which includes tree regeneration and shrubs, both being essential  
452 elements of vertical forest structure. The quality of LiDAR data for ecological applications in  
453 temperate regions thus depends on the time of the year they were acquired. Although we show that

454 combined leaf-on and leaf-off data reveals the greatest potential for LiDAR applications in bat  
455 ecology, our results support the recommendation that with limited budgets, acquiring leaf-off data is  
456 preferable to leaf-on data.

457 **5. CONCLUSIONS AND OUTLOOK**

458           Bat activity is strongly influenced by forest vegetation structure and is also modulated by  
459 species-specific echolocation and flight characteristics. Although our correlative framework hampers  
460 conclusions about the effective drivers of the guild-specific activity patterns, our results support the  
461 assumption that factors related to canopy architecture and vertical forest structure have strong effects  
462 on bat habitat use. These effects can either be direct, e.g. via decreasing manoeuvrability in forest  
463 stands with highly scattered vegetation along the vertical profile, or indirect, e.g. via increased  
464 resource abundance and diversity in stands with a complex canopy architecture. LiDAR remote  
465 sensing provides information on forest structure that is difficult or impossible to collect in the field,  
466 especially across large areas. LiDAR thus substantially improves our abilities to reliably map the  
467 entire 3D habitat space in forests at a relevant grain size, to the benefit of future studies investigating  
468 the ecological relevance of canopy structure. Combined leaf-on and leaf-off data holds more  
469 ecologically relevant structural information than the two individual datasets, and leaf-off appears to be  
470 the preferable choice over leaf-on for limited budgets. With the recent development of new  
471 technologies and techniques such as miniature GPS devices and flight path tracking (Matsuo et al.  
472 2014), extended use of LiDAR technology may push forward frontiers in the field of animal  
473 movement ecology, especially in structurally complex habitats such as forests.

474

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682

684 **Table 1.** Variables describing the vegetation structure of the sites where we investigated bat activity in the forest interior (FI) and in forest gaps (gap).

Variable	Short description	Unit	Source	Plot type
Vegetation layers	Number of vegetation layers according to Keller (2011)	number	Field	FI
Snags	Number of standing dead trees with diameter at breast height > 25 cm	number	Field	FI and gap
Density of trees	Number of trees higher than 5 m per hectare	trees/ha	Field	FI
LAI	Leaf area index estimated from hemispherical photographs using Hemisfer 1.5 (Schleppi et al. 2007, Thimonier et al. 2010)	index	Field	FI
Understory vegetation clutter	Vegetation clutter measured with a profile board (Nudds 1977)	index	Field	FI
Shrub vegetation cover	Visual estimation of shrub vegetation cover, i.e. cover of shrubs and small trees between 1.3 and 5 m in height (Keller 2011)	%	Field	FI and gap
Ground vegetation cover	Visual estimation of ground vegetation below 1.3 m (Keller 2011)	%	Field	FI and gap
Mean vegetation height	Mean of vegetation point cloud	m	LiDAR	FI and gap
Maximum vegetation height	Maximum of vegetation point cloud	m	LiDAR	FI and gap
SD of vegetation height	Standard deviation of vegetation point cloud	m	LiDAR	FI and gap
Proportion of lower vegetation	The number of vegetation points between 1.3 m and 5 m divided by the total number of all vegetation points	%	LiDAR	FI and gap
Canopy cover	The number of vegetation heights above 20 m divided by the total number of all returns, including terrain points (Morsdorf et al. 2006)	%	LiDAR	FI
Mean canopy height	Mean of interpolated outer canopy surface with a pixel size of 0.5 m (see text for details)	m	LiDAR	FI
SD of canopy height	Standard deviation of interpolated outer canopy surface with a pixel size of 0.5 m (see text for details)	m	LiDAR	FI
Canopy ruggedness	Terrain ruggedness index (TRI, Wilson et al. 2007) applied on a 3x3 pixel window of the outer canopy surface with a pixel size of 0.5 m (see text for details)	index	LiDAR	FI and gap



FHD	Foliage height diversity adopted from MacArthur and MacArthur (1961) to measure the degree of scatter of vegetation elements along the vertical forest profile (cf. Clawges et al. 2008) (see text for details)	index	LiDAR	FI
Gap size	Area of gap	m <sup>2</sup>	ArcGIS	gap
Edge structure	Visual classification of gap edge in either open or closed (Hamberg et al. 2009)	index	Field	gap

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686 **Table 2.** Sum of guild- and species-specific bat activity (number of 5 min intervals with  $\geq 1$  bat  
687 sequences) in 32 plots in the forest interior and in the forest gap, respectively. The two detectors in the  
688 forest interior were located at both ground and canopy. SRE: short-range echolocators; MRE: mid-  
689 range echolocators without *P. pipistrellus*; LRE: long-range echolocators.

<b>Taxa</b>	<b>Forest interior (two detectors/site)</b>	<b>Forest gap (one detector/site)</b>
<b>SRE</b>	<b>4,890</b>	<b>1,468</b>
<i>Myotis bechsteinii</i>	5	1
<i>Myotis bechsteinii-brandtii</i>	55	30
<i>Myotis brandtii</i>	59	31
<i>Myotis brandtii-daubentonii</i>	449	162
<i>Myotis brandtii-mystacinus</i>	220	93
<i>Myotis daubentonii</i>	507	156
<i>Myotis daubentonii-emarginatus</i>	63	19
<i>Myotis daubentonii-mystacinus</i>	452	118
<i>Myotis emarginatus</i>	293	43
<i>Myotis emarginatus-brandtii</i>	84	14
<i>Myotis myotis</i>	411	167
<i>Myotis mystacinus</i>	104	19
<i>Myotis mystacinus-emarginatus</i>	209	52
<i>Myotis mystacinus-nattereri</i>	45	11
<i>Myotis nattereri</i>	13	5
<i>Myotis</i> spp.	1,894	535
<i>Plecotus</i> spp.	27	12
<b>MRE</b>	<b>2,885</b>	<b>6,767</b>
<i>Hypsugo savii</i>	3	6
<i>Pipistrellus kuhlii</i>	408	616
<i>Pipistrellus nathusii</i>	890	3,254
<i>Pipistrellus nathusii-kuhlii</i>	312	670
<i>Pipistrellus pipistrellus-nathusii</i>	824	2,118
<i>Pipistrellus pygmaeus</i>	135	24
<i>Pipistrellus pygmaeus-pipistrellus</i>	312	72
<i>Pipistrellus</i> spp.	1	4
<i>Pipistrellus-Hypsugo</i>	0	3

<b>LRE</b>	<b>95</b>	<b>473</b>
<i>Eptesicus</i> spp.	45	183
<i>Eptesicus-Nyctalus</i>	8	41
<i>Eptesicus-Vespertilio</i>	0	7
<i>Eptesicus-Vespertilio-Nyctalus</i>	17	45
<i>Nyctalus leisleri-Vespertilio murinus</i>	0	1
<i>Nyctalus</i> spp.	25	177
<i>Nyctalus-Vespertilio</i>	0	15
<i>Vespertilio murinus</i>	0	4

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690

691

692 **Table 3.** Variables and their relative importance (effect size) represented by the Estimate from GLMMs relating standardized variables of forest vegetation  
693 structure to the activity of different bat guilds and *P. pipistrellus* in the forest interior and the forest gaps. SRE: short-range echolocators; MRE: mid-range  
694 echolocators without *P. pipistrellus*; LRE: long-range echolocators. The results are reported for each of the dataset containing variables recorded in the field  
695 and the respective LiDAR variables (leaf-on, leaf-off and combined).  
696  
697

Model	Variable	Leaf-on				Leaf-off				Combined leaf-on leaf-off			
		Estimate	SE	<i>t</i>	<i>P</i>	Estimate	SE	<i>t</i>	<i>P</i>	Estimate	SE	<i>t</i>	<i>P</i>
<b>Forest interior</b>													
SRE <sup>a</sup>	FHD	-0.18	0.08	-2.36	*	-0.22	0.07	-3.01	**	-0.20	0.07	-2.66	**
	Density of trees	-0.18	0.08	-2.30	*	-0.20	0.08	-2.70	**	-0.19	0.08	-2.47	*
	Temperature	0.02	0.01	1.70	.	0.02	0.01	1.78	.	-	-	-	-
MRE <sup>a</sup>	FHD	-	-	-	-	-0.30	0.14	-2.18	*	-0.42	0.14	-2.94	**
	Canopy ruggedness	-	-	-	-	0.28	0.13	2.13	*	0.48	0.15	3.22	**
	Mean canopy height	0.30	0.15	2.03	*	-	-	-	-	-	-	-	-
	LAI	-0.33	0.15	-2.24	*	-	-	-	-	-	-	-	-
LRE <sup>b</sup>	Mean canopy height	0.72	0.23	3.12	**	0.71	0.24	2.99	**	0.72	0.23	3.11	**
	Temperature	0.11	0.04	2.68	**	0.11	0.04	2.67	**	0.11	0.04	2.68	**
<i>P. pipistrellus</i> <sup>a</sup>	FHD	-	-	-	-	-0.28	0.14	-2.02	*	-0.44	0.14	-3.21	**
	Canopy ruggedness	-	-	-	-	-	-	-	-	0.56	0.14	3.94	***
	LAI	-0.40	0.14	-2.83	**	-0.40	0.14	-3.00	**	-0.37	0.12	-3.02	**
	Temperature	0.05	0.03	1.70	.	0.05	0.03	1.68	.	-	-	-	-
<b>Forest gap</b>													
SRE <sup>a</sup>	Ground vegetation cover	0.19	0.07	2.54	*	0.19	0.07	2.54	*	0.19	0.07	2.54	*

MRE <sup>a</sup>	Mean vegetation height	0.22	0.12	1.88	.	0.29	0.12	2.46	*	0.27	0.12	2.26	*
LRE <sup>b</sup>	Canopy ruggedness	-	-	-	-	-	-	-	-	0.32	0.13	2.37	*
<i>P. pipistrellus</i> <sup>a</sup>	Mean vegetation height	0.31	0.11	2.91	**	0.34	0.10	3.27	**	0.33	0.10	3.21	**

698

699 SE: standard error.

700 <sup>a</sup>GLMMs with a negative binomial distribution.

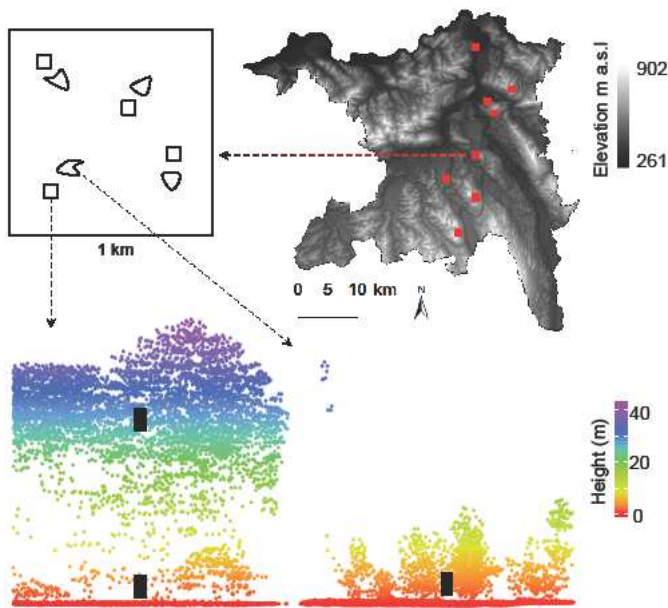
701 <sup>b</sup>GLMMs with a Poisson distribution.

702 .  $P < 0.1$ , \*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$

703 FHD: foliage height diversity; LAI: leaf area index

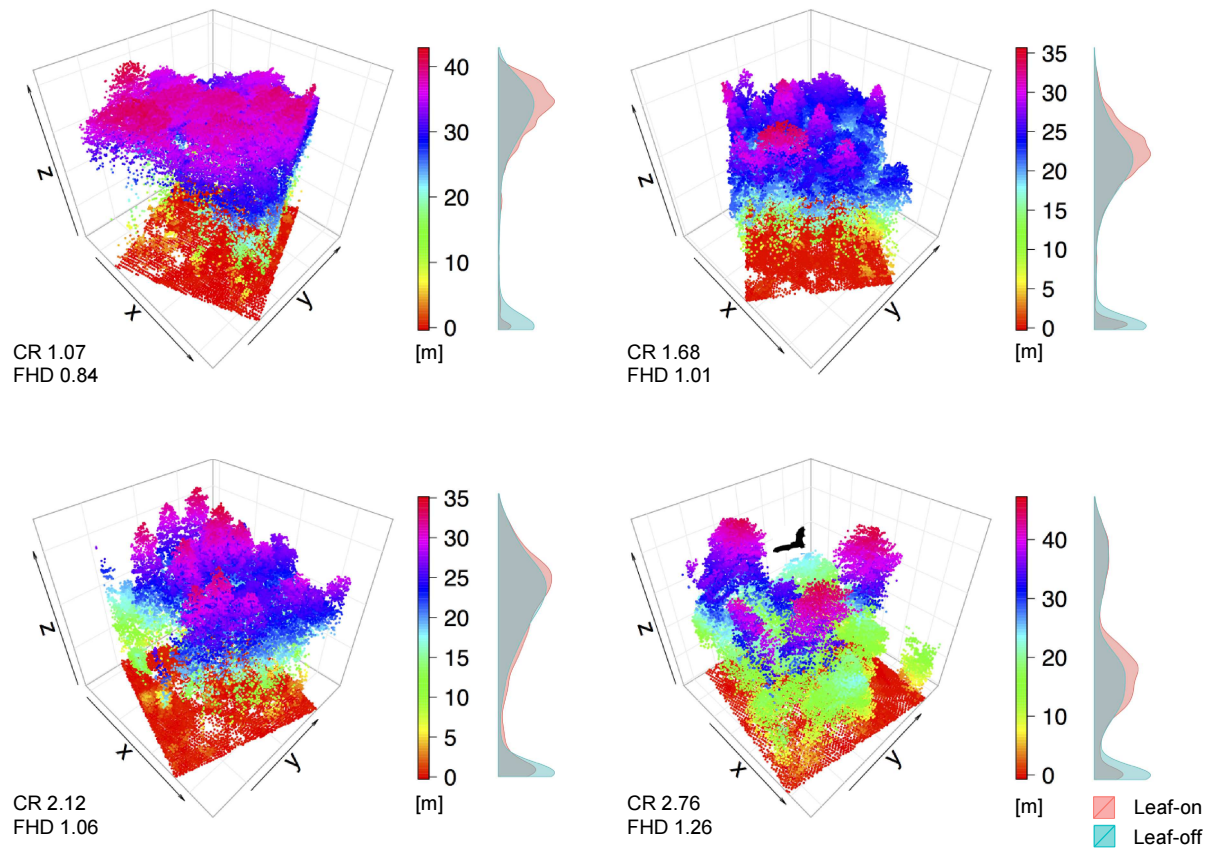
704 **FIGURES**

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706

707 **Fig 1.** Sampling design showing the eight 1-km<sup>2</sup>-sampling squares (red squares) in the elevation  
708 model of the study area (top right). The nested plot design within each km<sup>2</sup> (top left) includes four  
709 plots in the forest interior (small black squares) and the four corresponding gaps (small black  
710 polygons). The bottom figures show normalized LiDAR point clouds representing the forest floor and  
711 the 3D distribution of vegetation elements, as well as the location of the bat loggers (black boxes) in  
712 each plot. We placed two loggers in the forest interior (bottom left) and one in the forest gap (bottom  
713 right).



714

715 **Fig 2.** Normalized LiDAR point clouds from the combined leaf-on and leaf-off dataset for four plots  
 716 along a gradient of canopy ruggedness (CR) and foliage height diversity (FHD). The distribution of  
 717 return heights (in meters) along the vertical profile is shown by vertical density plots for the leaf-on  
 718 and leaf-off datasets separately, using the same scale as for the coloured scale bars.