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1 Research article

2 **Linking acoustic diversity to compositional and configurational heterogeneity**
3 **in mosaic landscapes**

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26

27

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42

43 **Abstract**

44 *Context* There is a long-standing quest in landscape ecology for holistic biodiversity metrics
45 accounting for multi-taxa diversity in heterogeneous habitat mosaics. Passive Acoustic Monitoring of
46 biodiversity may provide integrative indices allowing to investigate how soundscapes are shaped by
47 compositional and configurational heterogeneity of mosaic landscapes.

48 *Objectives* We tested the effects of dominant habitat and landscape heterogeneity on acoustic
49 diversity indices across a large range of mosaic landscapes from two long-term socio-ecological
50 research areas in Occitanie, France and Arizona, USA.

51 *Methods* We assessed acoustic diversity by automated recording for 44 landscapes distributed along
52 gradients of compositional and configurational heterogeneity. We analyzed the responses of six
53 acoustic indices and a composite multiacoustic index to habitat type and multi-scale landscape
54 metrics for three time periods: 24hr-diel cycles, dawns and nights.

55 *Results* Landscape mosaics dominated by permanent grasslands in Occitanie and woodlands in
56 Arizona produced the highest values of acoustic diversity. Moreover, several indices including H, ADI,
57 NDSI, NP and the multiacoustic index consistently responded to edge density in both study regions,
58 but with contrasting patterns, increasing in Occitanie and decreasing in Arizona. Landscape
59 configuration was a key driver of acoustic diversity for diel and nocturnal soundscapes, while dawn
60 soundscapes depended more on landscape composition.

61 *Conclusions* Acoustic diversity correlated more with configurational than compositional
62 heterogeneity in both regions, with contrasting effects explained by the interplay between
63 biogeography and land use history. We suggest that multiple acoustic indices are needed to properly
64 account for complex responses of soundscapes to large-scale habitat heterogeneity in mosaic
65 landscapes.

66

67 *Keywords*

68 Acoustic diversity, Edge density, Landscape heterogeneity, Multiacoustic index, Soundscapes

69

70 **Introduction**

71 Assessing the relative importance of habitat amount and configuration at the landscape level is
72 critical to understand how biodiversity cope with loss and fragmentation of semi-natural land covers
73 worldwide (Fahrig et al. 2011; Fletcher et al. 2018; Betts et al. 2019). Animal diversity is generally
74 considered to increase with habitat heterogeneity in mosaic landscapes (Tews et al. 2004; Fahrig et
75 al. 2011). However, whether species richness or abundance, ecological traits, behavioural parameters
76 or biotic interactions are accounted for when analyzing the responses to heterogeneity often leads to
77 contradictory conclusions (Fletcher et al. 2018; Betts et al. 2019; Semper-Pascual et al. 2021).
78 Furthermore, there are still few studies exploring the potential change in the direction of effects
79 between different biomes and habitats, because sampling biodiversity simultaneously on large
80 geographical gradients without observer biases remains difficult. Recording the sound of biodiversity
81 with autonomous devices is a promising way of limiting such observer biases in large-scale sampling
82 schemes (Ross et al. 2021; Yip et al. 2021). However, few studies to date have investigated how more
83 integrative biodiversity metrics such as multi-species acoustic indices could respond to landscape
84 heterogeneity at wider scales (but see Fuller et al. 2015; Dein and Rüdiger 2020; Dooley and Brown
85 2020).

86 Acoustic diversity is a major component of biodiversity which can be investigated at the landscape
87 level in the framework of soundscape ecology (Krause 2008; Pijanowski et al. 2011) and ecoacoustics
88 (Sueur and Farina 2015). It can be defined as a greater complexity of sounds in a given soundscape
89 and measured through either a higher number of occupied frequency bands, greater levels of
90 acoustic activity or sound energy, or more biophony, geophony and anthrophony intertwined (Sueur
91 et al. 2014). Acoustic diversity can therefore account for multiple biotic interactions and species
92 coexistence through the acoustic niche hypothesis (Farina et al. 2011; Azar and Bell 2016). Its large-
93 scale assessment has been strengthened in the recent years according to rapid technological
94 developments in Passive Acoustic Monitoring (Bradfer-Lawrence et al. 2019; Gibb et al. 2019; Sugai

95 et al. 2020; Wood et al. 2021). Passive Acoustic Monitoring (PAM) provides a holistic picture of
96 biodiversity through the recording and analysis of intricate patterns of sound, especially at larger
97 spatial scales (Krause 2008; Drake et al. 2021; Ross et al. 2021; Yip et al. 2021). Not only biodiversity -
98 notably breeding bird -surveys will benefit from the large-scale deployment of automated recorders,
99 but this will give more insights on how bird song attractiveness is connected to human well-being
100 and will help considering soundscape conservation as a cultural value (Ferraro et al. 2020; Barbaro et
101 al. 2021; Morrison et al. 2021).

102 Land use gradients and edge effects between adjacent habitats are expected to change the
103 interactions among soundscape components (Pijanowski et al. 2011), which can be captured by using
104 a large range of complementary indices of acoustic activity and diversity (Sueur et al. 2014; Buxton et
105 al. 2018; Bradfer-Lawrence et al. 2020). Such indices are not only useful for overall biodiversity
106 assessment (Gibb et al. 2019), they also allow tracking the spatio-temporal dynamics of multi-taxa
107 acoustic communities and how they respond to, or interact with, sound-producing human activities
108 (Fairbrass et al. 2017; Eldridge et al. 2018). Using a large range of acoustic metrics is considered
109 necessary because of their complementary performance and sensitivity to different sonic conditions
110 of background sound (Sueur et al. 2014; Ross et al. 2021). These indices are thus expected to respond
111 differently along habitat and landscape gradients (Fuller et al. 2015; Grant and Samways 2016)
112 because they reflect different facets of acoustic diversity, acoustic species richness and community
113 structure (Gasc et al. 2015; Machado et al. 2017; Eldridge et al. 2018).

114 Despite the study of spatial heterogeneity in sounds being one of the main objectives of soundscape
115 ecology (Pijanowski et al. 2011; Bormpoudakis et al. 2013), the relationships between acoustic
116 indices and landscape metrics are still unclear. Among landscape metrics measuring compositional
117 and configurational heterogeneity, only patch-scale fragmentation effects (i.e., their size and
118 connectivity) on acoustic diversity have been investigated to date (Tucker et al. 2014; Fuller et al.
119 2015; Dixon et al. 2020; Müller et al. 2020). The effect of land use intensity has been explored more

120 extensively (Joo et al. 2011; Dein and Rüdiger 2020; Dooley and Brown 2020; Dröge et al. 2021;
121 Shamon et al. 2021), yet few studies have attempted to compare the response of acoustic indices to
122 a large range of landscape structures measured at several spatial scales in different biomes.

123 Investigating the acoustic diversity of mosaic landscapes using standard recording devices and
124 sampling schemes is now easier, for example to compare the relative effects of habitat composition
125 and configuration on multi-taxa biodiversity metrics based on replicated acoustic sampling across
126 wide landscape gradients. Soundscape ecology may also contribute to both the Several Small Or
127 Single Large habitat patches (SLOSS) and land sharing vs land sparing debates, by providing
128 meaningful insights on the coexistence between biodiversity and human activities in heterogeneous
129 habitat mosaics (Fahrig 2020; Grass et al. 2021).

130 Here, we aimed at analyzing the relationships between acoustic diversity and landscape
131 compositional and configurational heterogeneity in two biogeographically contrasted areas with
132 different land use histories, in Occitanie, France and Arizona, USA. Both study regions were located
133 within long-term socio-ecological research areas (Zone Atelier Pyrénées Garonne, Occitanie,
134 France and Observatoire Hommes Milieux Pima County, Arizona, USA) holding large amounts of
135 semi-natural habitats of high importance for biodiversity conservation (Felger and Wilson 1995;
136 Gaüzère et al. 2020). These habitats included woodlands, permanent grasslands, scrublands and
137 semi-deserts, all hosting species-rich acoustic bird, mammal and insect communities, and where
138 human-driven processes of land management were predominant (urban, agriculture and forestry).
139 We selected these two contrasting study regions to build on local long-term biodiversity and land use
140 change surveys, and in order to (i) test whether acoustic indices showed consistent responses to the
141 same set of landscape metrics applied to mosaic landscapes mixing anthropized and natural habitats
142 in different bioclimatic contexts, and (ii) to challenge the generality of these relationships between
143 AIs and landscape heterogeneity across study regions that have experienced different historical rates
144 of human disturbance (Betts et al. 2019).

145 We specifically tested the response of six acoustic indices (BI, H, ACI, ADI, NDSI and NP) and their
146 combination into a new multiacoustic index summing their scaled values for three different time
147 periods (24hr-diel cycles, dawns and nights) to (i) the dominant habitat type of the landscape mosaic
148 where the recorder was installed; and (ii) the compositional and configurational heterogeneity of the
149 surrounding landscapes measured at increasing buffer scales. We predicted contrasting responses of
150 AIs to landscape composition and configuration in the two regions in accordance with distinct land
151 use histories, and an increase in the diversity of multi-taxa acoustic communities with the amount of
152 semi-natural habitats at both local and landscape scales.

153

154 **Methods**

155 **Study areas**

156 The first study region is the Aurignac county, located between the Garonne and Gers rivers in
157 Occitanie, south-western France (43°12'58.1"N; 0°52'51.4"E). The area is part of the European
158 network of Long-Term Ecological Research sites (<https://www.lter-europe.net>) as 'Zone Atelier
159 Pyrénées Garonne' (<http://www.za-inee.org/fr/reseau>). Elevation ranges from 200m to 400m asl,
160 with an Atlantic sub-climate subject to Mediterranean influences. The main habitat types include
161 farmland, meadows, grasslands, scrubland, hedgerows and oak woodlands (Fig. 1a). In that area, we
162 acoustically sampled 30 sites of comparable sizes located along a landscape gradient spanning from
163 only agricultural to large woodlands through mosaics mixing crops, grasslands and forests, as
164 follows : farmlands (n = 5), mixed farmland-grassland mosaics (n = 10), permanent grasslands (n = 9)
165 and woodlands (n = 6).

166 The second study region is located in the Pima county, southern Arizona, USA, within the Man-
167 Environment Observatory OHMi (<https://ohmi-pima-county.in2p3.fr/en>) around the city of Tucson
168 (32°12'17.2"N; 110°57'45.2"W) and in the Santa Rita range north of Patagonia (31°32'25.4"N
169 110°45'18.2"W), close to the Mexican border (Fig. 1b). Elevation spans between 800 and 1800 m asl

170 and climate is semi-arid with summer monsoon, with an Alpine influence at higher altitudes. We
171 sampled 14 sites on a landscape gradient ranging from periurban areas mixing gardens and deserts-
172 scrubland patches to saguaro and mesquite deserts, and higher-elevation grasslands and forests, as
173 follows : periurban gardens (n = 4), saguaro deserts (n = 4), mesquite deserts (n = 3) and mountain
174 oak-pine-aspen woodlands (n = 3).

175

176 **Sound recording methods and sampling scheme**

177 The same standard recording methods were used in both Occitanie and Arizona to allow
178 reproducible and comparable recordings and analyses. We used a total of six identical SoundMeter4
179 devices (SM4, Wildlife Acoustics, Inc., Maynard, Massachusetts, USA), with a minimal distance
180 between two adjacent recorders of 1 km. We recorded with the two internal omnidirectional
181 microphones at a sample rate of 24 kHz to capture overall sound activity within the human audible
182 range, and used only recordings from the left channel to compute acoustic indices (Gasc et al. 2018).
183 A discontinuous recording schedule was set to record 30 minute per hour (30 min on / 30 min off)
184 during a continuous time period of several 24-hr diel periods in a row for each site (Burivalova et al.
185 2018). We used relatively short recording periods compared to the ones conducted in tropical
186 biomes, to allow sampling the acoustic diversity of multiple sites by rotating the recorders across the
187 landscape (Sugai et al. 2020; Cifuentes et al. 2021), while still being within the peak seasonal period
188 of breeding bird vocal activity in both study regions.

189 In Occitanie, devices were installed between 21st of April and 19th of June in spring 2019, 2020 and
190 2021, and in Arizona, between 10th April and 18th of June in spring 2018 and 2019. These recording
191 time periods encompassed the local peaks in songbird choruses during the core of breeding season in
192 each study area, but also in amphibian choruses at dusk and night and in vocalizing mammal activity
193 (e.g., roe deer *Capreolus capreolus* in Occitanie or coyotes *Canis latrans* in Arizona) as well as the
194 beginning of the period of acoustically active insects such as orthopterans or cicadas (Grant and

195 Samways 2016; Gasc et al. 2018). The period also matches a peak in agricultural activities, especially
196 in Occitanie, that results in typical rural soundscapes of low-intensity farming mixing crops,
197 permanent grasslands and pastures, all producing significant anthrophony intertwined with local
198 biophony. Such a recording time period is therefore relevant to capture diel patterns of multi-species
199 acoustic activity and overall sound diversity in mosaic landscapes of temperate and semi-arid biomes
200 (Depraetere et al. 2012; Gasc et al. 2018; Müller et al. 2020). Compared to tropical biomes, temperate
201 and semi-arid bioclimates show more seasonality and diel variation in temperature, so that acoustic
202 activity peaks in spring or summer periods, contrarily to what is observed in tropical biomes (Joo et
203 al. 2011; Eldridge et al. 2018; Bateman et al. 2021). High seasonality also implies that intra-day
204 acoustic activity varies more than between several consecutive days, pointing out the importance of
205 analyzing dawn and nocturnal soundscapes separately. We also made careful attention not to record
206 during periods of high geophony (heavy rain or wind), or to discard recordings obtained during bad
207 weather periods (Fairbrass et al. 2017; Ross et al. 2021).

208

209 **Acoustic diversity indices**

210 We obtained 1,251 recordings of 30 min wav files totalling 625.5 hr that were further cut down in
211 37,530 one-minute samples for acoustic analyses (Towsey et al. 2014). For each one-minute sample,
212 we calculated 10 acoustic indices (Table 1) as follows: Acoustic Complexity Index ACI ; Acoustic
213 Diversity Index ADI ; Acoustic Evenness Index AEI; Bioacoustic Index BI ; temporal, spectral and total
214 acoustic entropy Ht, Hf and H ; median of amplitude envelope M ; Normalised Difference Sound
215 Index NDSI and Number of frequency Peaks NP (Sueur et al. 2014; Bradfer-Lawrence et al. 2019)
216 using *soundecology* version 1.3.3 (Villanueva-Rivera and Pijanowski 2014) and *seewave* version 2.1.6
217 R-packages (Sueur et al. 2008) and a R-script from A.G. available in GitHub
218 (<https://github.com/agasc/Soundscape-analysis-with-R>). We used the default parameters available
219 for each index for all calculations (Machado et al. 2017). We calculated the means and medians of

220 the 10 AIs for three complementary time periods (Dröge et al. 2021): 24hr-diel cycles (720 one-
221 minute periods from 00.00 am to 23.30 pm per site), dawns (120 one-minute periods from 6.00 am
222 to 9.30 am) and nights (240 one-minute periods from 22.00 pm to 05.30 am). We selected these time
223 periods because they are biologically relevant (Metcalf et al. 2021), while also capturing substantial
224 sound-producing human activities. Dawns are the peak periods for quantifying multi-species songbird
225 vocalizations (i.e., morning choruses) and nocturnal acoustic surveys are especially relevant for
226 amphibian or insect sound diversity, while diel cycles of 24 hours summarize all possible patterns of
227 acoustic activity and account for all possible sound sources in a given day (Tucker et al. 2014; Grant
228 and Samways 2016; Dröge et al. 2021).

229 We discarded four indices that were highly redundant with others by construction (Hf, Ht and M with
230 H, and AEI with ADI; see Villanueva-Rivera et al. 2011 and Sueur et al. 2014) and further analyzed the
231 responses of six remaining AIs (see below). High and low values of these AIs indicate high and low
232 acoustic diversity levels, respectively, as illustrated by example sonograms (Fig. 2). We also
233 computed for each time period a new index combining the scaled median values of these six indices
234 into a multiacoustic index in order to summarize the response of acoustic diversity to landscape
235 metrics (Gasc et al. 2015; Buxton et al. 2018), as follows:

$$236 \textit{Multiacoustic index} = \Sigma (\textit{scaled BI} + \textit{scaled H} + \textit{scaled ACI} + \textit{scaled ADI} + \textit{scaled NDSI} + \textit{scaled NP})$$

237 We constructed our index in a way to be as simple as possible both in terms of calculation and
238 computation, while giving the same weight to all AIs regardless of their absolute values, variation of
239 magnitude and direction of response patterns. We therefore used the sum of the scaled median
240 values, as used for example in the multidiversity index of Allan et al. (2014). Scaling the values of all
241 AIs allowed both their direct comparisons and their combination into a single index designed to
242 capture the dominant patterns in acoustic activity and diversity across all sites and time periods
243 sampled, as well as their response to habitat type and landscape metrics. We used the generic 'scale'
244 function in R which centers all values by the mean and scales them by dividing the values by standard

245 deviation. We further tested for other scaling options, such as the maximum values (Allan et al. 2014)
246 and we tested its sensitivity to the sequential removing of AIs. We also computed intra-set
247 correlations to check that the multiacoustic index was positively correlated with all six AIs in all sites
248 and time periods (Appendix S1).

249

250 **Landscape metrics**

251 Landscape metrics were computed from GIS mapping (ArcGIS 10.6, ESRI, Redlands, CA, USA) using
252 online available land cover databases of OSO2018 at 10 m of pixel spatial resolution for France
253 (<http://osr-cesbio.ups-tlse.fr/oso>) and North American Land Cover 2015 at 30m of pixel spatial
254 resolution for Arizona, USA (<https://www.mrlc.gov/data>). The same four metrics were calculated in
255 circular buffers of 250, 500, 1000, 2500m and 5000m-radii around recorders in both study regions, as
256 follows : two metrics of habitat composition, i.e., the covers of woodlands and urban areas; and two
257 standardized metrics of landscape compositional and configurational heterogeneity, namely Shannon
258 habitat diversity and total edge density (Fahrig et al. 2011), using Fragstats software version 4.2
259 (<https://www.umass.edu/landeco/research/fragstats>).

260 These buffer scales were selected because they were biologically meaningful for most vocalizing taxa
261 recorded regarding habitat selection, daily movements and dispersal ecology, for birds, mammals
262 and insects (Paradis et al. 1998; Holland et al. 2004; Laforge et al. 2021). They have also proven
263 relevant for soundscape assessment in previous studies and were compatible with the resolution of
264 land cover maps from both areas (Dein and Rüdissler 2020). While most previous soundscape studies
265 have generally focused on finer landscape scales (typically 500m; see Fuller et al. 2015), we included
266 also larger buffer scales because we attempted to question the effect of landscape matrix
267 composition and configuration on AIs at larger scales than previously investigated. Using five
268 distance radii allowed us testing for the scale of effect (Holland et al. 2004) by building correlation
269 matrices between the two best performing landscape metrics and AIs diel values for the two study

270 regions (Appendix S2). As we used GIS land cover data with different pixel resolutions between the
271 two study regions (10 m for France and 30 m for USA), we also checked that resampling the region
272 with finer resolution of 10 m (France) at the coarser resolution of 30 m did not affect the values of
273 the two main landscape predictors (Appendix S3).

274

275 **Data analysis**

276 Median and mean AIs were calculated for each three recording time scales (24hr-diel cycles, dawns
277 and nights). We systematically found during exploratory analyses that median values performed
278 better than means, likely because they are non-parametric and less sensitive to extreme values, as
279 shown by other studies (Eldridge et al. 2018; Bradfer-Lawrence et al. 2019; Dröge et al. 2021). We
280 therefore used medians of each index values across three time periods as response metrics of
281 soundscape acoustic diversity. To avoid collinearity in response metrics, we discarded four indices
282 that were highly redundant from further analyses (Ht, Hf, M and AEI) and modelled the responses of
283 the six remaining indices (BI, ACI, NDSI, ADI and NP) and the multiacoustic index. We also conducted
284 preliminary analyses to reduce collinearity among landscape predictors and test the predictive
285 efficiency of the same landscape metrics measured at five different scales, at 250, 500, 1000, 2500
286 and 5000 m-radii around recorders. We found that 2500 m was the best trade-off scale to optimize
287 correlations between AIs and landscape metrics for both study regions (Appendix S2). Moreover, the
288 same metrics had significant effects at all scales and their directions were consistent across scales,
289 especially edge density and woodland cover (Appendix S2). We therefore used further only the 2500
290 m scale for modelling AIs responses to habitat type and landscape metrics.

291 To compare their responses to the same set of predictors, we built a full model with identical
292 structure for all six AIs and multiacoustic index in the two areas for the three recording time periods
293 (24hr-diel cycles, dawns and nights) leading to six models for each AIs. We performed Linear Mixed
294 Models (LMMs) using Gaussian family models in glmmTMB R-package (Brooks 2020) with recording

295 year as random factor. Als such as NDSI and H have bounded scales and were therefore logit-
296 transformed before modelling. We first tested the separate effect of dominant habitat type on the
297 Als median values. Habitat type was defined as a fixed factor with four categories in each study
298 region, i.e., farmland, grassland, mixed farmland-grassland and woodland for Occitanie and
299 periurban gardens, mesquite, saguaro desert and woodland for Arizona. Post-hoc Tukey tests were
300 applied with the Kenward-Roger method to adjust for multiple comparisons.

301 In a second step, we modelled the responses of the six median Als and the multiaoustic index to the
302 same four landscape metrics, measured at 2500 m around recorders, which were included in the full
303 model as four scaled fixed predictors as follows: (i) woodland cover, (ii) urban area cover, (iii) edge
304 density and (iv) landscape-scale Shannon's habitat diversity. To fit the responses of Als to landscape
305 predictors irrespective of dominant habitat type, we added to these full models a second random
306 habitat effect in addition to the year effect. We performed automatic backward selection from the
307 full model using step function in lmerTest R-package to drop out non-significant predictors by
308 stepwise elimination using AICc and considered the final best model for each response variable
309 (Kuznetsova et al. 2017). We computed marginal and conditional R^2 of significant predictors for each
310 best model to account for variances explained by fixed effects and fixed and random effects, using
311 MuMin R package (Barton 2020). We checked all LMMs residuals for normality, homoscedasticity and
312 the absence of spatial autocorrelation. Prediction plots were obtained with ggplot2 R-package
313 (Wickham 2016) using 100 bootstrap iterations.

314

315 **Results**

316 **Effect of habitat type on acoustic diversity**

317 In Occitanie, the effect of dominant habitat type was significant on 24h-diel medians for ACI, ADI, NP
318 and multiaoustic index (Fig. 3 and Appendix S4). Post-hoc tests performed after LMMs indicated
319 that grasslands had significantly higher ADI, NP and multiaoustic index than farmlands and higher

320 ACI than woodlands (see Appendix S4). For dawns, we found significantly higher BI in grasslands and
321 woodlands than farmlands, higher ADI and multiacoustic index in grasslands than farmlands and
322 mixed farmlands, and higher ACI in grasslands than woodlands (Fig. 3). Nocturnal values of ACI, NP
323 and multiacoustic index were also significantly higher in grasslands than farmlands and woodlands
324 (Appendix S4).

325 In Arizona, woodlands displayed significant greater H, ADI and multiacoustic index for 24hr-diel
326 cycles than periurban areas, mesquite and saguaro deserts (Fig. 4 and Appendix S4), while other Als
327 did not significantly differ between habitats. For dawns, BI was significantly higher in periurban
328 gardens than in saguaro deserts while, in contrast, H was significantly higher in woodlands and
329 saguaro deserts compared to gardens (Fig. 4). For nocturnal soundscapes, H and multiacoustic index
330 were significantly higher in woodlands than in mesquite (Appendix S4).

331

332 **Effect of landscape metrics on acoustic diversity**

333 In Occitanie, edge density at 2500 m around recorders was the best predictor of acoustic indices,
334 having a positive effect on median values for ADI, NDSI, NP and multiacoustic index during 24hr-diel
335 cycles (see Table 2, Appendix S5 and Fig. 5 for the most significant biplots). Woodland cover at 2500
336 m was the only other significant predictor, with a negative effect on ACI. No landscape metrics were
337 significantly correlated to BI and H. For dawns, H and multiacoustic index were positively correlated
338 to edge density, while woodland cover had positive effects on H and negative effects on ACI and NP
339 (Table 2 and Fig. 6). No landscape metrics were correlated with BI, ADI or NDSI. For nocturnal
340 soundscapes, edge density was also the best predictor and was positively correlated to ACI, ADI,
341 NDSI, NP and multiacoustic index (Table 2 and Fig. 6). In addition, woodland cover had reverse
342 effects on H and ACI, respectively positive and negative.

343 For 24hr-diel cycles in Arizona, we found significant negative effects of edge density at 2500 m on
344 ADI, NDSI and multiacoustic index (Table 2; see Fig. 7 for significant biplots). Woodland cover at 2500

345 m had a positive effect on H while NP decreased with landscape diversity. For dawns, woodland
346 cover had a positive effect on BI and multiacoustic index, edge density had a negative effect on H and
347 urban cover a negative effect on NDSI (Table 2). No predictors were significant for ACI, ADI and NP.
348 Finally, woodland cover positively affected H and edge density negatively affected ADI, NDSI and
349 multiacoustic index for nocturnal soundscapes (Table 2).

350 In Occitanie, random effects of year and habitat measured by the difference between marginal and
351 conditional effects are ca 15-20% of additional variance explained for diel periods for all AIs except
352 NDSI (Table 2). For dawns, the random effects became negligible except for the multiacoustic index,
353 while for nights it was variable, depending on the AI considered, from 0% for H and NDSI to 29% for
354 the multiacoustic index. In Arizona, the additional variance explained by the random effects of year
355 and habitat is also variable for diel periods and dawns, ranging between 0 for NDSI to 46% for BI, and
356 became negligible for nocturnal soundscapes (Table 2).

357

358 **Discussion**

359 Our aim was to assess how median values of six complementary acoustic indices and a composite
360 multiacoustic index computed for three recording periods could be modelled by landscape
361 composition and configuration metrics at large spatial scales in two contrasting regions. We found
362 that (i) permanent grasslands in Occitanie and woodlands in Arizona produced the highest acoustic
363 diversity (i.e., the highest diversity of sounds across frequency bands, see Fig. 2), and that (ii) edge
364 density at 2500 m around recorders was the best predictor of acoustic indices in both Occitanie and
365 Arizona, but with contrasting patterns. In Occitanie, median values for all AIs except H and BI
366 increased with landscape configurational heterogeneity in all time periods and spatial scales, while
367 they decreased with landscape heterogeneity in Arizona (Appendix S2). Consistently with the local
368 habitat effect, BI, H, ADI and multiacoustic index increased with woodland cover and NDSI decreased
369 with urban cover in Arizona, while all AIs except H tended to decrease with woodland cover in

370 Occitanie. Overall, surrounding landscape composition (i.e., individual land cover types) had weaker
371 effects on acoustic diversity than landscape configurational heterogeneity (i.e., edge density) in both
372 study areas, especially for diel and nocturnal soundscapes.

373

374 **Effect of habitat type on acoustic diversity**

375 One key assumption of soundscape ecology is that ambient sound is not only spatially heterogeneous
376 by nature, but that it directly relates to habitat type and structure, and therefore produces distinct
377 habitat-specific acoustic signatures (Bormpoudakis et al. 2013; Grant and Samways 2016). These
378 signatures are not only linked to habitat structure but indirectly reflect habitat-specific composition
379 of multi-species acoustic communities (Merchant et al. 2015), which can only be accounted for by
380 the computation of multiple AIs (Eldridge et al. 2018). In forests, vegetation structure influences
381 directly acoustic diversity, which peaks in higher-complexity habitats, such as old-growth tree
382 patches (Machado et al. 2017; Müller et al. 2020). Most AIs are expected to increase with vegetation
383 complexity, i.e., local habitat heterogeneity, including ADI, NDSI, ACI, BI, AEI and H (Myers et al.
384 2019; Dröge et al. 2021; Shamon et al. 2021). However, we found that higher-complexity habitats
385 with greater vegetation heterogeneity (woodlands and shrublands) supported the highest acoustic
386 diversity in Arizona, but not in Occitanie where permanent grasslands were on the contrary the
387 acoustically-richer habitats. This is in support of temperate semi-natural grasslands supporting high
388 biodiversity of vocal taxa (birds, mammals, anurans and orthopterans), while it also means that
389 landscape-level habitat structure has a mitigating effect on acoustic activity in local habitats.

390 In accordance with other studies indicating that more intensively managed or disturbed habitats had
391 lower acoustic diversity (Burivalova et al. 2018; Gasc et al. 2018; Myers et al. 2019), we found less
392 diverse soundscapes in landscapes dominated by homogeneous farmland with low edge density than
393 in more complex mosaics of high edge density mixing crops, hedgerows and grasslands in Occitanie.
394 Surprisingly, we found that periurban gardens had high bioacoustic activity measured by BI in Arizona

395 while NDSI or H were low in the same sites, which may be an indication of high acoustic coexistence
396 between anthrophony and biophony (Sueur et al. 2008; Carruthers-Jones et al. 2019). In southern
397 Arizona, the extensive use of bird feeders and the low urban density allow gardens to support
398 species-rich urban bird communities, including several hummingbird species (Trochilidae) whose
399 buzzes produce acoustic signals that are typical components of garden soundscapes in semi-arid
400 regions (Emlen 1974; McCaffrey and Wethington 2008; see Appendix S6).

401 We also found a significant variation in Als among habitat types between the different recording
402 periods considered, pointing out the usefulness of investigating dawn and nocturnal soundscapes
403 separately. For example, there was higher acoustic diversity at night in semi-natural permanent
404 grasslands, shrublands and saguaro deserts due to insect sounds as well as to intense activity of
405 nocturnal birds and mammals (Gasc et al. 2015; Grant and Samways 2016). Nocturnal soundscapes of
406 semi-natural permanent grasslands or saguaro deserts are particularly important to quantify because
407 of their importance for diel rhythms in activity for many taxa of high conservation interest and/or
408 more sensitive to human disturbance (e.g., bats, terrestrial mammals, amphibians, nocturnal birds,
409 bush-crickets) while also constituting a key issue in soundscape management (Dumyahn and
410 Pijanowski 2011). Grassland soundscapes are less well-known and studied than forest soundscapes
411 but appears as contributing significantly to acoustic diversity at the landscape scale and their
412 importance for biodiversity conservation is increasingly acknowledged (Shamon et al. 2021). As dawn
413 choruses are important to songbird fitness and long-term survival and are regulated by coexisting
414 acoustic niches of vocalizing passerines (Duquette et al. 2021), it is interesting to note that we found
415 a positive effect of woodland cover on dawn acoustic diversity in Arizona, irrespective of landscape
416 configuration. The importance of riparian woodlands under semi-arid climate to sustain bird diversity
417 has been also pointed out by other bioacoustic studies in the same area (Bateman et al. 2021). These
418 results tend to support the idea that even small patches of semi-natural habitats sustain significant
419 songbird activity and are highly beneficial to both bird conservation and function in fragmented
420 landscapes (Barbaro et al. 2014; Müller et al. 2020).

421

422 **Effect of landscape heterogeneity on acoustic diversity**

423 A second key assumption of soundscape ecology is that acoustic diversity is also driven by the spatial
424 heterogeneity of habitats at larger scales (Bormpoudakis et al. 2013). However, soundscape
425 ecologists have rarely attempted to directly relate AIs to landscape metrics of compositional and
426 configurational heterogeneity, especially at wider scales (but see Fuller et al. 2015 and Dixon et al.
427 2020), while patch-scale fragmentation has been consistently proven detrimental to acoustic activity
428 and diversity in various biomes (Tucker et al. 2014; Burivalova et al. 2018; Müller et al. 2020). To
429 date, landscape-scale fragmentation effects on acoustic diversity are still virtually unexplored,
430 although they likely constitute key drivers of all bio-, geo- and anthrophony components of
431 soundscapes in various field conditions (Krause 2008; Pijanowski et al. 2011), as expected by
432 landscape ecology theory (Fahrig et al. 2011). Another key question rarely investigated to date is the
433 grain (i.e., its spatial extent) of the soundscape mosaic (Sueur and Farina 2015), as well as the ‘best
434 scale’ for landscape effects on acoustic diversity (Holland et al. 2004).

435 Here, we show that acoustic diversity is primarily driven by landscape configurational heterogeneity
436 at large scale (i.e., edge density at 2500m around recorders), and that the direction of the effect
437 reverses between temperate and semi-arid biomes. Such a positive or negative effect of edge density
438 on acoustic diversity likely depends on surrounding matrix composition (Barbaro et al. 2021), socio-
439 ecological legacy of mosaic soundscapes and their historical habitat uses (Semper-Pascual et al.
440 2021), as well as the evolutionary responses of vocalizing species to long-term experienced
441 disturbances and ambient noise (Paton et al. 2012; Duquette et al. 2021). Our results confirm
442 previous findings of soundscape studies, such as a large scale of effect of landscape metrics on
443 acoustic diversity (well above 1000m around recorders), the predominance of landscape over local
444 habitat effects, as well as the effect of individual land cover classes on acoustic diversity (Dein and
445 Rüdissler 2020; Dixon et al. 2020). We also found that, together with our multiacoustic index, H, ADI,

446 NP and NDSI were the AIs performing best to relate overall soundscape diversity to landscape
447 configuration in two contrasting study regions and across a large range of acoustic habitats (Fuller et
448 al. 2015; Ross et al. 2021; Shamon et al. 2021). As a ratio measuring the relative dominance of
449 biophony or anthrophony, NDSI is also best to capture the effect of urbanization on soundscapes at
450 large spatial scales (Fairbrass et al. 2017; Machado et al. 2017; Doser et al. 2020).

451

452 **Monitoring acoustic diversity in mosaic landscapes**

453 Our study follows previous recommendations in Passive Acoustic Monitoring and soundscape
454 assessment methodology that rotating recorders across the landscape is the most cost-efficient
455 design for the best trade-off in sound data acquisition at larger spatial and temporal scales (Sugai et
456 al. 2020; Drake et al. 2021), while keeping the volume of data storage under a reasonable threshold
457 (Cifuentes et al. 2021; Wood et al. 2021). While in tropical forest biomes, the minimal recording time
458 period required to stabilize the variance in acoustic indices across time for a given site is ca 120hr
459 (Bradfer-Lawrence et al. 2019), in temperate and semi-arid biomes where intra-day variation is often
460 higher than inter-day variation due to higher seasonality in acoustic activity (Gasc et al. 2018),
461 continuous recording across 24-48hr is generally accurate if the relevant season is targeted for
462 surveys (Metcalf et al. 2021). Here, we targeted spring to account for peaks in both breeding
463 songbird, mammal and insect acoustic activity.

464 A second requirement for an adequate soundscape assessment is the computation of multiple AIs to
465 capture the variability of sounds from different biophonic, geophonic or anthrophonic sources across
466 sites and time periods. While several indices are needed to reveal diel and seasonal soundscape
467 patterns (Bradfer-Lawrence et al. 2019), AIs have been shown to be often weakly correlated to
468 biophony assessed independently because of signal masking by non-target sounds (Fairbrass et al.
469 2017; Metcalf et al. 2021). Moreover, a combination of indices is generally required to successfully
470 predict biodiversity values (Towsey et al. 2014; Buxton et al. 2018; Yip et al. 2021). Here, we

471 modelled the responses of six AIs that are increasingly used as a standard analysis path to
472 characterize spatial or temporal changes in acoustic biodiversity (Sueur et al. 2014; Bradfer-Lawrence
473 et al. 2020). As most previous studies, we found limited congruence among metrics, but
474 complementary patterns in soundscape characterization for each suite of indices (Fuller et al. 2015;
475 Eldridge et al. 2018; Ross et al. 2021), while using a multiacoustic index helped summarizing the
476 dominant response of acoustic diversity to landscape heterogeneity.

477

478 **Relative performance of acoustic indices in complex soundscapes**

479 We found that correlative patterns in AIs were remarkably similar across study regions and time
480 periods. Our results support previous findings that ADI, H and NDSI are especially suitable at
481 predicting acoustic diversity across different habitats under various ambient sound conditions,
482 possibly because they reflect better the intertwining of biophony and anthrophony in complex
483 soundscapes (Fuller et al. 2015; Machado et al. 2017; Ross et al. 2021). Moreover, NDSI also tended
484 to better account for diel acoustic patterns while H and ADI seemed more efficient at characterizing
485 nocturnal soundscapes often dominated by pure tone signals such as owl calls, insect stridulations or
486 amphibian choirs (Gasc et al. 2015; Ross et al. 2021). In our study, H and NDSI were the two indices
487 that responded significantly to both local habitat and landscape metrics for all recording periods in
488 the two study regions. As pointed out by several authors, NDSI is designed to capture daily shifts
489 between dominant anthrophony and biophony while diversity-based indices such as H or ADI
490 incorporate anthrophony levels into biophonic soundscapes to produce high diversity values (Fuller
491 et al. 2015; Eldridge et al. 2018; Ross et al. 2021). By contrast, BI, NP and ACI are designed to capture
492 biophony and to be less sensitive to anthrophonic noise (Gasc et al. 2015). However, ACI does not
493 account for constant sound signal produced by many arthropods (Pieretti et al. 2011; Gasc et al.
494 2015; Fairbrass et al. 2017) and can therefore display inverse responses to habitat heterogeneity and
495 bird diversity, especially in grasslands (Shamon et al. 2021). While most AIs can be potentially biased

496 by high road traffic noise in urban habitats, ACI was specifically developed to be impervious to
497 constant sound (Pieretti et al. 2011; Fairbrass et al. 2017; Carruthers-Jones et al. 2019; Bradfer-
498 Lawrence et al. 2020; Ross et al. 2021). Using NDSI and ADI, Machado et al. (2017) concluded that
499 they were both affected by the distance with anthropic sound sources. As a result, the use of
500 compound indices might be relevant to survey acoustic diversity in mosaic soundscapes of various
501 biomes where biophony and anthrophony narrowly intertwine to shape complex spatio-temporal
502 sound patterns (Eldridge et al. 2018).

503

504 **Conclusion : socio-ecological processes underlying soundscape dynamics**

505 Our results suggest that edge density and landscape configurational heterogeneity are key to
506 understand soundscape structure and dynamics at larger scales in complex habitat mosaics. While
507 habitat heterogeneity generally increases animal diversity (Tews et al 2004; Fahrig et al. 2011), edges
508 enhance biotic interactions and are increasingly created by land use changes in mosaic landscapes
509 (Barbaro et al. 2014; Fletcher et al. 2018). Acoustic diversity can be affected by edge effects and
510 landscape configuration through multiple processes, including bird habitat selection based on
511 acoustic cues implying various tolerance to noise among species (Paton et al. 2012); soundscape
512 patchiness created by anthropophony (low frequency permanent sounds) altering key sensorial traits
513 and communication for vital behaviours in the most sensitive vocalizing organisms (Duquette et al.
514 2021); and complex phonic interactions between bio-, geo- and anthrophony in mosaic landscapes
515 (Joo et al. 2011; Fuller et al. 2015). As soundscape structure depends on the surrounding
516 environment where the sound source is transmitted (Krause 2008), it is not surprising that landscape
517 heterogeneity affects acoustic diversity at larger scales than previously investigated. Consequently,
518 the grain of the soundscape mosaic is likely larger than expected, and an increase in anthrophony
519 does not necessarily coincide with decreased biophony in heterogeneous landscapes (Pijanowski et
520 al. 2011; Sueur and Farina 2015).

521 As concluding remarks, we suggest that soundscape conservation is narrowly connected to human
522 well-being (Dumyahn and Pijanowski 2011; Morrison et al. 2021), notably because biophony and bird
523 songs have high cultural and emotional significance for humankind (Moscoso et al. 2018; Ferraro et
524 al. 2020). More insights on how acoustic diversity correlates with other cultural services provided by
525 landscapes are now required to go further into an integrated management of soundscapes. We thus
526 advocate for systematically integrating acoustic diversity as a key socio-ecological cue to understand
527 complex processes linking biodiversity and spatial heterogeneity in mosaic landscapes. By providing
528 relevant measures of the intertwining between biodiversity and human activities, it would also help
529 to solve some issues in landscape conservation planning arising from the land sharing vs land sparing
530 debates (Grass et al. 2021). Further research is needed to test the hypothesis that land sharing would
531 increase the diversity of soundscapes while land sparing would create acoustic preserves for
532 maintaining long-term relationships between biodiversity and human well-being across a large
533 diversity of landscapes worldwide.

534

535

536 **Author contributions**

537 LB and AS designed the study, LB, AS, JSPF, MC and FC conducted the field work, FC computed the
538 GIS data, AG provided the R code for acoustic diversity indices, LB conducted the analysis with inputs
539 by JSP, MC and AG, and all authors contribute to writing and editing the final manuscript.

540

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544

545 **Data availability**

546 Datasets on acoustic indices and landscape metrics per site and recording periods are available via
547 the Dryad Digital Repository at <https://doi.org/10.5061/dryad.XXXX>

548

549 **Code availability**

550 R codes for computing acoustic indices can be found in AG's GitHub site at
551 <https://github.com/agasc/Soundscape-analysis-with-R>

552

553 **Declarations**

554 **Conflict of interest**

555 The authors declare that the research was conducted in the absence of any commercial or financial
556 relationships that could be construed as a potential conflict of interest.

557

558 **Consent for publication**

559 All authors contributed to the article and approved the submitted version.

560

561

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707 **List of figures**

708 Fig. 1. Location of the two study areas and 44 sampling sites: a) Aurignac county, Occitanie, France;
709 b) Pima county, Arizona, USA. Main land cover types are indicated.

710 Fig. 2. Examples of 30s-sonograms with high and low acoustic diversity, i.e., high and low values for 5
711 acoustic diversity indices (BI, H, ACI, ADI and NP). a) semi-natural grassland; Benque, Aurignac
712 county, Occitanie, France; 6th of May 2021 at 7.00 am. Sounds include species-rich bird morning
713 chorus with wryneck *Jynx torquilla*, great tit *Parus major*, carrion crows *Corvus corone*, common
714 nightingale *Luscinia megarhynchos*, wood pigeon *Columba palumbus* and golden oriole *Oriolus*
715 *oriolus*, while human sounds include church bells, cars passing by and cattle calls. b) saguaro desert;
716 North Kinney Road, Tucson, Arizona, USA; 25th of May 2019 at 0.00 am. Sounds include a single
717 orthopteran calling song. See Table 1 for Als' codes.

718 Fig. 3. Effect of dominant habitat type on median acoustic indices Als computed for three time
719 periods (clock icon = 24hr-diel; bird icon = dawns 6.00 am – 9.30 am; moon icon = nights 22.00 pm –
720 5.30 am) in Aurignac county, Occitanie, France (N = 30). Codes and definitions of Als are listed in
721 Table 1. Significance levels from post-hoc Tukey tests adjusted for multiple comparisons as follows:
722 *** P < 0.001 ; ** P < 0.01 ; * P < 0.05.

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724 periods (clock icon = 24hr-diel; bird icon = dawns 6.00 am – 9.30 am; moon icon = nights 22.00 pm –
725 5.30 am) in Pima county, Arizona, USA (N = 14). Codes and definitions of Als are listed in Table 1.
726 Significance levels from post-hoc Tukey tests adjusted for multiple comparisons as follows: *** P <
727 0.001 ; ** P < 0.01 ; * P < 0.05.

728 Fig. 5. LMM prediction biplots of the effects of landscape composition and configuration on median
729 Als for 24hr-diel cycles (clock icon) in Aurignac county, Occitanie, France (N = 30). Marginal R^2 values
730 of fixed effect are indicated. See Table 1 for Als codes and definitions and Table 2 for significance
731 levels. Dotted lines indicate 95% confidence intervals.

732 Fig. 6. LMM prediction biplots of the effects of landscape composition and configuration on median
733 Als for dawns (bird icon = 6.00 am – 9.30 am) and nights (moon icon = 22.00 pm – 5.30 am) in
734 Aurignac county, Occitanie, France (N = 30). Marginal R^2 values of fixed effect are indicated. See
735 Table 1 for Als codes and definitions and Table 2 for significance levels. Dotted lines indicate 95%
736 confidence intervals.

737 Fig. 7. LMM prediction biplots of the effects of landscape composition and configuration on median
738 Als for three time periods (clock icon = 24hr-diel; bird icon = dawns 6.00 am – 9.30 am; moon icon =
739 nights 22.00 pm – 5.30 am) in Pima county, Arizona, USA (N = 14). Marginal R^2 values of fixed effect
740 are indicated. See Table 1 for Als codes and definitions and Table 2 for significance levels. Dotted
741 lines indicate 95% confidence intervals.

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744 **Supplementary information**

745 Appendix S1. Intra-set correlation plots for the six acoustic indices (BI, H, ACI, NDSI, ADI, NP) and
746 multiacoustic index (MI) from the three recording time periods (24hr-diel cycles, dawns and nights) in
747 the two study areas (upper panel = Occitanie ; lower panel = Arizona).

748 Appendix S2. Matrix correlation plots between the six median AI values for 24hr-diel cycles and the
749 two best landscape predictors (edge density and woodland cover) measured at five increasing buffer
750 scales (250, 500, 1000, 2500 and 5000m around recorders ; see Methods).

751 Appendix S3. Intra-set correlation matrices for the two main landscape predictors computed at 10 m
752 of pixel resolution and resampled at 30 m for Occitanie, France (left panel: woodland cover; right
753 panel: edge density)

754 Appendix S4. Results of post-hoc tests on Linear Mixed Models of AIs' responses to the dominant
755 habitat type in each study area. Codes and definitions of acoustic indices are listed in Table 1.
756 Significance levels from post-hoc Tukey tests adjusted for multiple comparisons as follows: *** $P <$
757 0.001 ; ** $P < 0.01$; * $P < 0.05$.

758 Appendix S5. Estimates \pm SE, z and P values of best LMMs obtained after stepwise backward
759 elimination of non-significant terms from the full model. AICc of best, full and null models are
760 indicated.

761 Appendix S6. Examples of 30s-spectrograms for dawn and nocturnal soundscapes in different
762 habitats of Aurignac county, Occitanie, France and Pima county, Arizona, USA. Spectrograms were
763 drawn with RavenLite software (Cornell Lab of Ornithology), using short-time Fourier transform
764 (STFT) and Hann window type (<https://ravensoundsoftware.com/software/raven-lite>). Red values
765 indicate low values for acoustic indices, green indicate high values and black close-to-average values.
766 See Table 1 for codes of acoustic indices.

767

768 Table 1. Summary of 10 acoustic indices (AIs) definitions and properties. The six AIs used in the present study are indicated in bold.

769

Acoustic indices	Code	Definition	High expected values	Low expected values	Main reference
Acoustic complexity index	ACI	Mean relative change in sound intensity across consecutive 5s time periods and frequency bins	High variation in sound intensity across frequencies and times	Constant levels of similar sound intensity, such as most anthropogenic sources	Pieretti et al. 2011
Acoustic diversity index	ADI	Shannon index adapted to measures the evenness of sound signals across frequency bins	Even sound across all frequencies or silent recordings	Pure tones dominating single frequency band	Villanueva-Rivera et al. 2011
Acoustic evenness index	AEI	Equal to the reverse of ADI, it measures unevenness of sound across frequencies	High sound intensity in a restricted range of frequencies	Either high or no acoustic activity across all frequency bins	Villanueva-Rivera et al. 2011
Bioacoustic index	BI	Area under the mean spectrum between 2-10 kHz in dB minus the minimum dB value	Increases with higher variation between loud and quiet frequency bins	Silent recordings above 2 kHz indicating no or low biophony	Gasc et al. 2018
Temporal entropy	Ht	Shannon evenness applied to the amplitude envelope	Sub-index used to calculate H	Sub-index used to calculate H	Sueur et al. 2008
Spectral entropy	Hf	Shannon evenness applied to the average frequency spectrum	Sub-index used to calculate H	Sub-index used to calculate H	Sueur et al. 2008
Total acoustic entropy	H	Product of Ht and Hf, it varies between 0 for pure tones and 1 for even signals or silence	Silent recordings or evenly distributed sounds across frequencies	Pure tones dominating single frequency band	Sueur et al. 2008
Median of amplitude envelope	M	Measures the sound amplitude of a recording	Increases with noise and sound intensity	Silent or very quiet recordings with low sound intensity	Depraetere et al. 2012
Normalised Difference Sound Index	NDSI	Ratio of biophony on anthrophony where anthrophony is the sum of sound below and biophony above 2 kHz	Tends towards 1 with no anthrophony and only biophony	Tends towards -1 with only anthrophony and no biophony	Eldridge et al. 2018
Number of frequency peaks	NP	Numbers of major frequency peaks from a mean spectrum scaled between 0 and 1	Increases with the level of vocalizing animal activity	Decreases with the level of vocalizing animal activity	Gasc et al. 2013

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771

772 Table 2. Summary results for linear mixed models linking acoustic indices to landscape metrics. H and NDSI values were logit-transformed prior to modelling.
 773 Predictor codes as follows : WOOD = woodland cover, EDGE = edge density, SHDIV = Shannon landscape diversity, URB = urban area cover. R²m indicates
 774 marginal R² for fixed effects and R²c conditional R² for fixed and random effects. Significance levels are indicated as follows: * P < 0.05 ; ** P < 0.01 ; *** P <
 775 0.001

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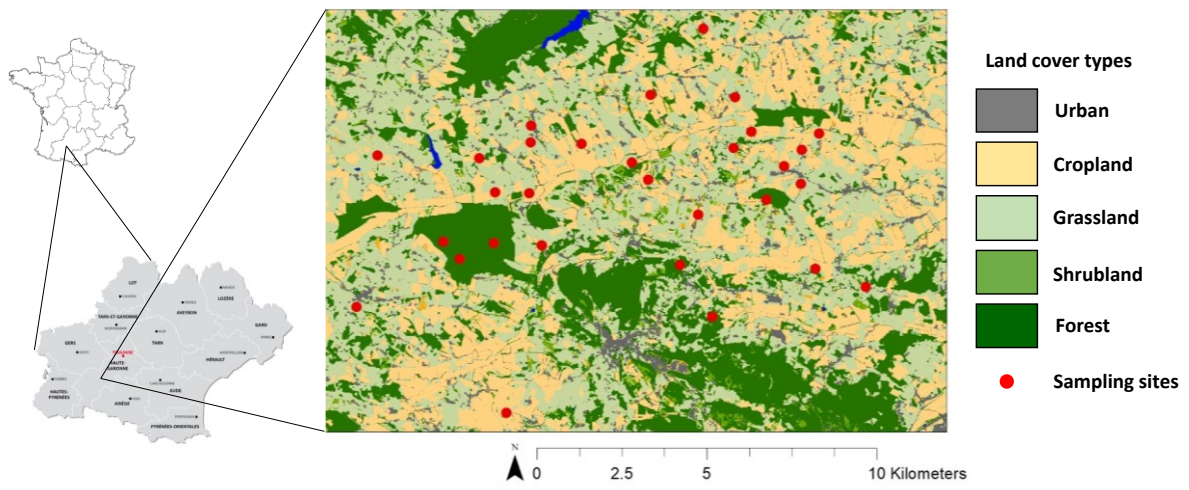
Acoustic indices	France – Aurignac county									Arizona – Pima county								
	24hr	R ² m	R ² c	Dawns	R ² m	R ² c	Nights	R ² m	R ² c	24hr	R ² m	R ² c	Dawns	R ² m	R ² c	Nights	R ² m	R ² c
Bioacoustic index BI	ns	-	-	ns	-	-	ns	-	-	ns	-	-	WOOD*	0.18	0.64	ns	-	-
Acoustic entropy H	ns	-	-	EDGE* WOOD*	0.15	0.15	WOOD*	0.16	0.16	WOOD*	0.29	0.66	-EDGE***	0.61	0.62	WOOD*	0.29	0.29
Acoustic complexity ACI	-WOOD***	0.25	0.46	-WOOD***	0.32	0.39	-WOOD*	0.11	0.26	ns	-	-	ns	-	-	ns	-	-
Acoustic diversity ADI	EDGE**	0.24	0.39	ns	-	-	ns	-	-	-EDGE*	0.34	0.56	ns	-	-	-EDGE**	0.40	0.40
NDSI	EDGE**	0.22	0.23	ns	-	-	EDGE**	0.20	0.20	-EDGE**	0.45	0.45	-URB*	0.31	0.31	-EDGE***	0.59	0.60
Number of peaks NP	EDGE***	0.36	0.57	-WOOD*	0.15	0.18	EDGE**	0.21	0.44	-SHDIV*	0.21	0.21	ns	-	-	ns	-	-
Multiacoustic index	EDGE**	0.26	0.41	EDGE*	0.11	0.47	EDGE**	0.18	0.47	-EDGE**	0.41	0.61	WOOD*	0.23	0.33	-EDGE***	0.55	0.55

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a



b

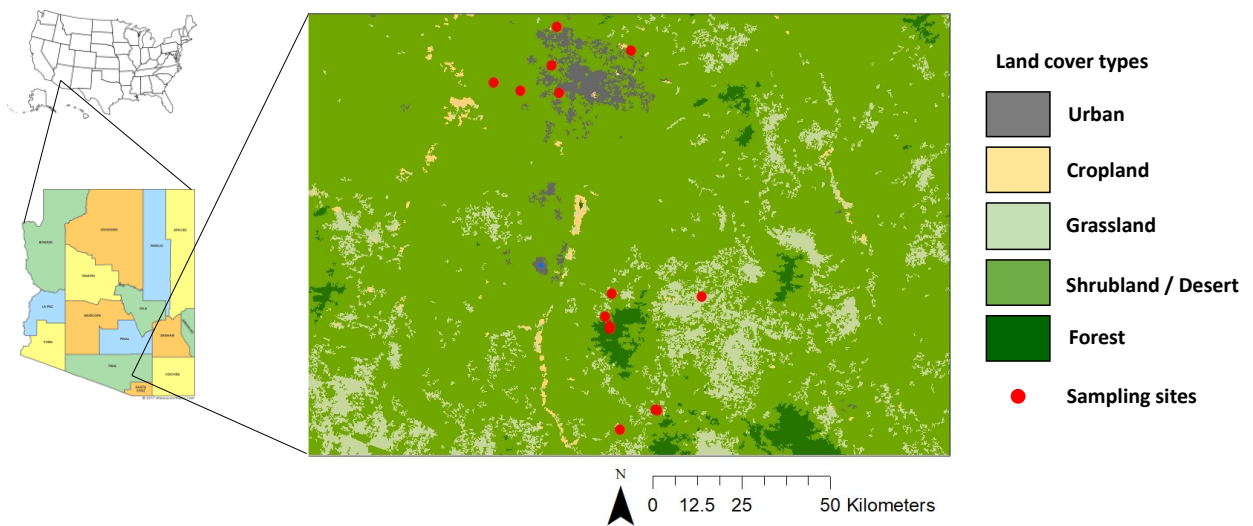
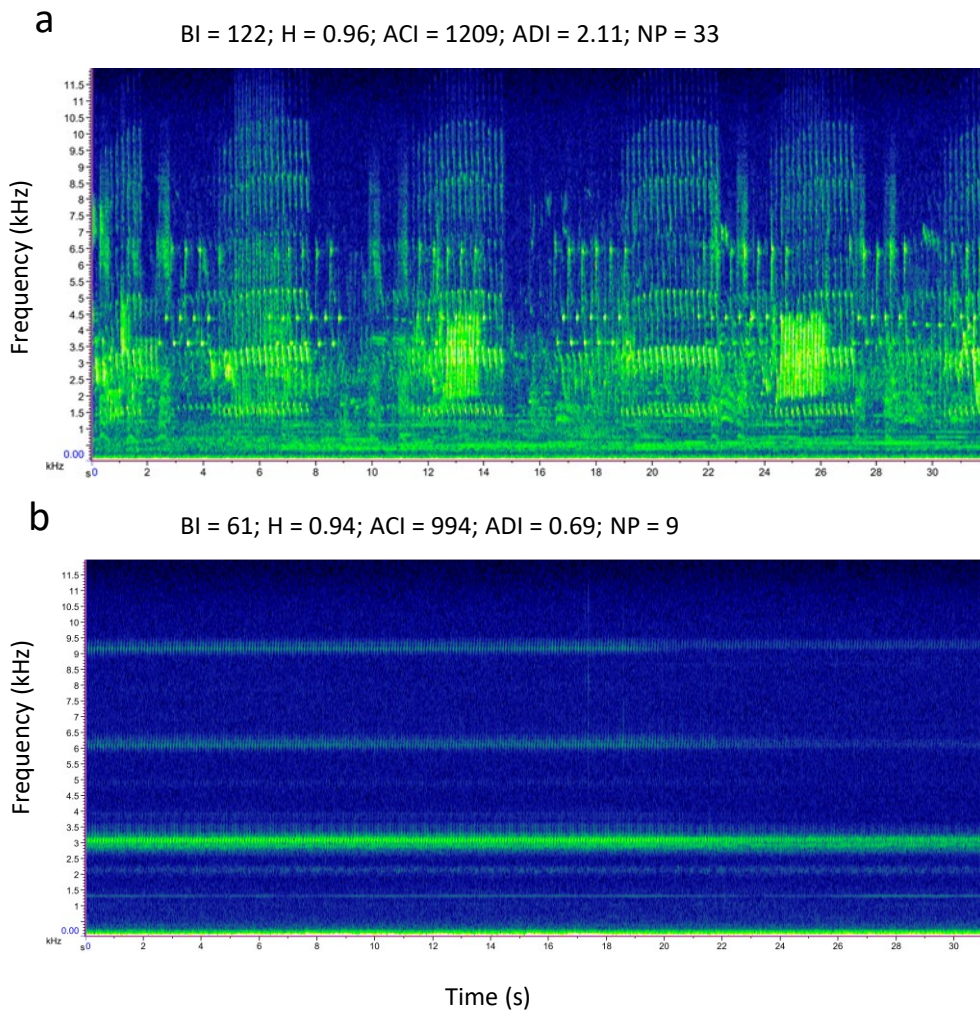


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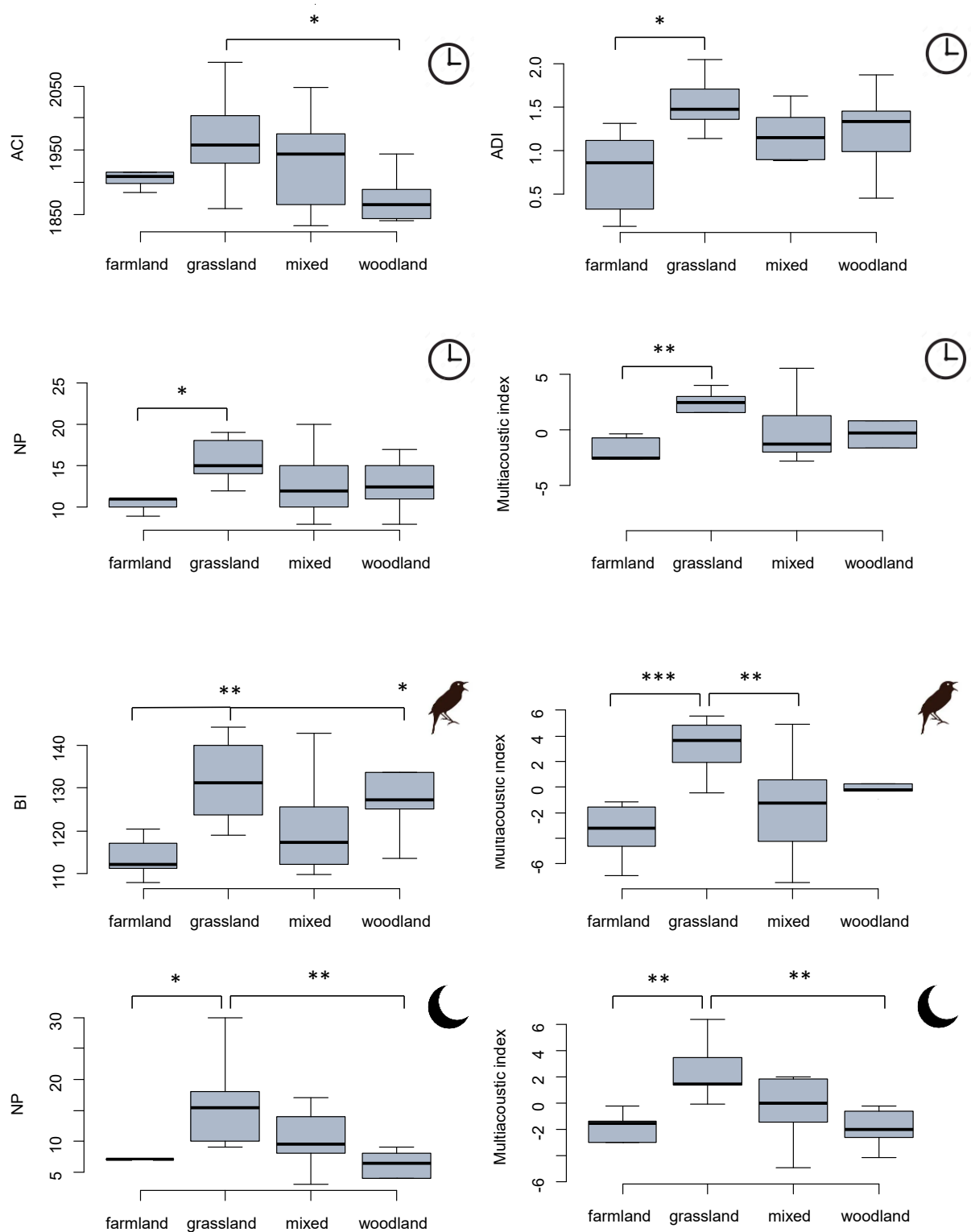


Fig. 3. Effect of dominant habitat type on median acoustic indices AIs computed for three time periods (clock icon = 24hr-diel; bird icon = dawns 6.00 am – 9.30 am; moon icon = nights 22.00 pm – 5.30 am) in Aurignac county, Occitanie, France (N = 30). Codes and definitions of AIs are listed in Table 1. Significance levels from post-hoc Tukey tests adjusted for multiple comparisons as follows: *** P < 0.001 ; ** P < 0.01 ; * P < 0.05.

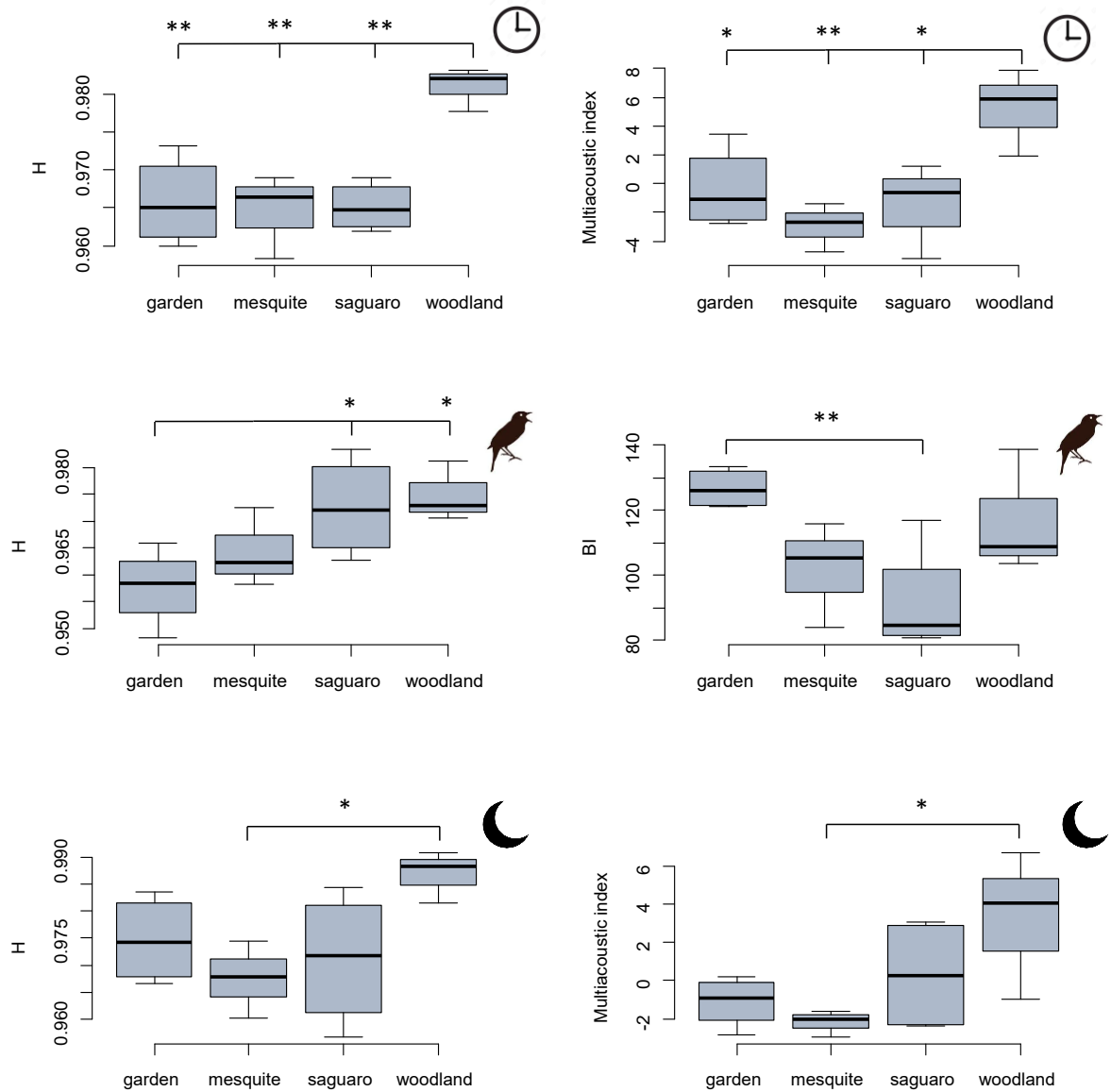


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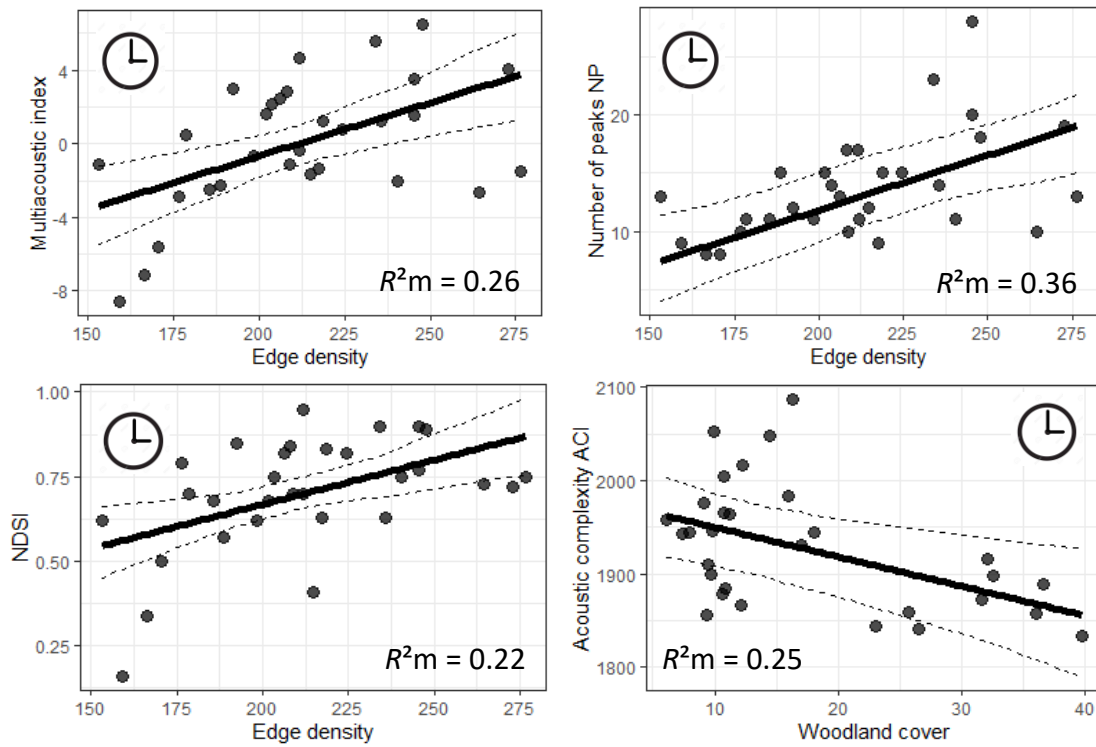


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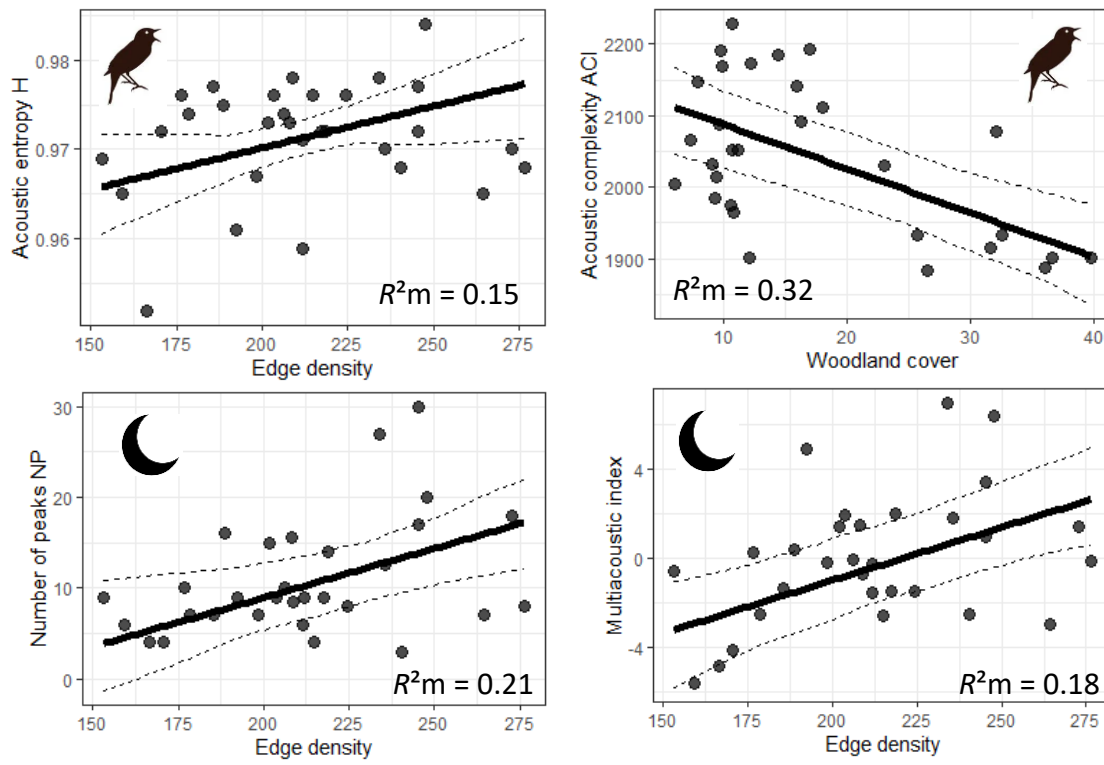


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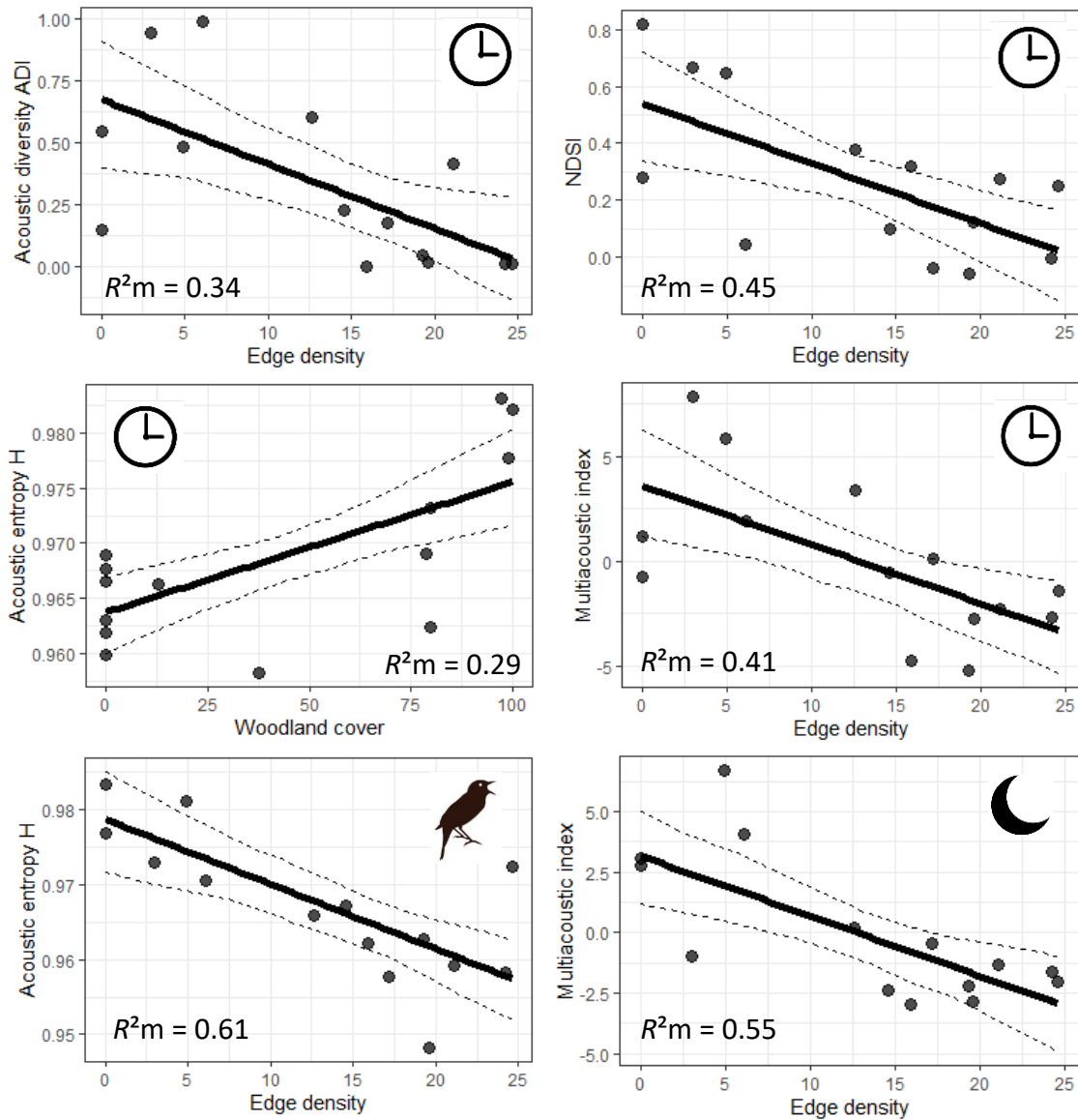


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