Research article

Linking acoustic diversity to compositional and configurational heterogeneity in mosaic landscapes

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Abstract

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

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

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

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

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

Keywords

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

Introduction

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

Acoustic diversity is a major component of biodiversity which can be investigated at the landscape level in the framework of soundscape ecology (Krause 2008; Pijanowski et al. 2011) and ecoacoustics (Sueur and Farina 2015). It can be defined as a greater complexity of sounds in a given soundscape and measured through either a higher number of occupied frequency bands, greater levels of acoustic activity or sound energy, or more biophony, geophony and anthrophony intertwined (Sueur et al. 2014). Acoustic diversity can therefore account for multiple biotic interactions and species coexistence through the acoustic niche hypothesis (Farina et al. 2011; Azar and Bell 2016). Its large-scale assessment has been strengthened in the recent years according to rapid technological developments in Passive Acoustic Monitoring (Bradfer-Lawrence et al. 2019; Gibb et al. 2019; Sugai et al. 2020; Wood et al. 2021). Passive Acoustic Monitoring (PAM) provides a holistic picture of biodiversity through the recording and analysis of intricate patterns of sound, especially at larger spatial scales (Krause 2008Drake et al. 2021; Ross et al. 2021; Yip et al. 2021). Not only biodiversity - notably breeding bird -surveys will benefit from the large-scale deployment of automated recorders, but this will give more insights on how bird song attractiveness is connected to human well-being and will help considering soundscape conservation as a cultural value (Ferraro et al. 2020; Barbaro et al. 2021; Morrison et al. 2021).

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

Despite the study of spatial heterogeneity in sounds being one of the main objectives of soundscape ecology (Pijanowski et al. 2011; Bormpoudakis et al. 2013), the relationships between acoustic indices and landscape metrics are still unclear. Among landscape metrics measuring compositional and configurational heterogeneity, only patch-scale fragmentation effects (i.e., their size and connectivity) on acoustic diversity have been investigated to date (Tucker et al. 2014; Fuller et al. 2015; Dixon et al. 2020; Müller et al. 2020). The effect of land use intensity has been explored more extensively (Joo et al. 2011; Dein and Rüdisser 2020; Dooley and Brown 2020; Dröge et al. 2021; Shamon et al. 2021), yet few studies have attempted to compare the response of acoustic indices to a large range of landscape structures measured at several spatial scales in different biomes. Investigating the acoustic diversity of mosaic landscapes using standard recording devices and sampling schemes is now easier, for example to compare the relative effects of habitat composition and configuration on multi-taxa biodiversity metrics based on replicated acoustic sampling across wide landscape gradients. Soundscape ecology may also contribute to both the Several Small Or Single Large habitat patches (SLOSS) and land sharing vs land sparing debates, by providing meaningful insights on the coexistence between biodiversity and human activities in heterogenous habitat mosaics (Fahrig 2020; Grass et al. 2021).

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

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

Methods

Study areas

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

The second study region is located in the Pima county, southern Arizona, USA, within the Man-Environment Observatory OHMi (https://ohmi-pima-county.in2p3.fr/en) around the city of Tucson (32°12'17.2"N; 110°57'45.2"W) and in the Santa Rita range north of Patagonia (31°32'25.4"N 110°45'18.2"W), close to the Mexican border (Fig. 1b). Elevation spans between 800 and 1800 m asl and climate is semi-arid with summer monsoon, with an Alpine influence at higher altitudes. We sampled 14 sites on a landscape gradient ranging from periurban areas mixing gardens and deserts-scrubland patches to saguaro and mesquite deserts, and higher-elevation grasslands and forests, as follows : periurban gardens (n = 4), saguaro deserts (n = 4), mesquite deserts (n = 3) and mountain oak-pine-aspen woodlands (n = 3).

Sound recording methods and sampling scheme

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

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

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

Acoustic diversity indices

We obtained 1,251 recordings of 30 min wav files totalling 625.5 hr that were further cut down in 37,530 one-minute samples for acoustic analyses (Towsey et al. 2014). For each one-minute sample, we calculated 10 acoustic indices (Table 1) as follows: Acoustic Complexity Index ACI ; Acoustic Diversity Index ADI ; Acoustic Evenness Index AEI; Bioacoustic Index BI ; temporal, spectral and total acoustic entropy Ht, Hf and H ; median of amplitude envelope M ; Normalised Difference Sound Index NDSI and Number of frequency Peaks NP (Sueur et al. 2014; Bradfer-Lawrence et al. 2019) using *soundecology* version 1.3.3 (Villanueva-Rivera and Pijanowski 2014) and *seewave* version 2.1.6 R-packages (Sueur et al. 2008) and a R-script from A.G. available in GitHub (https://github.com/agasc/Soundscape-analysis-with-R). We used the default parameters available for each index for all calculations (Machado et al. 2017). We calculated the means and medians of the 10 AIs for three complementary time periods (Dröge et al. 2021): 24hr-diel cycles (720 one-minute periods from 00.00 am to 23.30 pm per site), dawns (120 one-minute periods from 6.00 am to 9.30 am) and nights (240 one-minute periods from 22.00 pm to 05.30 am). We selected these time periods because they are biologically relevant (Metcalf et al. 2021), while also capturing substantial sound-producing human activities. Dawns are the peak periods for quantifying multi-species songbird vocalizations (i.e., morning choruses) and nocturnal acoustic surveys are especially relevant for amphibian or insect sound diversity, while diel cycles of 24 hours summarize all possible patterns of acoustic activity and account for all possible sound sources in a given day (Tucker et al. 2014; Grant and Samways 2016; Dröge et al. 2021).

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

Multiacoustic index = Σ (scaled BI + scaled H + scaled ACI + scaled ADI + scaled NDSI + scaled NP)

We constructed our index in a way to be as simple as possible both in terms of calculation and computation, while giving the same weight to all AIs regardless of their absolute values, variation of magnitude and direction of response patterns. We therefore used the sum of the scaled median values, as used for example in the multidiversity index of Allan et al. (2014). Scaling the values of all AIs allowed both their direct comparisons and their combination into a single index designed to capture the dominant patterns in acoustic activity and diversity across all sites and time periods sampled, as well as their response to habitat type and landscape metrics. We used the generic ‘scale’ function in R which centers all values by the mean and scales them by dividing the values by standard deviation. We further tested for other scaling options, such as the maximum values (Allan et al. 2014) and we tested its sensitivity to the sequential removing of AIs. We also computed intra-set correlations to check that the multiacoustic index was positively correlated with all six AIs in all sites and time periods (Appendix S1).

Landscape metrics

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

These buffer scales were selected because they were biologically meaningful for most vocalizing taxa recorded regarding habitat selection, daily movements and dispersal ecology, for birds, mammals and insects (Paradis et al. 1998; Holland et al. 2004; Laforge et al. 2021). They have also proven relevant for soundscape assessment in previous studies and were compatible with the resolution of land cover maps from both areas (Dein and Rüdisser 2020). While most previous soundscape studies have generally focused on finer landscape scales (typically 500m; see Fuller et al. 2015), we included also larger buffer scales because we attempted to question the effect of landscape matrix composition and configuration on AIs at larger scales than previously investigated. Using five distance radii allowed us testing for the scale of effect (Holland et al. 2004) by building correlation matrices between the two best performing landscape metrics and AIs diel values for the two study regions (Appendix S2). As we used GIS land cover data with different pixel resolutions between the two study regions (10 m for France and 30 m for USA), we also checked that resampling the region with finer resolution of 10 m (France) at the coarser resolution of 30 m did not affect the values of the two main landscape predictors (Appendix S3).

Data analysis

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

To compare their responses to the same set of predictors, we built a full model with identical structure for all six AIs and multiacoustic index in the two areas for the three recording time periods (24hr-diel cycles, dawns and nights) leading to six models for each AIs. We performed Linear Mixed Models (LMMs) using Gaussian family models in glmmTMB R-package (Brooks 2020) with recording year as random factor. AIs such as NDSI and H have bounded scales and were therefore logit-transformed before modelling. We first tested the separate effect of dominant habitat type on the AIs median values. Habitat type was defined as a fixed factor with four categories in each study region, i.e., farmland, grassland, mixed farmland-grassland and woodland for Occitanie and periurban gardens, mesquite, saguaro desert and woodland for Arizona. Post-hoc Tukey tests were applied with the Kenward-Roger method to adjust for multiple comparisons.

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

Results

Effect of habitat type on acoustic diversity

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

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

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

Effect of landscape metrics on acoustic diversity

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

For 24hr-diel cycles in Arizona, we found significant negative effects of edge density at 2500 m on ADI, NDSI and multiacoustic index (Table 2; see Fig. 7 for significant biplots). Woodland cover at 2500 m had a positive effect on H while NP decreased with landscape diversity. For dawns, woodland cover had a positive effect on BI and multiacoustic index, edge density had a negative effect on H and urban cover a negative effect on NDSI (Table 2). No predictors were significant for ACI, ADI and NP. Finally, woodland cover positively affected H and edge density negatively affected ADI, NDSI and multiacoustic index for nocturnal soundscapes (Table 2).

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

Discussion

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

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

Effect of habitat type on acoustic diversity

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

In accordance with other studies indicating that more intensively managed or disturbed habitats had lower acoustic diversity (Burivalova et al. 2018; Gasc et al. 2018; Myers et al. 2019), we found less diverse soundscapes in landscapes dominated by homogeneous farmland with low edge density than in more complex mosaics of high edge density mixing crops, hedgerows and grasslands in Occitanie. Surprisingly, we found that periurban gardens had high bioacoustic activity measured by BI in Arizona while NDSI or H were low in the same sites, which may be an indication of high acoustic coexistence between anthrophony and biophony (Sueur et al. 2008; Carruthers-Jones et al. 2019). In southern Arizona, the extensive use of bird feeders and the low urban density allow gardens to support species-rich urban bird communities, including several hummingbird species (Trochilidae) whose buzzes produce acoustic signals that are typical components of garden soundscapes in semi-arid regions (Emlen 1974; McCaffrey and Wethington 2008; see Appendix S6).

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

Effect of landscape heterogeneity on acoustic diversity

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

Here, we show that acoustic diversity is primarily driven by landscape configurational heterogeneity at large scale (i.e., edge density at 2500m around recorders), and that the direction of the effect reverses between temperate and semi-arid biomes. Such a positive or negative effect of edge density on acoustic diversity likely depends on surrounding matrix composition (Barbaro et al. 2021), socio-ecological legacy of mosaic soundscapes and their historical habitat uses (Semper-Pascual et al. 2021), as well as the evolutionary responses of vocalizing species to long-term experienced disturbances and ambient noise (Paton et al. 2012; Duquette et al. 2021). Our results confirm previous findings of soundscape studies, such as a large scale of effect of landscape metrics on acoustic diversity (well above 1000m around recorders), the predominance of landscape over local habitat effects, as well as the effect of individual land cover classes on acoustic diversity (Dein and Rüdisser 2020; Dixon et al. 2020). We also found that, together with our multiacoustic index, H, ADI, NP and NDSI were the AIs performing best to relate overall soundscape diversity to landscape configuration in two contrasting study regions and across a large range of acoustic habitats (Fuller et al. 2015; Ross et al. 2021; Shamon et al. 2021). As a ratio measuring the relative dominance of biophony or anthrophony, NDSI is also best to capture the effect of urbanization on soundscapes at large spatial scales (Fairbrass et al. 2017; Machado et al. 2017; Doser et al. 2020).

Monitoring acoustic diversity in mosaic landscapes

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

A second requirement for an adequate soundscape assessment is the computation of multiple AIs to capture the variability of sounds from different biophonic, geophonic or anthrophonic sources across sites and time periods. While several indices are needed to reveal diel and seasonal soundscape patterns (Bradfer-Lawrence et al. 2019), AIs have been shown to be often weakly correlated to biophony assessed independently because of signal masking by non-target sounds (Fairbrass et al. 2017; Metcalf et al. 2021). Moreover, a combination of indices is generally required to successfully predict biodiversity values (Towsey et al. 2014; Buxton et al. 2018; Yip et al. 2021). Here, we modelled the responses of six AIs that are increasingly used as a standard analysis path to characterize spatial or temporal changes in acoustic biodiversity (Sueur et al. 2014; Bradfer-Lawrence et al. 2020). As most previous studies, we found limited congruence among metrics, but complementary patterns in soundscape characterization for each suite of indices (Fuller et al. 2015; Eldridge et al. 2018; Ross et al. 2021), while using a multiacoustic index helped summarizing the dominant response of acoustic diversity to landscape heterogeneity.

Relative performance of acoustic indices in complex soundscapes

We found that correlative patterns in AIs were remarkably similar across study regions and time periods. Our results support previous findings that ADI, H and NDSI are especially suitable at predicting acoustic diversity across different habitats under various ambient sound conditions, possibly because they reflect better the intertwining of biophony and anthrophony in complex soundscapes (Fuller et al. 2015; Machado et al. 2017; Ross et al. 2021). Moreover, NDSI also tended to better account for diel acoustic patterns while H and ADI seemed more efficient at characterizing nocturnal soundscapes often dominated by pure tone signals such as owl calls, insect stridulations or amphibian choirs (Gasc et al. 2015; Ross et al. 2021). In our study, H and NDSI were the two indices that responded significantly to both local habitat and landscape metrics for all recording periods in the two study regions. As pointed out by several authors, NDSI is designed to capture daily shifts between dominant anthrophony and biophony while diversity-based indices such as H or ADI incorporate anthrophony levels into biophonic soundscapes to produce high diversity values (Fuller et al. 2015; Eldridge et al. 2018; Ross et al. 2021). By contrast, BI, NP and ACI are designed to capture biophony and to be less sensitive to anthrophonic noise (Gasc et al. 2015). However, ACI does not account for constant sound signal produced by many arthropods (Pieretti et al. 2011; Gasc et al. 2015; Fairbrass et al. 2017) and can therefore display inverse responses to habitat heterogeneity and bird diversity, especially in grasslands (Shamon et al. 2021). While most AIs can be potentially biased by high road traffic noise in urban habitats, ACI was specifically developed to be impervious to constant sound (Pieretti et al. 2011; Fairbrass et al. 2017; Carruthers-Jones et al. 2019; Bradfer-Lawrence et al. 2020; Ross et al. 2021). Using NDSI and ADI, Machado et al. (2017) concluded that they were both affected by the distance with anthropic sound sources. As a result, the use of compound indices might be relevant to survey acoustic diversity in mosaic soundscapes of various biomes where biophony and anthrophony narrowly intertwine to shape complex spatio-temporal sound patterns (Eldridge et al. 2018).

Conclusion : socio-ecological processes underlying soundscape dynamics

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

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

Author contributions

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

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Data availability

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

Code availability

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

Declarations

Conflict of interest

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

Consent for publication

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

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

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

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.

Fig. 4. 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 Pima county, Arizona, USA (N = 14). 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.

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

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

Fig. 7. LMM prediction biplots of the effects of landscape composition and configuration on median AIs 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 Pima county, Arizona, USA (N = 14). Marginal R^2 values of fixed effect are indicated. See Table 1 for AIs codes and definitions and Table 2 for significance levels. Dotted lines indicate 95% confidence intervals.

Supplementary information

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

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

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

Appendix S4. Results of post-hoc tests on Linear Mixed Models of AIs' responses to the dominant habitat type in each study area. Codes and definitions of acoustic indices 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.

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

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

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

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

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

Acoustic indices	France – Aurignac county									Arizona – Pima county								
	24hr	R^2m	R^2c	Dawns	R^2m	R^2c	Nights	R^2m	R^2c	24hr	R^2m	R^2c	Dawns	R^2m	R^2c	Nights	R^2m	R^2c
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

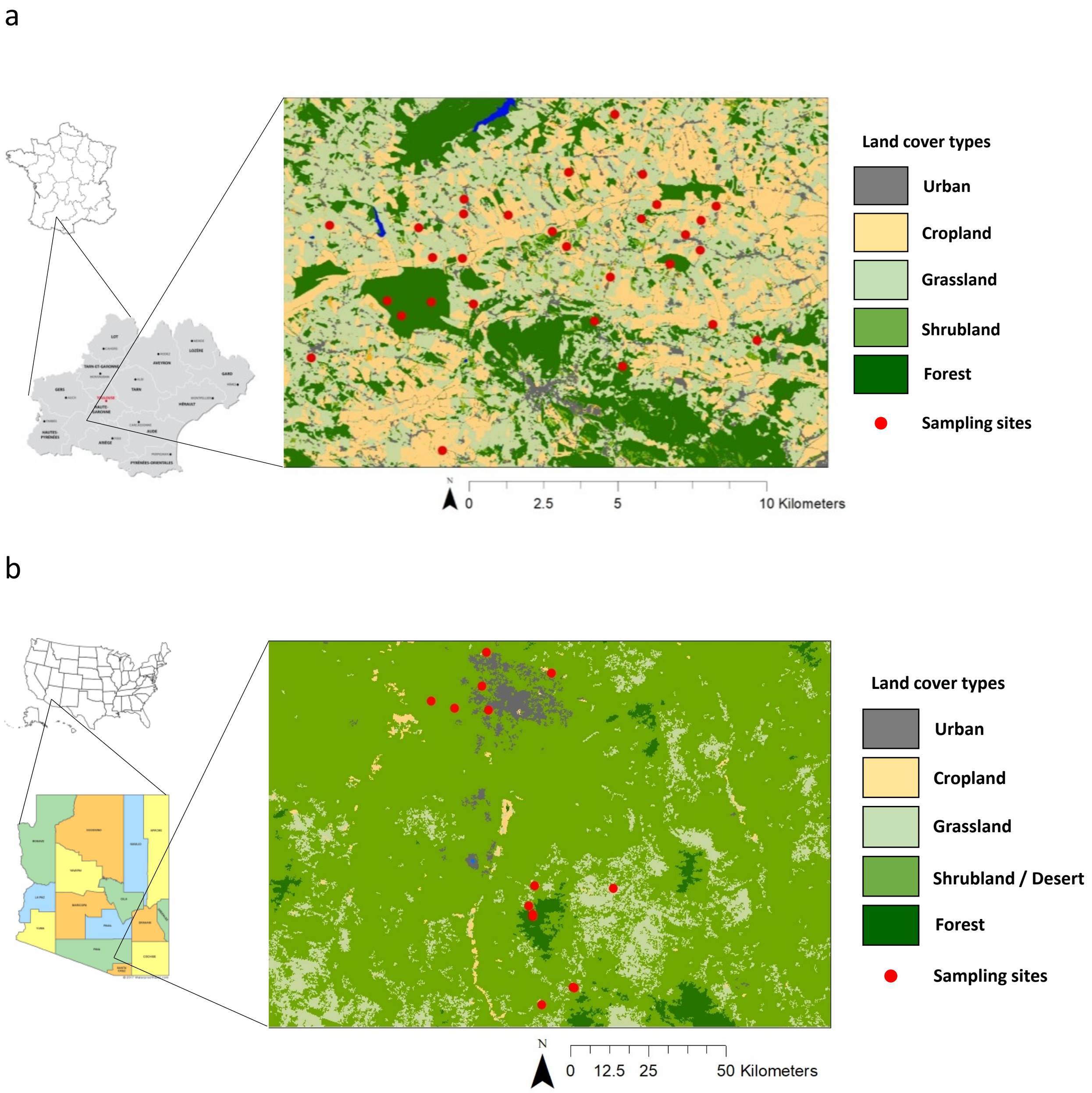
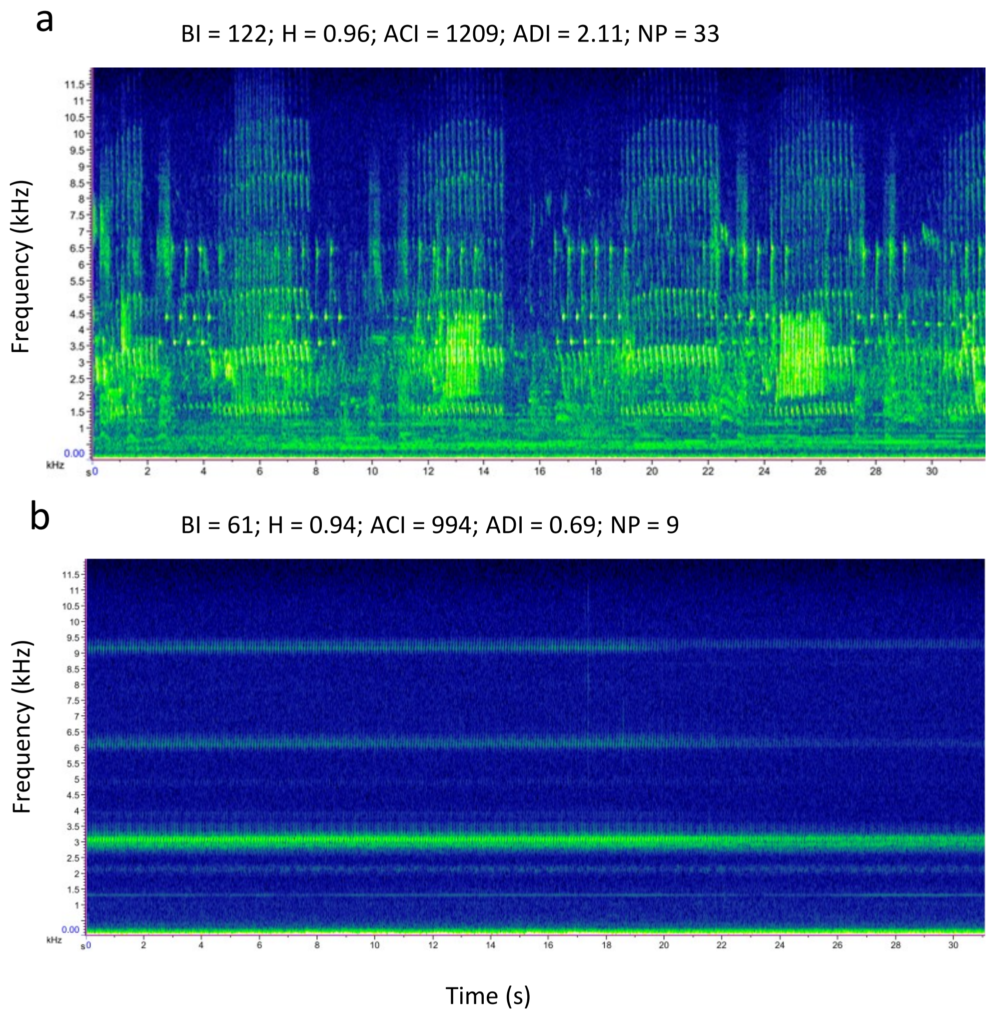


Fig. 1. Location of the two study areas and 44 sampling sites: a) Aurignac county, Occitanie, France; b) Pima county, Arizona, USA. Main land cover types are indicated.

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



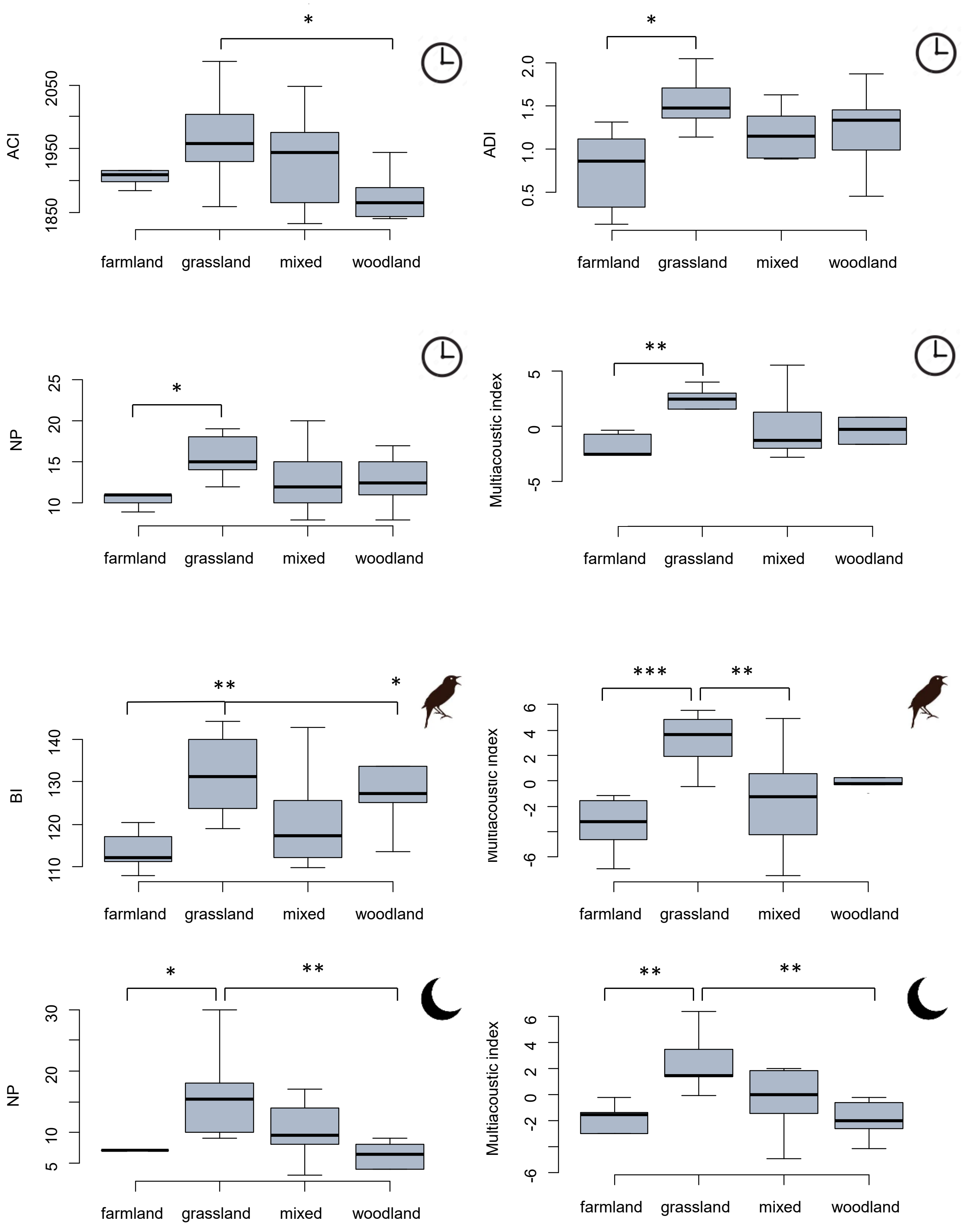


Fig. 3. Effect of dominant habitat type on median acoustic indices AIs computed for three time periods (clock icon = 24hr-diel; bird icon = dawns 6.00 am – 9.30 am; moon icon = nights 22.00 pm – 5.30 am) in Aurignac county, Occitanie, France (N = 30). Codes and definitions of AIs are listed in Table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

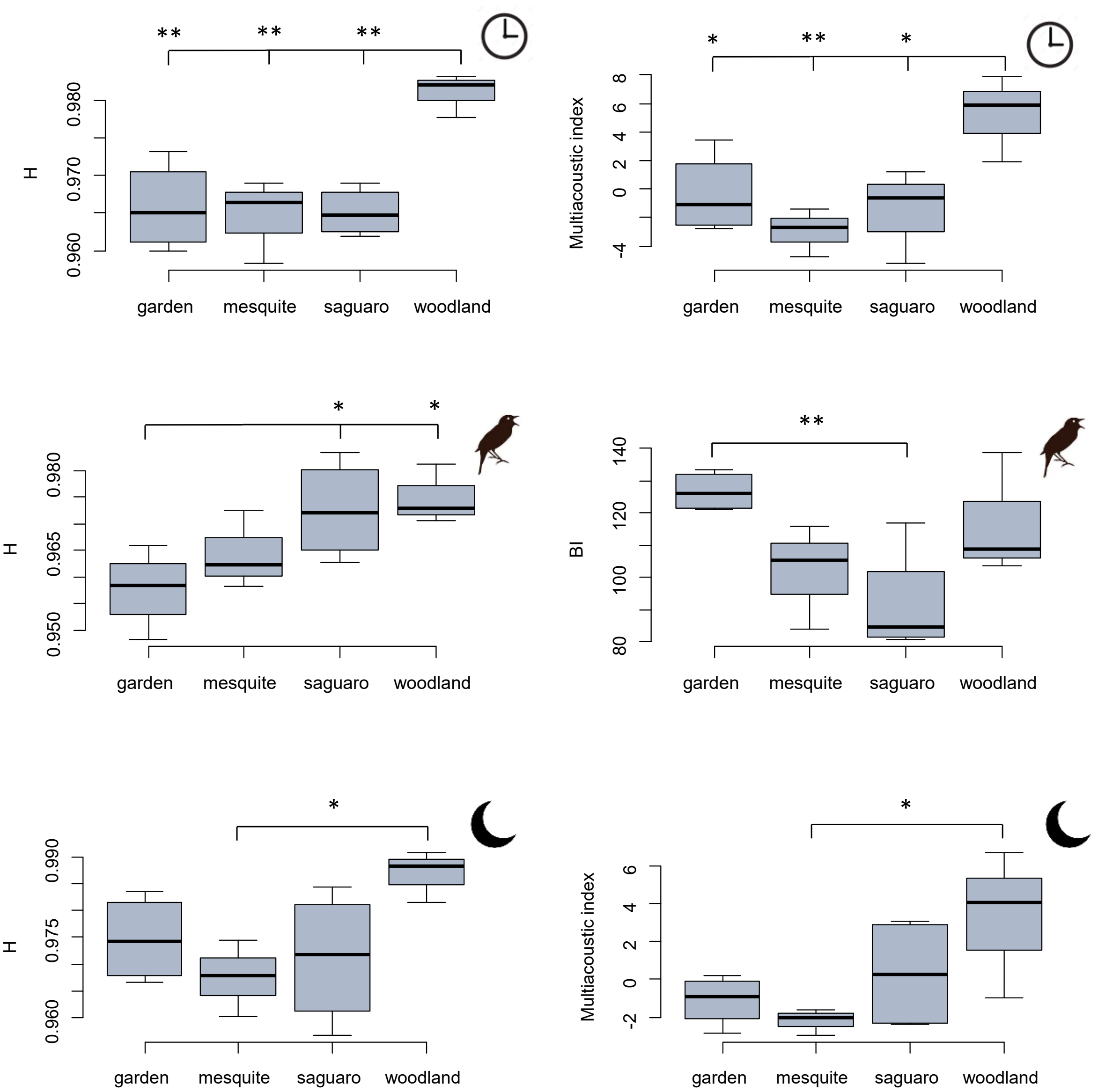


Fig. 4. Effect of dominant habitat type on median acoustic indices AIs computed for three time periods (clock icon = 24hr-diel; bird icon = dawns 6.00 am – 9.30 am; moon icon = nights 22.00 pm – 5.30 am) in Pima county, Arizona, USA (N = 14). Codes and definitions of AIs are listed in Table 1. Significance levels from post-hoc Tukey tests adjusted for multiple comparisons as follows: *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$.

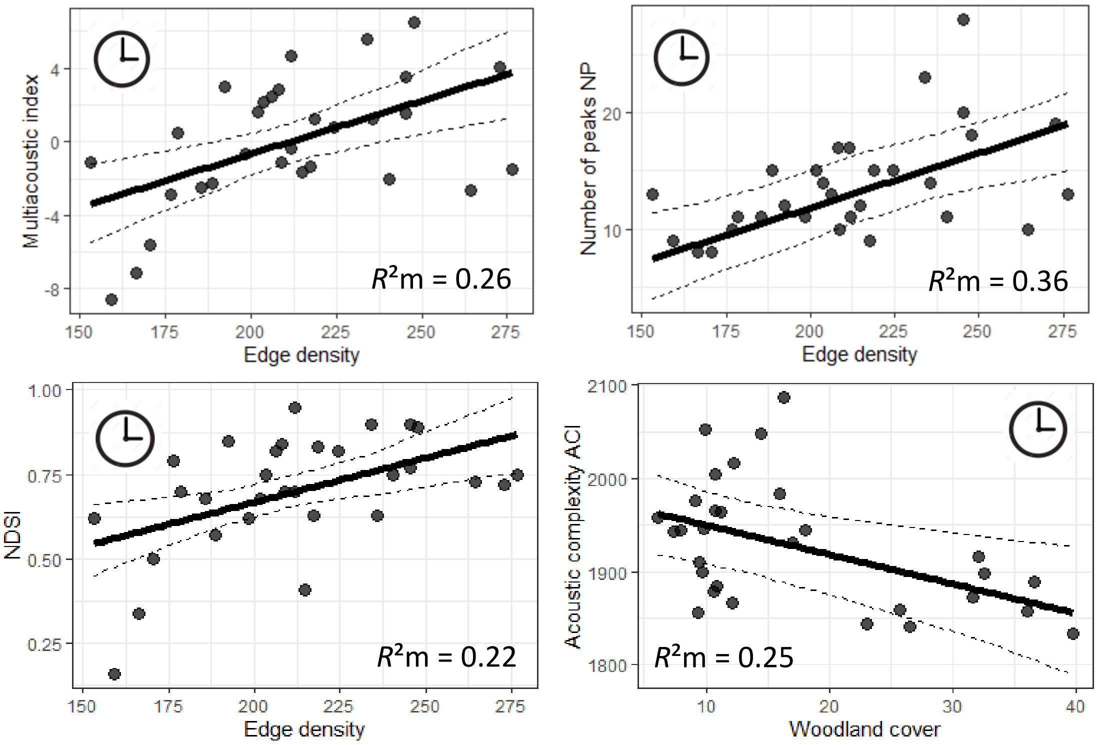


Fig. 5. LMM prediction biplots of the effects of landscape composition and configuration on median AIs for 24hr-diel cycles (clock icon) in Aurignac county, Occitanie, France (N = 30). Marginal R^2 values of fixed effect are indicated. See Table 1 for AIs codes and definitions and Table 2 for significance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

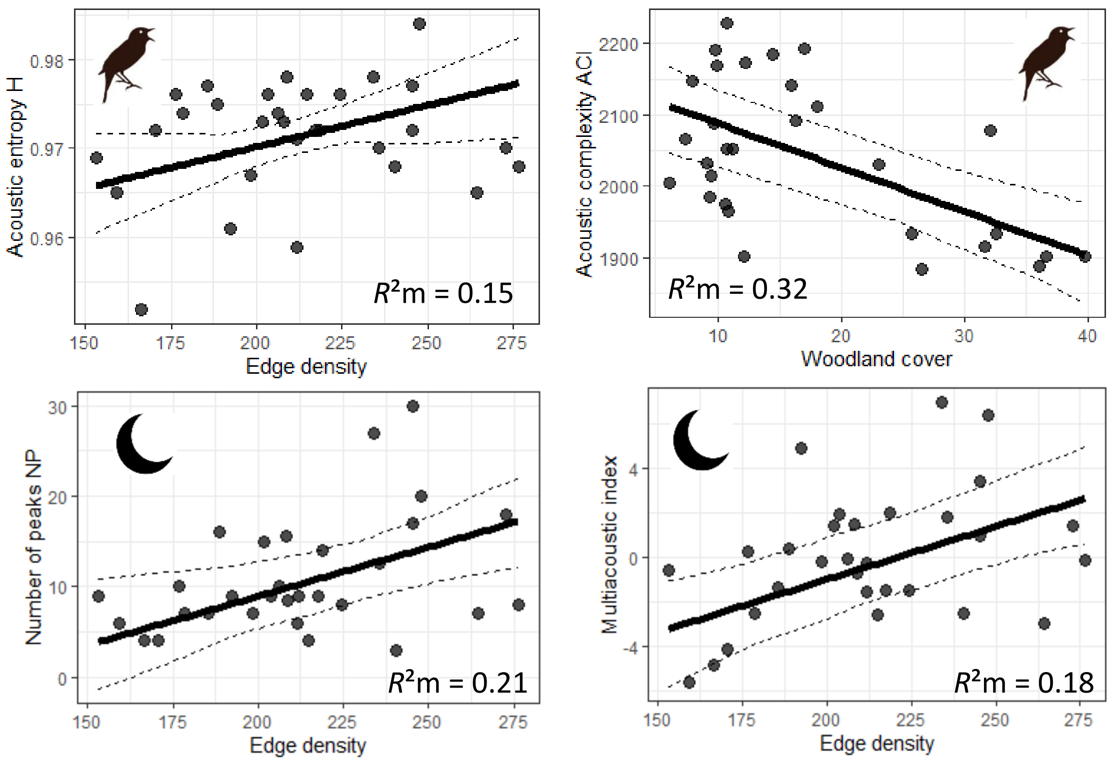


Fig. 6. LMM prediction biplots of the effects of landscape composition and configuration on median AIs for dawns (bird icon = 6.00 am – 9.30 am) and nights (moon icon = 22.00 pm – 5.30 am) in Aurignac county, Occitanie, France (N = 30). Marginal R^2 values of fixed effect are indicated. See Table 1 for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

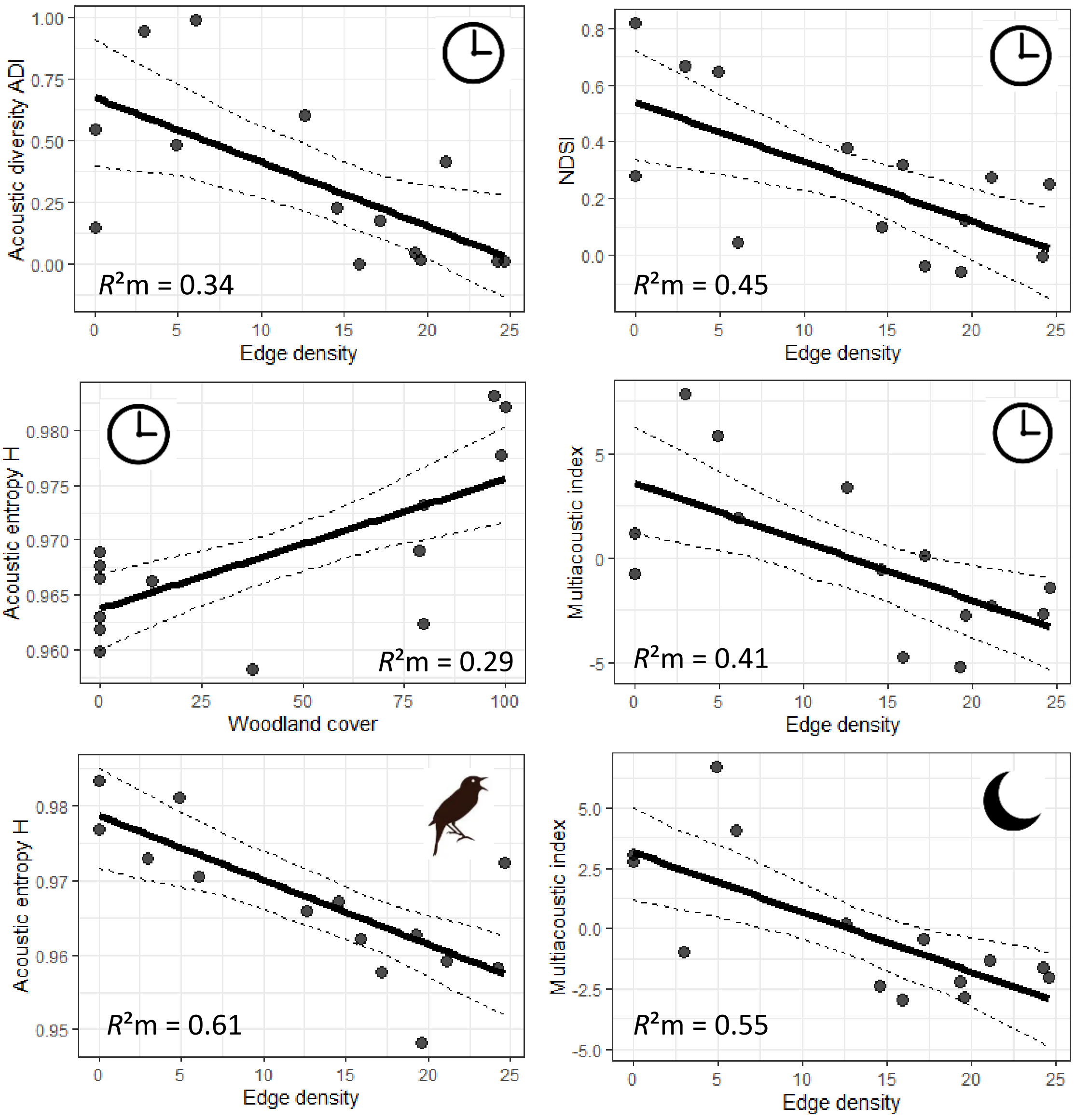


Fig. 7. LMM prediction biplots of the effects of landscape composition and configuration on median AIs for three time periods (clock icon = 24hr-diel; bird icon = dawns 6.00 am – 9.30 am; moon icon = nights 22.00 pm – 5.30 am) in Pima county, Arizona, USA (N = 14). Marginal R^2 values of fixed effect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