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Listening to a changing landscape: Acoustic indices reflect bird species richness and plot-scale vegetation structure across different land-use types in north-eastern Madagascar

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A R T I C L E I N F O

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A B S T R A C T

New technologies like ecoacoustic surveys promise time and cost efficiency for biodiversity assessments, serve as a basis for effective conservation policies, and are particularly appealing for remote and highly diverse tropical areas. Acoustic indices facilitate the analysis of large acoustic datasets but no consensus on their performance has been reached yet. We evaluated the efficacy of four acoustic indices (Acoustic Complexity Index, Acoustic Diversity Index, Acoustic Evenness Index, Acoustic Entropy) for sound data analysis and biodiversity assessments inside a national park and the agricultural mosaic landscape of north-eastern Madagascar, a global biodiversity hotspot. We used self-built sound recorders to continuously record soundscapes on 80 plots across seven land-use types (old-growth forest, forest fragment, forest–derived and fallow-derived vanilla agroforest, herbaceous and woody fallow, rice paddy) and compared index values between land–use types, assessed the correlation with bird species richness as measured by point counts, and related the acoustic indices to plot- and landscape-scale parameters. The Acoustic Diversity Index, Acoustic Evenness Index (inverse) and Acoustic Entropy were highest in old-growth forest and lowest for rice paddies and fallow land. Index values for structurally similar land-use types did not differ significantly from each other. The correlation of the three acoustic indices with bird species richness was strongest during daytime ($R^2 \geq 0.30$). Differences in the index values were best explained by land-use type and vegetation density. Our results showed that all investigated indices except the Acoustic Complexity Index were suitable biodiversity indicators for a tropical, agricultural landscape. Soundscape diversity was positively affected by plot-scale vegetation structure, emphasizing the importance of forests and particularly old-growth forest for conservation. We demonstrated that acoustic indices and sound recordings are a useful tool for assessing biodiversity in tropical agricultural mosaic landscapes. To realize the full potential of ecoacoustics in conservation, sampling guidelines and user-friendly analysis packages will be key to facilitate a wider implementation.

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1. Introduction

The anthropogenic alteration and overexploitation of the planet's ecosystems lead to global biodiversity loss at an unprecedented rate (Jantz et al., 2015; Newbold et al., 2015). Despite ambitious global targets to reduce biodiversity loss (Tittensor et al., 2014), pressure on biodiversity has increased notably over the past four decades (Butchart et al., 2010). Currently, agricultural expansion and intensification are the main drivers of the biodiversity crisis (Díaz et al., 2019).

Detailed accounts of the state and trends of biodiversity at a local scale are thus needed to inform effective conservation policies and environmental management practices (Díaz et al., 2019). However, field surveys, especially in remote tropical areas with high species diversity, can be time-consuming as well as logistically and taxonomically challenging (Gardner et al., 2008; Digby et al., 2013). Ecoacoustic surveys are a promising tool to overcome these limitations by reducing survey costs substantially through the use of open–source acoustic hardware and software (Whytock and Christie, 2017; Hill et al., 2018).

Ecoacoustic surveys rely on the Acoustic Niche Hypothesis which posits that each environment has a soundscape (Schafer, 1977; Pijanowski et al., 2011). The partitioning of the soundscape in time and frequency range results into a limited number of acoustic niches (Krause, 1993). The occupancy of acoustic niches by vocalizing species is regarded as an indicator for ecological integrity (Servick, 2014) and the

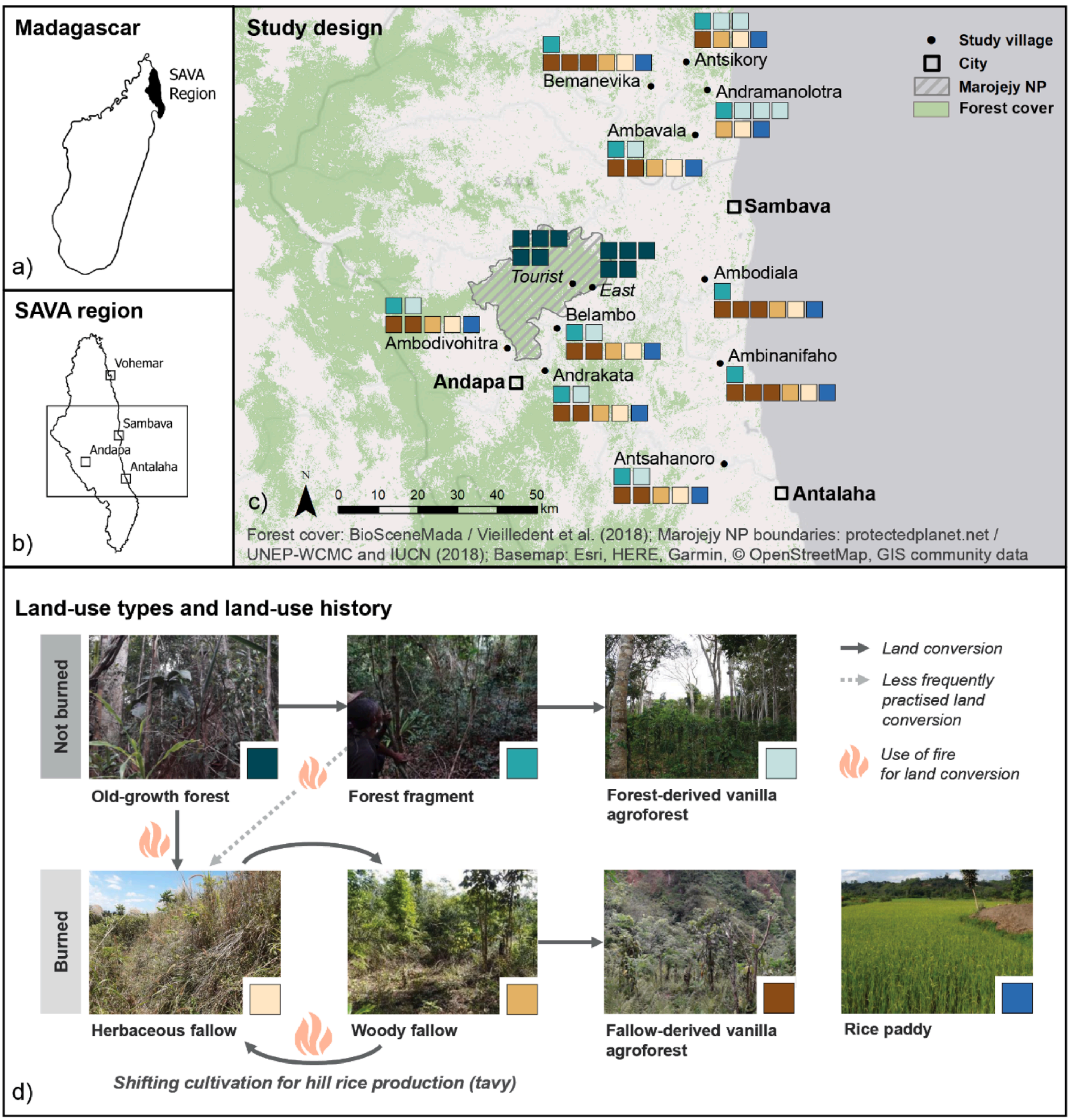

Fig. 1. Study area, study design and land-use types. a) Location of SAVA region in north-eastern Madagascar and b) study region therein. c) Distribution of 80 plots across 10 different villages and Marojejy National Park in the SAVA region. d) Overview of studied land-use types and typical transformation pathways.

number of species in a habitat is expected to increase the variety and complexity of acoustic signals (Sueur et al. 2008). In this context, it is important to note that vocalizing communities are not limited to the audible range and surveys may also include infra- and ultrasonic sounds.

Continuing developments in data storage capacities allow ecologists to gather large acoustic datasets in short time, but manual analysis of full datasets remains time-consuming. One alternative to a manual or species-focused sound data analysis is to assess the complete soundscape by computing various acoustic indices that determine, for example, the amplitude and frequency variation within a recording (Sueur et al., 2008; Buxton et al., 2018).

Rapid biodiversity assessment tools are particularly helpful in highly diverse tropical regions such as Madagascar. The country is a global biodiversity hotspot with exceptional endemism (Myers et al., 2000) and has lost 44% of its forest cover over the last six decades (Vieilledent et al., 2018). In north-eastern Madagascar, shifting cultivation of hill rice is the main driver of deforestation (Zaehringer et al., 2015). Successional stages within the shifting cultivation cycle and permanent small-scale vanilla agroforestry lead to a diverse landscape mosaic. The potential of vanilla agroforests for conservation is still poorly studied but likely depends on land-use history, that is whether an agroforest is established inside forest or on fallow open land formerly forested (Martin et al., 2020a).

The aim of this study was to investigate the efficacy of acoustic indices as a biodiversity indicator in the tropical, agricultural landscapes of north-eastern Madagascar. Specifically, we tested (i) if acoustic indices vary systematically across 80 plots covering the seven predominant land-use types of the study region (old-growth forest, forest fragments, forest-derived vanilla agroforests, fallow-derived vanilla agroforests, woody fallow, herbaceous fallow, rice paddy); (ii) if acoustic indices serve as a reliable proxy for biodiversity; and (iii) which environmental parameters co-vary with acoustic indices.

2. Materials and methods

2.1. Study area and design

We conducted this study in the SAVA region in north-east Madagascar (Fig. 1). The climate is tropical-humid with a mean annual temperature of 24 °C and annual rainfall of 2220 mm. The rainy season lasts from November to April (Tattersall and Sussman, 1975).

In our study area, there are seven prevalent land-use types (Fig. 1): i) Old-growth forests, which represent lowland tropical rainforests, the natural vegetation in the region; ii) Forest fragments, which are small remnants of old-growth forest, typically used for timber extraction by private landowners. Furthermore, we included two types of vanilla agroforests: iii) forest-derived vanilla agroforests, established inside of remaining forests, and iv) fallow-derived vanilla agroforests, established by conversion of fallow land that was formerly part of the shifting cultivation cycle. In forest–derived vanilla agroforests, the forest understory is thinned or cleared but native trees usually remain as shade trees and smaller trees are kept or additionally planted as support structures for the vanilla vines. In fallow-derived vanilla agroforests, in turn, shade and support trees either represent secondary regrowth or were subsequently planted. Additionally, we distinguished v) herbaceous and vi) woody fallows as successional stages within the shifting cultivation cycle of rainfed upland rice farming (*Malagasy: tavy*), different from vii) irrigated rice paddies. Herbaceous fallows last burned ~ 1 year before the start of our study in late 2017, while woody fallows last burned 4–16 years before.

For studying the seven land-use types, we selected 80 plots of 25 m radius, with 10 replicates for each land-use type (20 replicates for fallow-derived vanilla agroforests). The old-growth forest plots were at two sites within Marojejy National Park (241 to 701 m above sea level). The plots in the remaining land-use types were in 10 villages (7 to 819 m above sea level), placed using a nested design with one plot per land-use type per village, except for the two types of vanilla agroforest, which could not be equally distributed across villages (see Fig. 1c). The mean minimum distance from one plot to the closest neighbouring plot, regardless of land-use type, was 719 m (SD = 438 m) with a minimum of 260 m.

2.2. Plot characteristics

To quantify the structural complexity of the focal plots, we assessed basal area and vegetation density. Firstly, we calculated the basal area of all living trees with a diameter at breast height ≥ 8 cm. Secondly, we estimated the overall vegetation density including non-woody vegetation. To this end, we established vegetation density profiles (adapted from van der Maarel 1970) based on photographs taken in cardinal directions from the plot centre. From the photos, we estimated the vegetation density of six 0.5 m-layers between 0 and 3 m above ground in % and used all layers to calculate the average vegetation density for each plot (more detail in Schwab et al., 2020). We further extracted the elevation above sea level of all plots from the digital elevation model AW3D30 (Japan Aerospace Exploration Agency, 2016). To assess landscape-level effects of forest on acoustic indices, we calculated the forest cover within a 250 m radius around the plot centre using 2017 binary forest cover data (Vieilledent et al., 2018).

2.3. Bird point counts

We conducted one point count per plot between October and December 2017 and one point count per plot between August and December 2018 based on Bibby et al., 2000 (Supplementary Tables III-IV, in SI). We reversed the sequence of plots in the second year to avoid possible biases due to seasonal changes. In the old-growth forest, we did point counts only in 2018 but repeated them at the beginning and end of the field season (August/September; December) to cover similar seasonal conditions as in the other land-use types. We call the two sampling periods ‘year’ in the rest of the manuscript.

Each point count lasted 40 min and was done by two observers starting around sunrise and finishing before 8:15 AM (Supplementary Tables III-IV, in SI). For identification of bird species, we followed the field guide of Hawkins et al. (2015) and BirdLife nomenclature (Handbook of the Birds of the World and BirdLife International, 2018). We combined the 2017- and 2018-point count data to calculate the cumulative bird species richness for each plot, including only detections within the 25 m plot radius and excluding detections of species only seen in flight. Further details of bird point counts are described in Martin et al. (2020b).

2.4. Sound recordings

We used self-built, autonomous Solo audio recorders (Whytock and Christie, 2017) with two omnidirectional microphones (Supplementary Sec. I, Fig. I and Table II, in SI) and deployed them in the plot centre at 130 cm height for at least 72 h (continuous recording). We did the sound recordings during the same field work as point counts (October - December 2017; August - December 2018) and followed the same sampling sequence as for point counts (Supplementary Tables III-IV, in SI).

2.5. Acoustic indices

We randomly selected one continuous recording section (24 h, starting at 12 AM) per year per plot (Supplementary Tables III-IV, in SI). We visually inspected spectrograms of the chosen recording section and selected a different 24-hour section of that recording if precipitation or anthropogenic noise was high. We could not use one corrupted 2017 recording, resulting in a total of 3,816 recording hours used for index calculation.

We used R version 3.5.0 (R Core Team, 2018) and the *multiple_sounds* function of the package *soundecology* (Villanueva-Rivera and Pijanowski, 2018) to calculate four acoustic indices: the Acoustic Complexity Index **ACI** (Pieretti et al., 2011), the Acoustic Diversity Index **ADI** (Villanueva-Rivera et al., 2011), the Acoustic Evenness Index **AEI** (Villanueva-Rivera et al., 2011) and Acoustic Entropy **H** (Sueur et al., 2008). We selected the four acoustic indices based on their frequent use in recent ecoacoustic studies. To limit computation time, we used the setting of a maximum frequency (12 kHz) available for the ACI, ADI and AEI. To exclude low frequency background noise, we used the setting of a minimum frequency (0.2 kHz) available for the ACI and a dB threshold (-40 dB) available for the ADI and AEI. We provide an overview of all computational settings for index calculation in Supplementary Tables I in the SI.

We calculated the acoustic indices on 1-min-basis, resulting into 1,440 index values per continuous recording. To receive a final value per plot, we calculated the median of the full 24–hour-recording duration using the 1-min-based values of the 2017 and 2018 recording per plot. We did the same for shorter time intervals, specifically the night-time (12 AM – 5 AM; 6 PM – 12 AM), dawn chorus (5 AM – 8 AM) and daytime interval (5 AM – 6 PM). Because high AEI values represent high evenness within a recording (few or no signals), and to facilitate comparability, we present the results of this index inverse (1-AEI).

2.6. Statistical analyses

We performed all statistical analysis in R version 3.5.0 (R Core Team, 2018). We used the Shapiro–Wilk test to assess whether the acoustic index values (medians) were normally distributed. To determine differences in acoustic indices between the land-use types and because of non–normal distribution of the data, we performed a Kruskal-Wallis test and a pairwise Wilcoxon rank-sum test including Bonferroni correction. To test for a correlation between observed bird species richness and acoustic indices, we fitted linear and second–order polynomial models and selected the most parsimonious model based on the Akaike Information Criterion (AIC) (Akaike, 1998). We used the polynomial model only if its AIC value was at least two units lower than the AIC value of the linear model, because models with AIC values less than two units apart are equivalent and do not justify the use of higher complexity to describe a relationship (Burnham and Anderson, 1998).

We followed the approach of Burivalova et al. (2018) to investigate differences in the acoustic index values between land-use types and over time. We used the *lmer* function of the package *lme4* (Bates et al., 2015) to build linear mixed-effect models for every minute of the day: we included basal area, elevation, forest area within 250 m radius around plot centres, land-use type and vegetation density of plots as fixed effects (Supplementary Tables V, in SI). We included the 10 study villages and the two old-growth forest sites as a random effect. We rescaled the fixed continuous variables between zero and one and excluded two fallow-derived vanilla agroforests due to missing basal area data.

We used the *dredgeDS* function of the package *MuMIn* (Bartoń, 2018) that produces models with all possible combinations of the five explanatory variables, resulting in 2^5 (=32) models. We then sorted all 32 models for each acoustic index and each minute of the day according to AIC (Akaike, 1998; Burnham and Anderson, 1998). Subsequently, we calculated the relative variable importance for each fixed effect by summing up the Akaike weights over all models in which the effect appears. We did this separately based on how the fixed effect was considered within the model (positive; negative).

3. Results

Three of the acoustic indices (ADI, 1-AEI, H) varied systematically between the seven land–use types in north-eastern Madagascar (Fig. 2). Values for these acoustic indices were highest for old-growth forest and forest fragments (Fig. 3) and showed a strong correlation with bird species richness (Fig. 4). The plot-level vegetation density explained the differences in acoustic indices among the land–use types best (Fig. 5).

3.1. Temporal variation of acoustic indices

The ADI, 1–AEI and H showed a distinct temporal pattern (Fig. 2): Index values were high during night-time for all land-use types. After sunrise, we observed a strong decrease of the three acoustic indices in rice paddies and herbaceous fallows and values were lowest between 11 AM and 3 PM. Index values for woody fallows, fallow-derived and forest-derived vanilla agroforests decreased moderately after sunrise. The old-growth forest and forest fragments had high values throughout the day. The ACI showed no distinctive pattern for the different land–use types.

3.2. Differences in acoustic indices among land-use types

The ADI, the 1-AEI and H showed strongest differences in index values between land-use types during daytime, between 5 AM and 6 PM (Fig. 3). Differences were less substantial but still apparent during the full recording and the dawn chorus and became indistinct during night–time. These three acoustic indices showed highest values for old-growth forest and lowest values for rice paddy. During daytime, the index values for rice paddies, herbaceous and woody fallows, and fallow–derived vanilla agroforests were significantly lower ($p < 0.05$) compared to old-growth forest and forest fragments, with the H in woody fallow being the only exception (Supplementary Tables VI-VIII, in SI). The ACI showed the lowest values for the old-growth forest and the highest values for the herbaceous fallow.

3.3. Correlation of acoustic indices with bird species richness

There was a significant positive correlation between bird species richness and ADI, 1–AEI and H, respectively, for all time intervals (except 1-AEI during dawn chorus) (Fig. 4). The strongest correlation between bird species richness and the ADI (adj. $R^2 = 0.38$), the 1-AEI (adj. $R^2 = 0.30$) and H (adj. $R^2 = 0.39$) occurred between 5 AM and 6 PM (daytime interval). The second order polynomial model outperformed the linear model during this time interval. During night and dawn chorus, adjusted R^2 values were low and the linear model performed better (Supplementary Table IV, in SI). For the ACI, the correlation with bird species richness was significantly negative. However, adjusted R^2 values were very low (adj. $R^2 < 0.09$), indicating only a weak correlation.

3.4. Structural parameters of plots driving acoustic indices

The most parsimonious models explaining differences in ADI, 1-AEI and H values among plots included most frequently the variables vegetation density (during the whole day) and land-use type (especially during daytime) (Fig. 5). Furthermore, the basal area was a positive determinant for the 1–AEI. For the ACI, the best models most frequently included basal area and land-use type as variables. A higher basal area was negatively associated with ACI values and the elevation and vegetation density played only a minor role. The forested area in 250 m radius around plot centres was of low relevance to all four acoustic indices.

4. Discussion

We tested the performance of sound recordings and acoustic indices to assess and monitor the biodiversity in old-growth-forest, forest fragments and agricultural land-use systems in north–eastern Madagascar. Evaluating the efficacy of this emerging rapid biodiversity assessment method, we found three acoustic indices to be useful proxies for biodiversity.

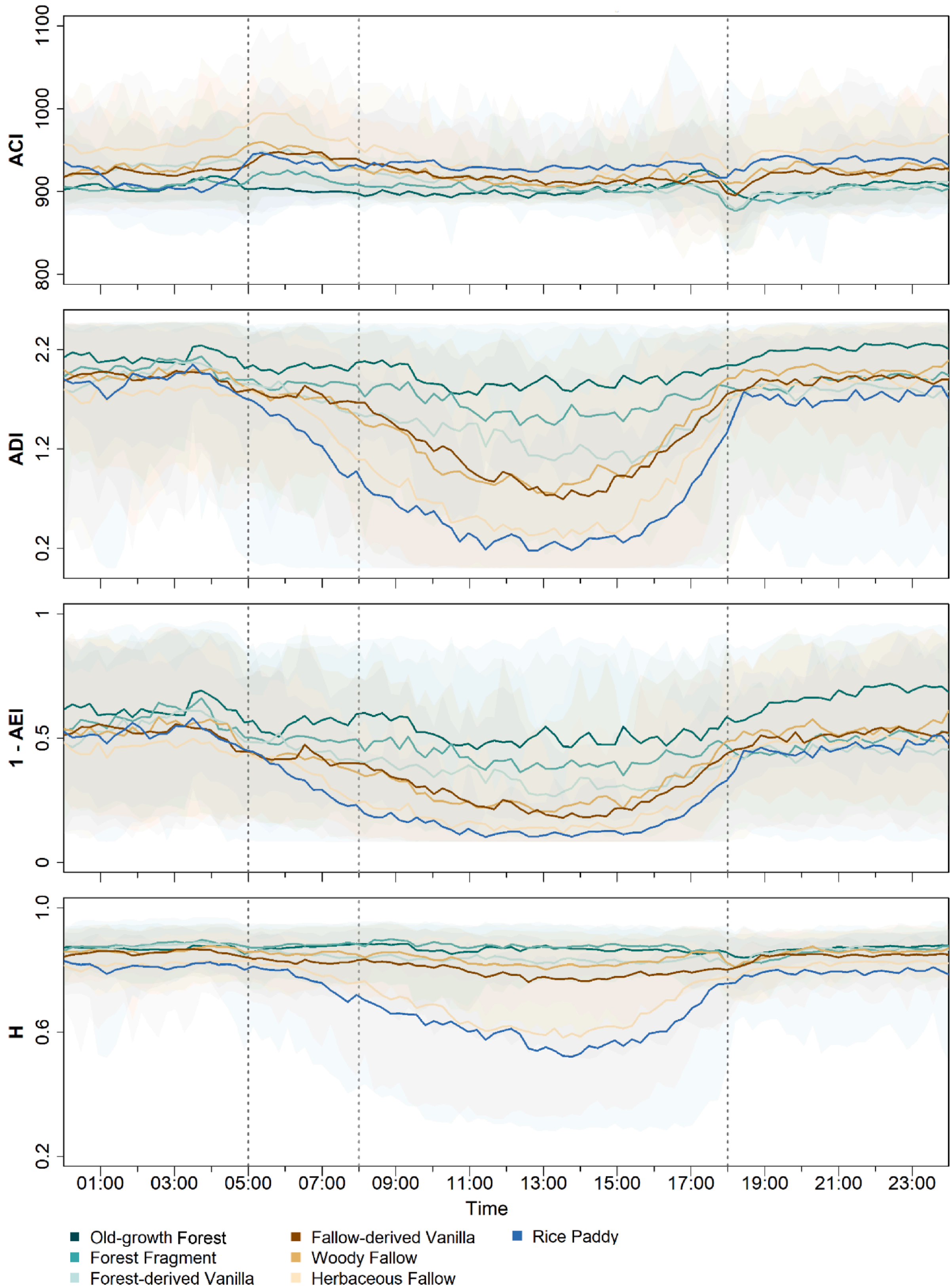

Fig. 2. Temporal variation of the Acoustic Complexity Index (ACI), the Acoustic Diversity Index (ADI), the inverse Acoustic Evenness Index (1-AEI) and Acoustic Entropy (H) for the different land–use types. We used one continuous recording of 24 h of each year (2017; 2018) per plot and calculated the acoustic indices on a 1-min-basis. Based on 10 replicates per land-use type (20 replicates for fallow-derived vanilla), we show the median (line) and 95%-confidence interval (background colour) for each land-use type. To facilitate interpretation and visualization, we applied locally weighted polynomial regression (LOWESS) on the medians and confidence intervals. Dotted lines mark sunrise (equivalent to start time of point counts), end time of point counts, and sunset.

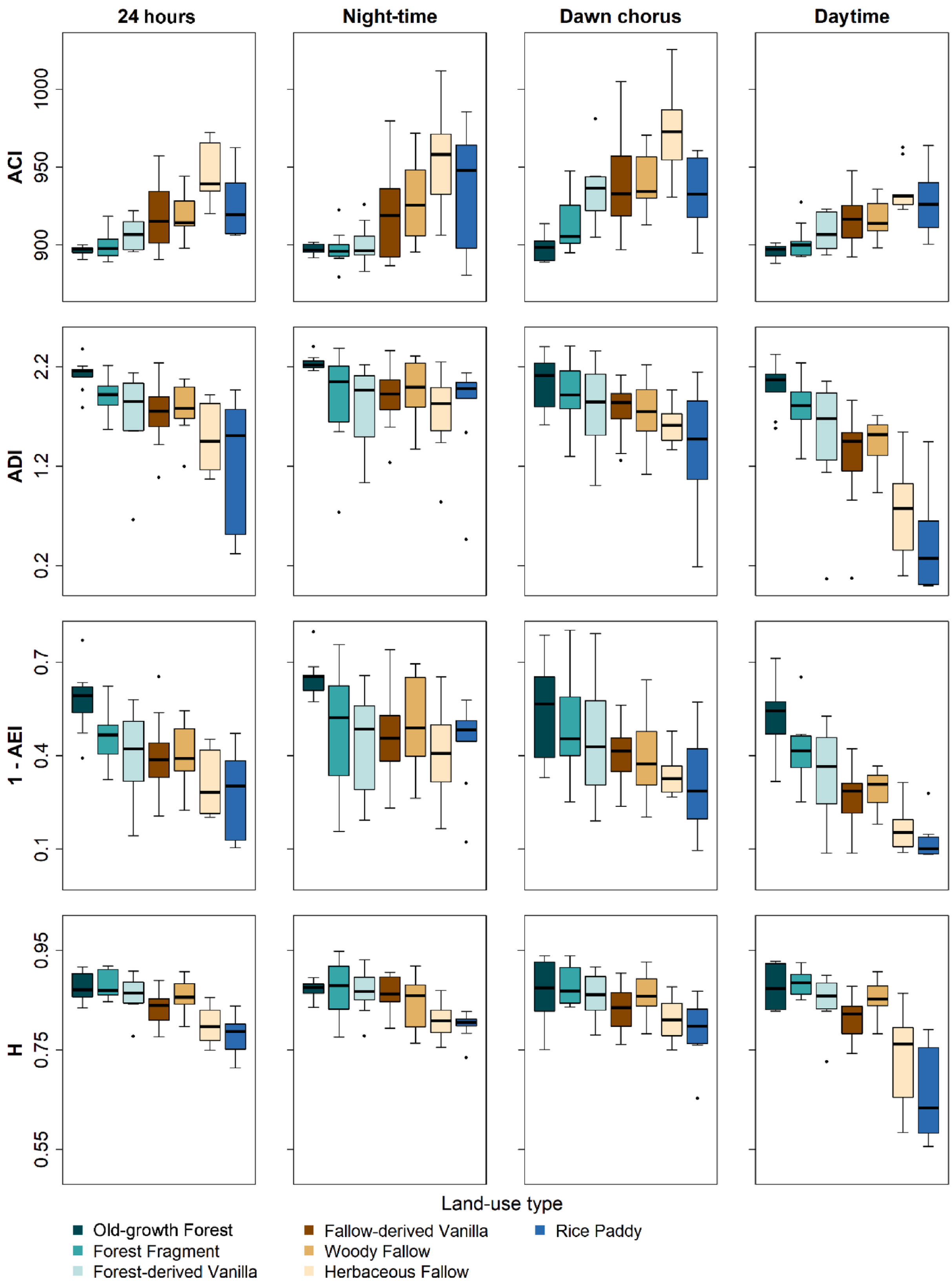

Fig. 3. Variation of the Acoustic Complexity Index (ACI), the Acoustic Diversity Index (ADI), the inverse Acoustic Evenness Index (1-AEI) and Acoustic Entropy (H) for 10 plots per land-use type (20 plots for fallow-derived vanilla). We used one continuous recording per recording seasons per plot (2017; 2018) and calculated the acoustic indices on 1-min basis. To receive a final value per plot, we used the 1-min-based values to calculate the median for the continuous 24 h recording, the night–time (12 AM – 5 AM; 6 PM – 12 AM), dawn chorus (5 AM – 8 AM) and daytime (5 AM – 6 PM). Box-and-whiskers represent lower extreme, lower quartile, median, upper quartile, upper extreme and outliers outside double interquartile range for each land-use type based on the plot medians.

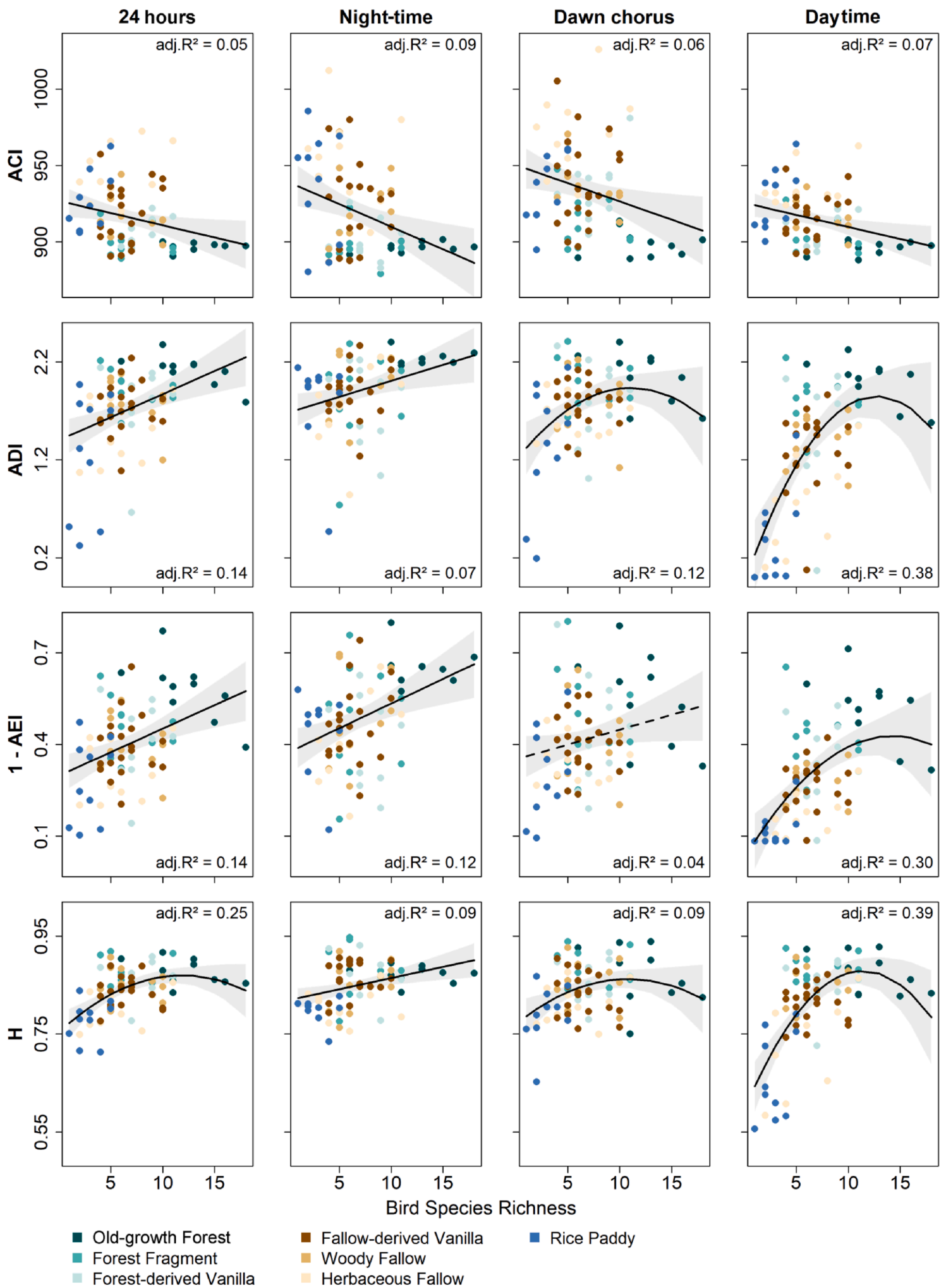

Fig. 4. Correlation between bird species richness and the Acoustic Complexity Index (ACI), the Acoustic Diversity Index (ADI), the inverse Acoustic Evenness Index (1-AEI) and Acoustic Entropy (H) for the different land-use types during the full 24 h recording duration, the night-time before 5 AM and after 6 PM, the morning chorus between 5 and 8 AM and the day-time between 5 AM and 6 PM. We tested a linear and a second-order polynomial model to describe the correlation. We display the simple linear model by default and only show the polynomial model if Δ AIC $\geq$ 2. The correlations are significant for all time intervals except one (dashed line). Grey ribbons indicate 95%-confidence intervals for each estimate.

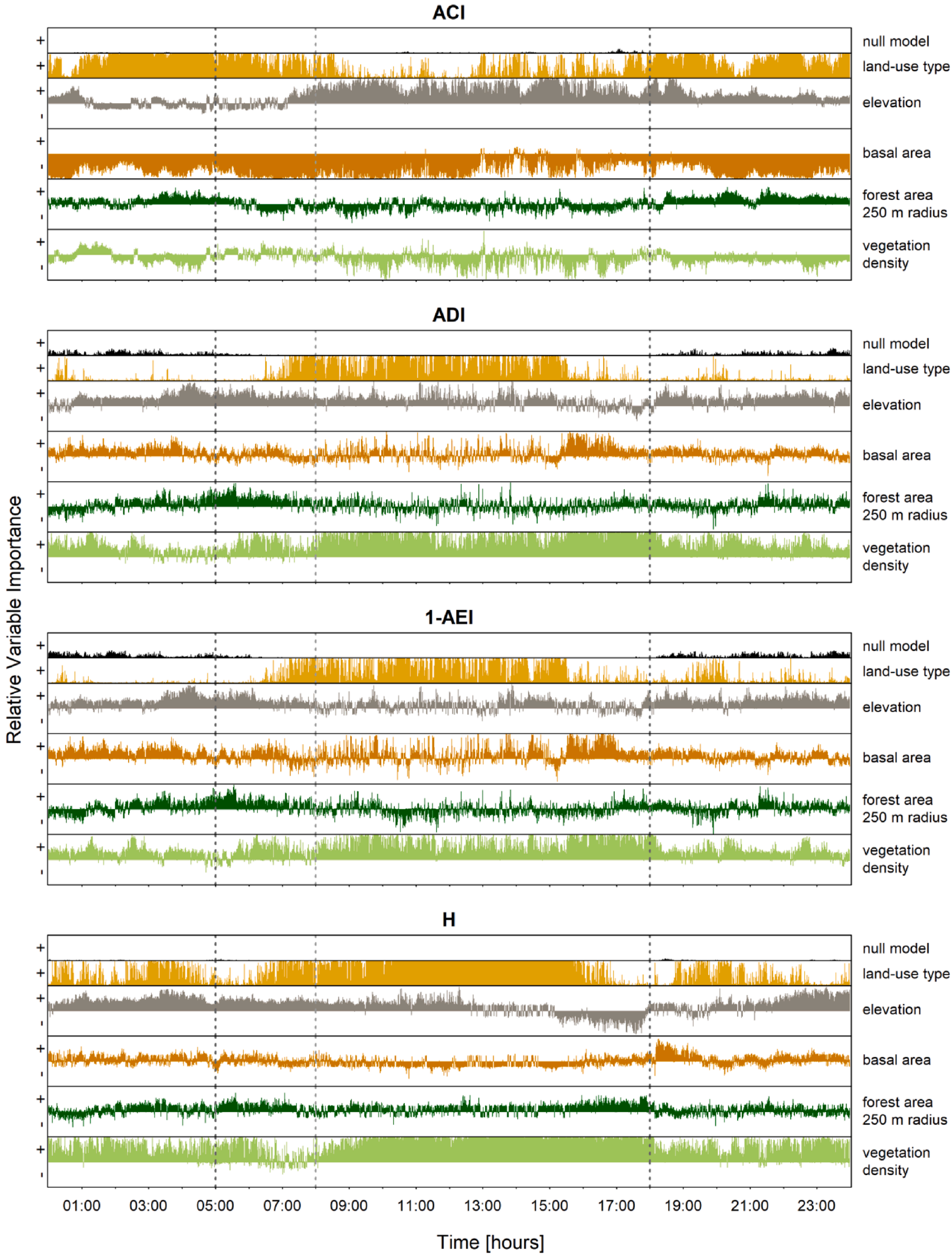

Fig. 5. Relative variable importance explaining differences in Acoustic Complexity Index (ACI), the Acoustic Diversity Index (ADI), the inverse Acoustic Evenness Index (1-AEI) and Acoustic Entropy (H). Model variables included land-use type, elevation, basal area, forested area within a 250 m radius around plot centre and vegetation density. Black colour represents the Akaike weight of the null model during that time of the day.

4.1. Systematic variation of acoustic indices among land-use types

We found that three acoustic indices varied systematically across the seven land–use types in north-eastern Madagascar (Fig. 3). The ADI, the 1-AEI and H showed the lowest index values for irrigated rice paddies and fallow land within the hill rice shifting cultivation cycle, typically facing highest land-use intensity and therefore indicating a lower value for biodiversity due to less suitable habitat. Acoustic index values for forest fragments and old-growth forest in particular were consistently high, emphasizing their importance for conservation, in line with results of previous studies relying on conventional methods (Rocha et al., 2015; Gardner et al., 2016).

As the ACI should theoretically be high in habitats with higher variability in biotic sound intensity (Pieretti et al., 2011), our results were contrary to our expectations and opposite to the other three indices studied: ACI values were highest in herbaceous fallows and rice paddies and lowest in old-growth forest (Fig. 3). This might be because irrigated rice paddies can be dominated by a single distinct signal, like the vocalizations of amphibians during night-time, therefore having a high variation in sound intensity. Additionally, boundaries of vocalizations of different species in a diverse habitat like an old-growth forest may overlap, ultimately leading to a lower variation in sound intensity over time and thus lower ACI values. Therefore, the ACI might not be a useful biodiversity indicator in a tropical, agricultural landscape.

4.2. Acoustic indices as a proxy for biodiversity

We found that the ADI, 1-AEI and H were correlated with bird species richness, a standard biodiversity indicator. This correlation was particularly strong during daytime. Our results are thus in line with a case study from South China, which reports the same three acoustic indices to be correlated with bird species richness (Mammides et al., 2017). Similarly, a case study from the Brazilian Cerrado showed a correlation of bird species richness and the ADI (Machado et al., 2017) and in the Brazilian Atlantic Rainforest, AEI was correlated with species richness (Jorge et al., 2018). The higher support for the polynomial models during daytime indicates a saturation in the soundscape as index values do not differ between species-rich plots (Fig. 4). Hence, losses in species richness within species-rich plots may not be reflected by acoustic indices, limiting the efficacy of these particular indices in hyper-diverse tropical forests. This limitation could be overcome by a multiple analysis approach including machine learning, as well as new variations of indices.

Contrary to our expectations, the ACI showed a negative and only weak correlation with bird species richness. Retamosa Izaguirre et al. (2018) reported the ACI to be useful to monitor bird abundance in a tropical dry forest in Costa Rica. Towsey et al. (2014) confirmed the viability of the index for species diversity for bushland in eastern Australia. However, our results do not provide evidence for the ACI being a good proxy for bird species richness in north-eastern Madagascar.

4.3. Plot-scale vegetational structure related to soundscape diversity

The three acoustic indices describing the soundscape diversity of the study plots were mainly related to the plot-specific vegetation structure. Vegetation density, and to a lesser extend basal area, were positively associated with higher index values. Our findings indicate that maintaining vegetation structure in the agricultural landscape and preventing forest degradation is key to preserve a high soundscape diversity.

The soundscape of natural environments is composed by vocalisations of birds, amphibians and insects. Therefore, we would not expect a perfect correlation of the four acoustic indices with bird species richness, as this is only one taxon representing a part of the acoustic fingerprint of a habitat. Furthermore, the contribution of understory-dependent amphibians and insects to the recorded soundscapes may explain why the plot-scale vegetational structure was of highest relevance for the soundscape diversity within our study. Supporting this theory, it has been observed that insects and frogs can dominate dusk and dawn chorus in tropical biomes (Farina and Gage, 2017). It also points out to the potential of ecoacoustics to assess biodiversity holistically through regarding the full soundscape instead of focusing on single indicator taxa, which may respond to land-use change very differently (Barlow et al., 2007).

4.4. Implications for the use of acoustic indices for biodiversity assessments

Three acoustic indices (ADI, 1-AEI, H) showed strongest differences in the soundscape of the different land-use types in north-eastern Madagascar during noon and afternoon (Fig. 2). Only few ecoacoustic studies have described similar patterns of high soundscape diversity during night–time and a decline during daytime (Gasc et al., 2013; Fuller et al., 2015). As demonstrated in this study, only continuous recordings are able to reveal such fine temporal patterns, yet many studies rely on a reduced sampling scheme, e.g. recording 1 min every 10 min (Gómez et al., 2018) or only dawn and dusk chorus (Depraetere et al., 2012), due to data storage capacities and battery power. Continuous sampling for several days in a row is desirable to capture the complete soundscape and diurnal trends. Moreover, it is the basis for the comparability of ecoacoustic surveys across different biomes, as advocated by Bradfer-Lawrence et al. (2019).

Currently, a limiting factor for conservation practitioners to use acoustic indices for rapid biodiversity assessments is the challenging nature of sound data analysis. Due to the variability of habitats and lack of standard protocols, the settings for index computation (e.g. frequency thresholds and dB-thresholds) are mainly set by trial and error. More research and case studies are needed to provide firm guidelines for ecoacoustic surveys, including, for example, user–friendly and open-source analyses packages.

The acoustic indices used in our study captured substantial differences between land-use types but were not suitable to detect the more subtle differences in the soundscape of structurally similar land-use types, particularly in species rich habitats. Furthermore, some acoustic indices rely on the same coefficients (Shannon-Index; ADI and H) or similar equations (ADI and AEI) used for computation. Some acoustic indices are hence correlated (Supplementary Fig. II, SI) and thus provide partly redundant information. An alternative might be a combination of analyses, including e.g. automated classification and machine learning, which currently focus on the identification of a single or few species (Aide et al., 2013). However, the latter approaches would require advanced knowledge in signal processing, large training data sets and available software may not be open source (Priyadarshani et al., 2018).

4.5. Implications on the potential of vanilla agroforests for biodiversity conservation

We found that forest-derived vanilla agroforests had similar acoustic index values as forest fragments, suggesting the maintenance of biodiversity after conversion of forest fragments into forest-derived vanilla agroforests (Fig. 3). Fallow-derived agroforests, on the other hand, had index values similar to woody fallows, the land-use type on which such agroforests are typically established. These results highlight the importance of land–use history when assessing the conservation value of agroforests (Martin et al. 2020a). Agroforests can increase landscape connectivity (Bhagwat et al., 2008) and previous studies in Madagascar showed that the agricultural landscapes can support a high number of the endemic birds if forest fragments remain within a landscape mosaic (Martin et al., 2012). Currently, expanding vanilla agroforestry could thus be biodiversity-friendly 1) if forest-derived agroforests contribute to tree maintenance by avoiding complete forest fragment loss and 2) if the establishment of fallow-derived agroforests on woody fallows leads to a cessation of the shifting cultivation cycle on this land. The potential of vanilla agroforests to complement and enhance the landscape mosaic will, however, need further research.

5. Conclusions

Autonomous sound recordings and acoustic indices are regarded as time-efficient assessment tools in the biodiversity conservation context. Based on an exceptionally large acoustic dataset, our study contributes to a better understanding of the relationship between acoustic indices and bird species richness as well as between acoustic indices and plot- and landscape-scale characteristics. We found that the Acoustic Diversity Index, the Acoustic Evenness Index, and the Acoustic Entropy are informative metrics to analyse sound data and estimate soundscape diversity in a biodiverse tropical landscape. Acoustic index values were highest for the old-growth forests, highlighting their importance for conservation, however, forest fragments also retained relatively high index values. Our results emphasize the potential of vanilla agroforests to contribute to the maintenance of biodiversity in the agricultural landscape. Nonetheless, the acoustic indices alone did not allow us to distinguish structurally similar land-use types due to high variations in soundscapes within land-use types. The Acoustic Complexity Index emerged as not useful in our study region. Using a multiple analysis approach, e.g. including machine learning, could overcome methodological limitations. Together with user-friendly analysis packages and firm guidelines this will facilitate a wider implementation of ecoacoustics in applied ecology and conservation.

6. Author's contributions

SD, DAM and HK designed the study. SD, DAM, RA, ER and TRF collected sound and bird data; KO collected basal area data and DS collected vegetation density data. DAM prepared the point count data; SD analysed the sound data and wrote the first manuscript draft. ZB contributed to the mixed effect modelling. All authors contributed to the manuscript and gave final approval for publication.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability statement

Data (plot parameters, acoustic index minute-based values, acoustic index median values, bird-species richness) are available via Mendeley Data, https://doi.org/10.17632/fxxnwtmynv.1 (Dröge et al., 2020).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2020.106929.

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