

RESEARCH ARTICLE

Forest edge structure from terrestrial laser scanning to explain bird biophony characteristics from acoustic indices

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Abstract

Forest edges can be important strongholds for biodiversity and play a crucial role in the protection of forest interiors against edge effects. However, their potential to host biodiversity is dependent on the structure of the forest: Abrupt edges often fail to realise this potential. Yet, methods to accurately characterise and quantify forest edge abruptness are currently lacking. Here, we combine three-dimensional forest structural data with biodiversity monitoring to assess the influence of forest edge structure on habitat suitability. We derived several structural metrics to determine forest edge abruptness using terrestrial laser scanning and applied these to six forest edge transects in Belgium. The local soundscapes were captured using audio recording devices (Audiomoths) and quantified using acoustic indices (AIs) (metrics on the soundscape characteristics). In each transect, the dawn choruses were recorded over a period of a week, both at the edge and the interior of the forest. No correlation between the AIs and bird species richness was found. There were clear differences between transects in the structural metrics and the recorded soundscapes. Some possible relations between both were found. In this proof of concept, we demonstrated innovative techniques to semi-automatically classify forest structure and rapidly quantify soundscape characteristics and found a weak effect of forest edge structure on bird biophony.

Introduction

Habitat loss is one of the key threats to global biodiversity (Almond et al., 2020). Human activities, such as urbanisation and agriculture, are continuously expanding at the expense of natural habitats and lead to habitat loss and fragmentation. Habitat fragmentation per se can have positive effects on biodiversity, mostly attributed to the formation of transition zones between different habitats (Fahrig, 2017). These transition zones, called ecotones,

are potential hotspots for biodiversity, housing both species from the two neighbouring habitats as well as ecotone-specific species (Duelli et al., 2002; Müller et al., 2007). This is possible due to the presence of gradients in environmental conditions, such as moisture and temperature, creating a wide range of possible niches. However, fragmentation is often a direct result of habitat loss and ecotone formation is often limited or even absent due to human interference. Forest edges are a prime example of an ecotone that is often affected. Temperate

deciduous forest particularly are overall strongly fragmented habitats (Haddad et al., 2015). In Europe for instance, 4% of the deciduous forest is already less than 4.5 m from the forest edge (Meeussen et al., 2021). The result is a landscape of fragmented forest patches in a non-forest matrix that often consists of low-quality habitat. Because the forest edges in these patches often lack a gradual, established ecotone, their potential for biodiversity is impaired (Wuyts et al., 2009). The negative effect of abrupt edges has been demonstrated extensively for invertebrate communities via insect inventory studies (Duelli et al., 2002; Müller et al., 2007; Wermelinger et al., 2007), which found lower species numbers in abrupt forest edges. Adverse effects of abrupt and exposed edges on vertebrate communities have also been reported, for instance on nesting success rate in bird populations (Flaspohler et al., 2001).

Forest edge abruptness can also be linked to forest edge openness. Openness here refers to the presence of gaps and openings in the canopy. It is the canopy in forests that shields the understorey against direct sunlight and high winds, resulting in reduced temperature and moisture fluctuations (De Frenne et al., 2021), which contributes to the microclimate of the typical forest interior. However, the presence of gaps in the canopy in open forests allows more light to penetrate into the forest, reducing this sheltering effect (Meeussen et al., 2021). Offsets are indeed generally lower in open forests and it takes a significantly longer distance into the forest before the interior microclimate conditions are reached. This is in line with previous work on nitrogen deposition that reported an increased penetration of edge effects in more open forest edges (Wuyts et al., 2009). Because it takes longer for the interior forest conditions to be reached, the transition from edge to core is more gradual and thus can be seen as less abrupt. This results in a more clear ecotone formation. The caveat to this is that the forest edges in these open forests are broader, limiting the development of interior forest habitat in smaller forest patches.

Whereas the negative effect of abrupt forest edges has been extensively studied, the abruptness itself is rarely quantified. Rather, most studies qualitatively define edges as either smooth, abrupt or somewhere in between. Due to the complex three-dimensional (3D) structure of forest edges (and forests in general), quantifying edge structure is a challenging task. Terrestrial laser scanning (TLS) can produce highly detailed 3D structural data in forests, from which quantitative structural metrics can be derived (Calders et al., 2020). Using such a quantitative approach allows for a more objective comparison between different forest edges. The applicability of TLS in forest edge research has been demonstrated multiple times in the last years. Meeussen et al. (2020) used TLS-derived metrics,

such as the Plant Area Index, to model edge-to-core patterns in forest structure and carbon stocking in temperate forest edges. Recently, similar edge-to-interior models were also constructed for seven transects in the Amazon and were used to investigate the impact of edge effects on forest structural traits and diversity (Maeda et al., 2022; Nunes et al., 2022). This type of quantitative approach to forest structure could also be used to explore the effects of forest edge structure on the ecological communities they house.

Sound is an important aspect in the ecology of many animal species, across all types of habitats. It is often used as a means of exchanging information between individuals and plays an important role in numerous ecological events, such as breeding, hunting or territorial behaviour (Farina & Gage, 2017). Therefore, sound contains a significant level of data regarding many ecological processes, which means that sound can be a powerful resource for monitoring biodiversity. This idea has opened up a new field of research, called ecoacoustics (Sueur & Farina, 2015). The framework of ecoacoustics revolves around the analysis of soundscapes to monitor dynamics over time or differences between locations. Shifts in the soundscape over time can provide new insights into the dynamics of ecological communities, for instance the response of animal communities to forest disturbances such as fires or logging (Rappaport et al., 2020). This new framework, combined with an increasing technical feasibility of large-scale remote acoustic sensing, has sparked an interest in the development of metrics that provide fast, quantitative information of recorded soundscapes. Over the last years, a wide array of these so-called acoustic indices (AIs) have been developed (Eldridge et al., 2016). These AIs allow us to rapidly derive information from sound recordings without the need for expert knowledge. Many of these AIs have been developed on birds in temperate regions (Pieretti et al., 2011; Sueur, Pavoine, et al., 2008) to assess either activity or biodiversity. While fast analysis speed is a major benefit when analysing large volumes of data, certain drawbacks regarding AIs need to be considered. They can be heavily impacted by noise from sources such as insect sound, traffic or rain, which should therefore be avoided during recordings (Eldridge et al., 2016; Pieretti et al., 2011; Sueur, Pavoine, et al., 2008). Secondly, some biodiversity AIs become less reliable for recordings with a low species richness (Sueur, Pavoine, et al., 2008). Finally, there is a trade-off in terms of detail compared to traditional inventories, as species lists are missing.

Here, we provide a proof of concept on the combination of highly detailed structural data with ecological monitoring via sound in temperate forest edge-to-core transects. The study was performed in six contrasting

forest transects (thinned and unthinned) in temperate deciduous oak forests in Belgium. We derive TLS-based structural metrics describing the abruptness and openness of the forest edges. We then couple these forest-structural data with AIs, derived from bird recordings in those edge-to-core transects, to explore the effects of forest edge structure on the recorded soundscapes. We demonstrate how TLS data can be used to more objectively quantify forest edge structure and how this can be applied in ecological research. We hypothesise to find a negative effect of both forest edge abruptness on bird biodiversity.

Materials and Methods

Study design

Data were acquired from six different edge-to-interior transects in temperate forest stands in Belgium. The forest stands were distributed over three different regions (labelled R1, R2 and R3). Each region contained two transects, one of which was unthinned, while the other

was recently thinned (Fig. 1A). In each transect, two sampling plots were located, one at the forest edge and one in the forest interior (Fig. 1B). The interior plots were located at approximately 100 m from the edge plot, and at least 100 m from any other forest edge. The edge plots were located 1.5 m from the forest edge. All transects were located in south orientated edges and were laid out perpendicular to the forest edge. All forest stands were oak dominated (*Quercus robur*, *Q. petraea*). The most prominent secondary species were beech (*Fagus sylvatica*), hornbeam (*Carpinus betulus*) and sycamore (*Acer pseudo-platanus*). The layout of the transects is described in detail by Govaert et al. (2020) and Meeussen et al. (2020).

Data collection

Acoustic data

Acoustic data were collected at all sites using digital sound recorders (AudioMoth; Open Acoustic Devices, UK). Two recordings were installed in each transect, one

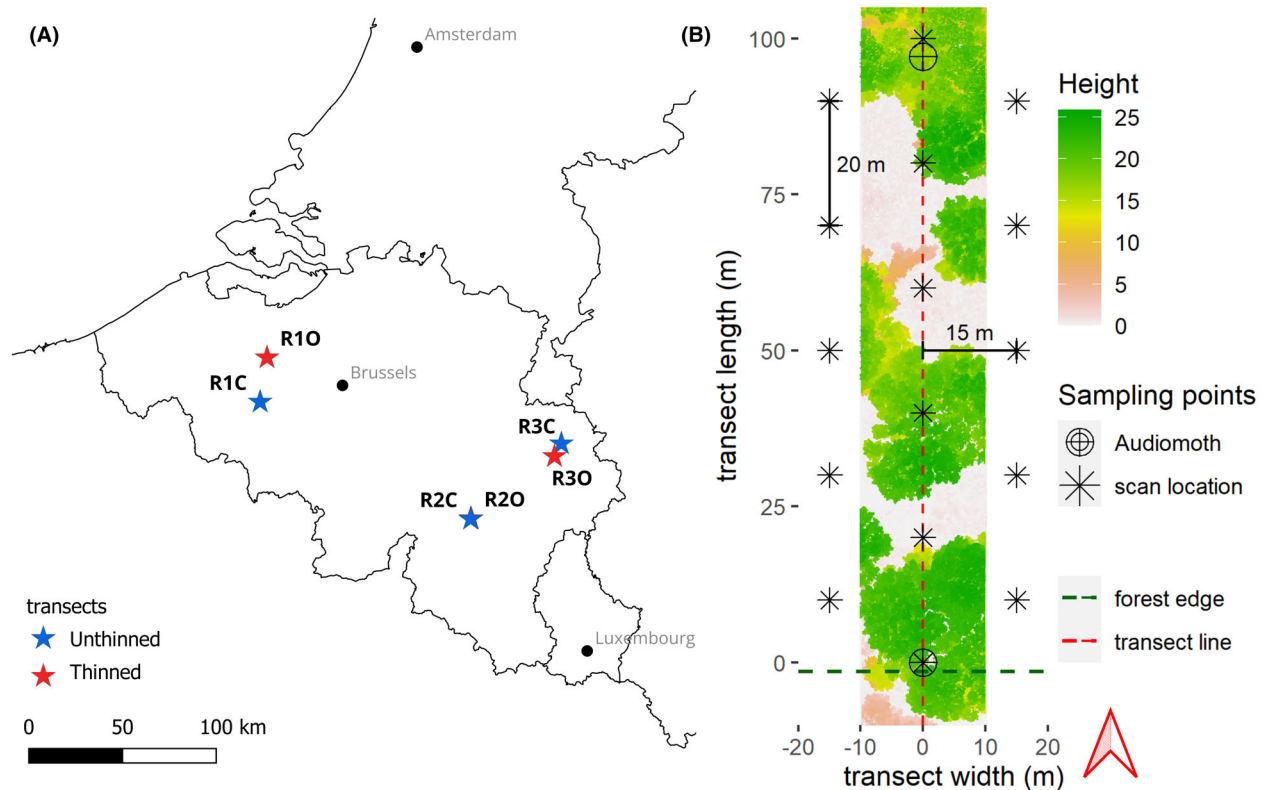


Figure 1. (A) Map of the geographical distribution of the transects in Belgium. The stars in R2 overlap, because the transects in this region were located in the same forest. (B) Overview of the data collection protocol. Terrestrial laser scanning data were collected in three staggered rows parallel to the edge-to-core transect line. The middle row was located on the transect line. The rows were 15 m apart and the scan locations in each row were 20 m apart. Finally, two additional scan locations were also included, one outside of the forest and one deeper into the forest core (not shown on the figure). Audiomoths (Open Acoustic Devices) were installed on the edge (0 m) and core plot (~100 m).

at the edge plot and one at the core plot (Fig. 1B). The AudioMoths were programmed to record for 5 min every 15 min during the dawn chorus from roughly 1.5 h before to 2.5 h after sunrise. Recordings at region 2 and region 3 were held from 29 March 2021 to 04 April 2021, while the recordings at region 1 were held from 21 April 2021 to 28 April 2021. A sampling frequency of 48 kHz was used, allowing for frequency analysis from zero up to 24 kHz, which ensures the typical bird activity range of 2–8 kHz is completely included (Gage et al., 2001). The recordings were scheduled during the dawn chorus in the breeding season, as the highest amount of bird activity was expected during these periods. Previous studies have shown this can increase the reliability of certain indices as a predictor for species richness (Sueur, Pavoine, et al., 2008). Furthermore, insect broadcasting typically starts around July in temperate Europe (Farina et al., 2011), so by recording in spring, insect interference was largely avoided. Lastly, a 1 kHz high-pass filter was applied over the recordings to filter out background noise, such as traffic, which is often characterised by low-frequency sounds (<1 kHz).

Structural data

Highly detailed structural data were acquired for the transects using TLS. Leaf-on TLS data were obtained from the forest edges using a RIEGL VZ400 (RIEGL Laser Measurement Systems GmbH, Horn, Austria) in July 2020 (Fig. 1B). The field of view of this scanner is 100° along the zenith and 360° along the azimuth. To overcome the zenith range limitations, two scans were taken at each scan location, one vertical and one tilted at a 90° angle. This allowed for a complete sampling of the canopy structure at each scan location. Before scanning, 48 retro-reflective co-registration targets were semi-randomly placed across the entire transect so that at least three reflectors would be visible on each scan. A scan resolution

of 40 mdeg was used, which results in a point spacing of 34 mm at 50 m distance from the scanner. A 300 kHz laser pulse repetition rate was used.

Data processing

Acoustic data

The sound recordings were analysed using a suite of AIs commonly used in research to monitor bird activity and species richness (Table 1). The AIs are computed using the R packages *soundecology* (Villanueva-Rivera & Pijanowski, 2018) and *seewave* (Sueur, Aubin, et al., 2008). The Normalised Difference Soundscape Index (NDSI) was used as a selection criterion for recording quality. This index ranges between −1 and 1, where low values indicate high anthropogenic activity, low bird activity or both, which could potentially interfere with the other AIs (Kasten et al., 2012; Pieretti et al., 2011; Sueur, Pavoine, et al., 2008). Recordings with a negative NDSI value were discarded as this indicates high anthropogenic disturbance. The other selected AIs we then calculated for all remaining recordings on a 1-min basis, so five values were computed per recording for each AI. For these AIs, the daily median values were then calculated.

Finally, the recorded bird species were identified by a bird expert for a sample of sixty 1-min chunks. This was used to validate the use of the AIs as direct proxies for biodiversity metrics, specifically species richness. Five recording chunks of 1 min were randomly selected from each sampling plot, resulting in a total of 60 recordings. For these chunks, all audible bird species were identified and given a dominance score between 1 and 4. One indicating that the species was only heard once, four indicating that the species was vocalising for almost the entire duration. Two metrics were derived using this species information, the species richness and a Shannon diversity index based on the dominance scores. Correlations with the AIs were then explored.

Table 1. Overview of the selected acoustic indices calculated from the sound recordings in forest edges (Bradfer-Lawrence et al., 2019).

Acoustic index	Proxy for	Value	Reference
Normalised difference soundscape index (NDSI)	Anthropogenic noise	$-1 \leq \text{NDSI} \leq 1$ (anthropogenic – biotic)	Kasten et al. (2012)
Acoustic complexity index (ACI)	Bird activity/number of bird vocalisations	Dependent on recording length	Pieretti et al. (2011)
Acoustic diversity index (ADI)	Species richness/distribution	0–4 ⁺ (one species – ...) (Shannon–Weaver index)	Villanueva-Rivera et al. (2011)
Acoustic evenness index (AEI)	Species richness/distribution	0–1 (even – uneven)	Eldridge et al. (2016)
Bioacoustic index (BI)	Species richness	BI = ^a	Boelman et al. (2007)
Acoustic entropy index (H)	Species richness	0–1 (pure tones – noise)	Sueur, Aubin, et al. (2008)

^aSDF = sound density function/bioacoustic spectrum.

Structural data

The TLS data of individual scan locations were co-registered into one large point cloud using RiSCAN PRO v2.10 (RIEGL). The transect was cut out of this point cloud as a 20-m wide rectangle around the transect line. This new transect point cloud was filtered using a deviation filter (>12) to keep high-quality points (Calders et al., 2017).

The total number of data points in the point clouds was reduced using a 0.02-m subsampling and the default SOR filter in *CloudCompare v2.12.0* (CloudCompare, 2022). Finally, all transects were rotated in order to align the transect lines with the y -axis. A translation was then applied to move the edge plot to the origin of the coordinate system. The computation of further structural metrics was done using R (R Core Team, 2021), using the *lidR* v4.0.1 package (Roussel et al., 2020; Roussel & Auty, 2021).

Forest edge abruptness

The forest edge abruptness was evaluated based on the presence of sudden height jumps and the rate at which the vegetation height increased from edge to core. To achieve this, lateral height profiles of the transects were first constructed (Fig. 2). These height profiles were based

on height grids that were computed using the *lidR* function *gridmetrics()*. This function divides an input point cloud into a grid of a certain resolution and then applies a user-defined function on each pixel in this grid. A resolution of 0.1 m was chosen. Two user-defined functions were created as input for *gridmetrics()*, a canopy height and a terrain height function. The canopy height function calculated the maximum z -axis value in each pixel, while the terrain height function calculated the minimum z -axis value. As a result, 16 grids were created, one canopy height grid and one terrain height grid for each transect. These grids were then transformed into the lateral height profiles of the canopy and terrain along the transect. This was done by taking the 90% quantile for each pixel row along the transect length (Figure A1). The 90% quantile was chosen over the mean to reduce the impact of gaps in the canopy or local depressions in the terrain, as that could lead to an underestimation of the overall height.

Finally, the vegetation height profile was calculated by subtracting the terrain height profile from the canopy height profile. This new profile represents the actual height of vegetation along the transect. For most transects, this difference was mostly conceptual and the actual values were similar or nearly identical. However, at transects with a significant topography, large differences existed. The vegetation height profiles were used to

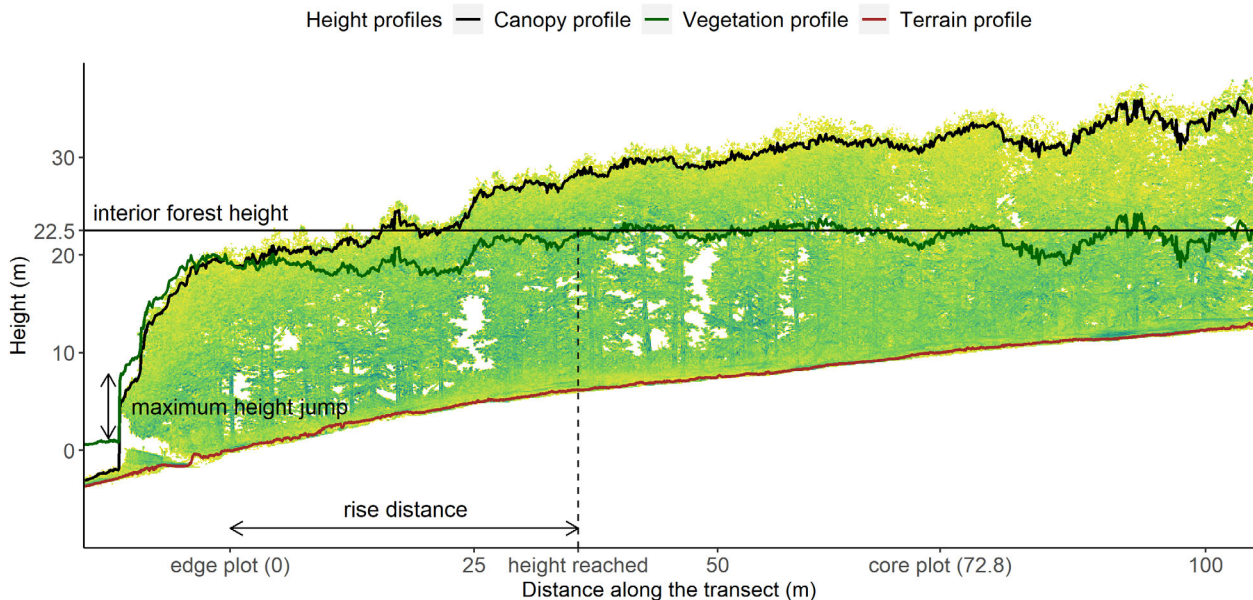


Figure 2. An overview of the lateral height profiles and the corresponding structural metrics for the open transect in region 3. The conceptual difference between the canopy and vegetation height profiles can be clearly seen on this transect due to its location on a hill (continuously rising terrain height profile). The location of the sampling plots (edge and core plot) where the Audiomoths were installed are also indicated on the x -axis. The core plot in this specific transect is located at 72.8 m due to the presence of a road around the 100 m mark. The height profiles are displayed over the sideview of this transect for visual reference, which was created by plotting the mean point count value for each row in the yz -plane.

calculate two different structural metrics (Fig. 2; Figure A2). The first metric was the maximal height jump between consecutive points in the vegetation height profile. The second metric was the rise distance, which was defined as the distance between the edge plot and the point where the vegetation height profile first reaches the interior forest height (negative distance if this point is reached before the edge plot). Both metrics relate to the forest edge abruptness, but indicate slightly different aspects. Large maximal height jumps indicate the presence of overhangs in the forest edge, while the rise distance indicates the general abruptness of the forest edge.

Forest edge openness

The forest edge openness was quantified using two different gap fractions, the canopy gap fraction (CGF) and the edge gap fraction (EGF). The CGF was used to indicate the presence of canopy gaps along the transects. These canopy gaps increase the penetration of light through the canopy, affecting the light availability and microclimate conditions in the forest. The EGF was used to evaluate the presence of openings in the façade of the forest edge, as it is known that these can affect edge conditions and biodiversity (Wuyts et al., 2009). Both metrics quantify the openness of the transect, but from different viewpoints.

A voxelisation was first applied on the transect point clouds using the function *voxelmetrics()* in the *lidR* package. This function functions similarly to *gridmetrics()*, but also divides the point cloud along the z-axis. The result is a 3D grid of cubes, also called voxels. A 10-cm voxel size was used. In each of these voxels, the number of data points was counted, that is, the point count (PC). The final result was a 3D matrix of the transect in which the values equal the PC in the corresponding voxels. Four different vegetation layers were established within this 3D matrix based on a study on the effects of undergrowth on bird communities (Camprodon & Brotons, 2006). These layers were a low shrub layer between 0 and 0.5 m, a high shrub layer between 0.5 and 4 m and a low arboreal layer from 4–8 m. The remaining layer (8 m-max) was considered the canopy layer. These layers were then divided in an inner and outer section based on the location of the edge plot (Figure A3). The CGF was calculated by summing the inner canopy layer in the direction of the z-axis to create a horizontal plane. A custom *gapfraction()* function was then applied on the resulting raster. This function computes the proportion of 0 elements in a matrix. The EGF was calculated in a similar fashion, but the PC values in the outer edge between 0 and 8 m were summed in the direction of the y-axis instead to create a vertical plane.

Two vegetation layer profiles were then constructed based on the hypothesis that more foliage leads to more

voxels containing data points. To do this, a 'reverse' *gapfraction()* function was applied on each slice along the y-axis in the 3D transect matrix, that is, calculation of the proportion of non-zero elements in each slice. The hypothesis was tested by graphically comparing the vegetation layer profiles with the sideview of the normalised transects. These vegetation layer profiles were then used to derive two final structural metrics, the shrub layer trends, which were defined as the regression coefficient from a linear regression through the vegetation layer profiles from edge to core.

Linking the soundscape to forest structure

Correlations between the AIs and the structural metrics were investigated to see which structural components might have an impact on the recorded soundscapes. This was done separately for the AI values from the forest edge plot and the forest core plot, because the structure of the forest edge might have different effects on the soundscapes in the forest core. The strongest correlations between the AIs and the structural metrics were then further analysed using linear regressions.

Results

Acoustic indices

Species identification

A total of 30 different species were identified in the selected sample of 60 recordings. The species richness on the recordings ranged from three to nine. The most prominent species were the European robin (*Erithacus rubecula*), common chiffchaff (*Phylloscopus collybita*), common chaffinch (*Fringilla coelebs*), Eurasian blue tit (*Cyanistes caeruleus*) and the song thrush (*Turdus philomelos*). The Shannon index ranged between one and six, where low values consistently indicated recordings with a dominant vocaliser. A correlation analysis revealed that there was little correlation between the AI values and species richness (Fig. 3). There were moderate correlations between most AI values and the Shannon index, indicating that the AI values are affected by dominant vocalising species.

Soundscape differences between recording locations

There were significant differences in the AI values between transects and between plot locations (Fig. 4). Differences in AI values between plots were often not statistically significant. The values from transect R1C consistently stand out as either lowest or highest (depending on the AI) and show very little variance. Another notable result is the low NDSI values in transect R1O, which was

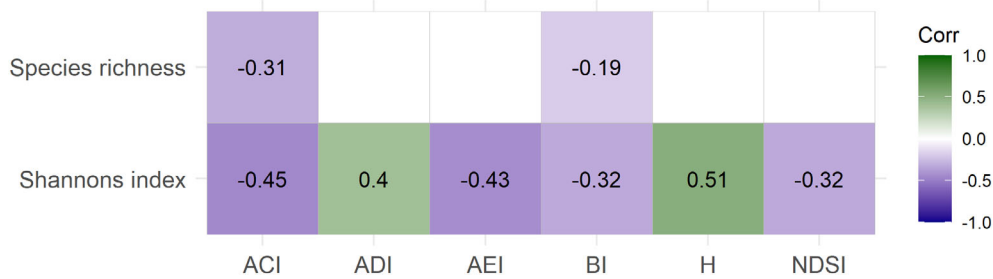


Figure 3. Correlation matrix between the acoustic indices and two biodiversity metrics derived from 60 recording samples. Insignificant correlation coefficients ($P > 0.05$) were omitted from the matrix. The Shannon–Weaver index was calculated using a dominance score that was assigned to every identified bird species in the sample and relates to the presence of dominant vocalisers on the recording. Lower values indicate more dominantly vocalising species.

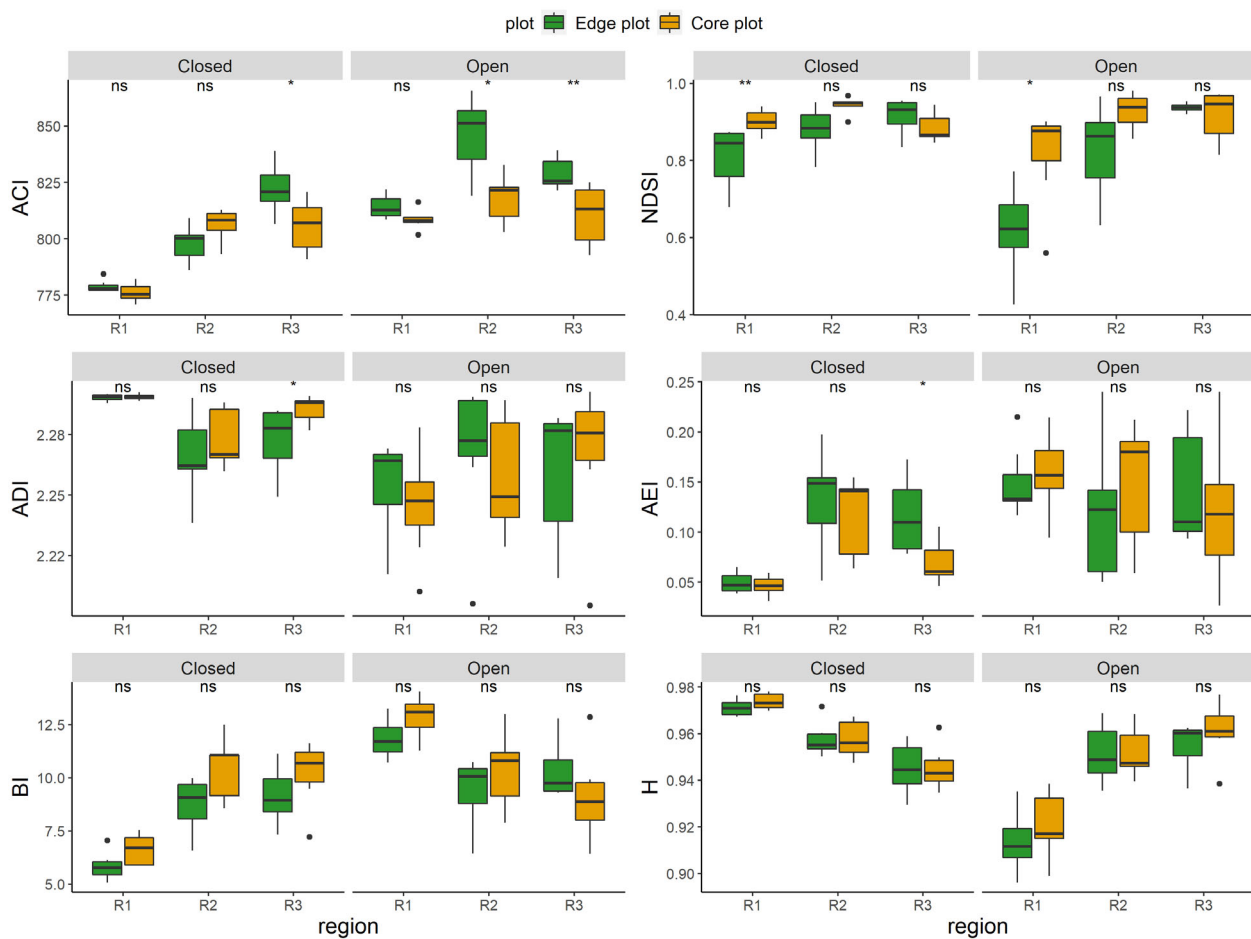


Figure 4. Overview of the acoustic index (AI) values from the recordings at each sampling plot. The boxplots represent of the daily median AI values associated with each transect. The significance of the difference between the AI values at the edge plot versus the core plot is indicated above the boxplots ('***' 0.001 '**' 0.01 '*' 0.05 'ns').

located next to a road. Finally, the acoustic evenness index (AEI) and acoustic diversity index (ADI) values had a higher variance in open transects compared to closed transects.

Structural metrics

No distinct patterns were found in the edge abruptness metrics. The maximum height jumps were never smaller

Table 2. Overview of the structural metrics in every transect.

Metric	Layer	Region 1		Region 2		Region 3	
		Closed	Open	Closed	Open	Closed	Open
Maximum height jump (m)	/	3.91	5.60	11.9	19.6	6.67	6.14
Edge distance (m)	/	23.9	15.4	−4.5	−4.9	7.3	35.7
Canopy gap fraction	/	0.04	0.14	0.10	0.34	0.05	0.14
Edge gap fraction	/	0.04	0.12	0.15	0.33	0.05	0.10
Shrub layer trend	High shrub	−0.94	−0.18	−0.47	0.61	−0.65	0.86
Shrub layer trend	Low arboreal	−0.74	0.06	−0.21	1.07	0.43	0.70

than 6 m (Table 2). This indicates that large overhangs were present in all transects. The two calculated gap fractions (CGF and EGF) were both consistently higher for the open transects compared to the closed transects.

The visual comparison of the vegetation profiles with the side view of the transects showed a good match with the foliage patterns in the vegetation layers (Fig. 5). The vegetation profiles peaked in areas of dense undergrowth and dropped in open sections. They were thus used to derive the shrub layer trends using a linear regression (Table 2). The shrub layer trends in the closed transects were consistently smaller than those in open forests for both the high shrub and low arboreal layer. Furthermore, they were often negative in the closed transects, whereas those in the open transects were mostly positive. There was thus an overall decrease in foliage from edge-to-core in the closed forest edges opposed to an increase in the open edges.

Linking sound and structure

The correlation analysis between the AI values and the structural metrics showed several moderate to strong

correlations (Fig. 6). At the forest edge plot, the acoustic complexity index (ACI) and bioacoustic index (BI) showed the strongest correlations with the forest structure. At the core plots, correlations were different compared to the edge plots. The ACI was this correlated with most structural metrics, although lower. Interestingly, the ADI and AEI now show moderate correlations with the structural metrics, which was not the case at the forest edge.

The strongest regressions were found between the structural metrics and the ACI values (Fig. 7). The linear regressions were significant for five out of the six structural metrics, although the extreme maximum height jump, CGF and EGF values at transect R20 likely skew these regressions.

Discussion

Acoustic indices

The usage of the AIs proved to be a very fast method to analyse a large amount of sound recordings. A total of 1344 five-minute recordings were collected, resulting in 112 h of audio. Using the presented workflow, the

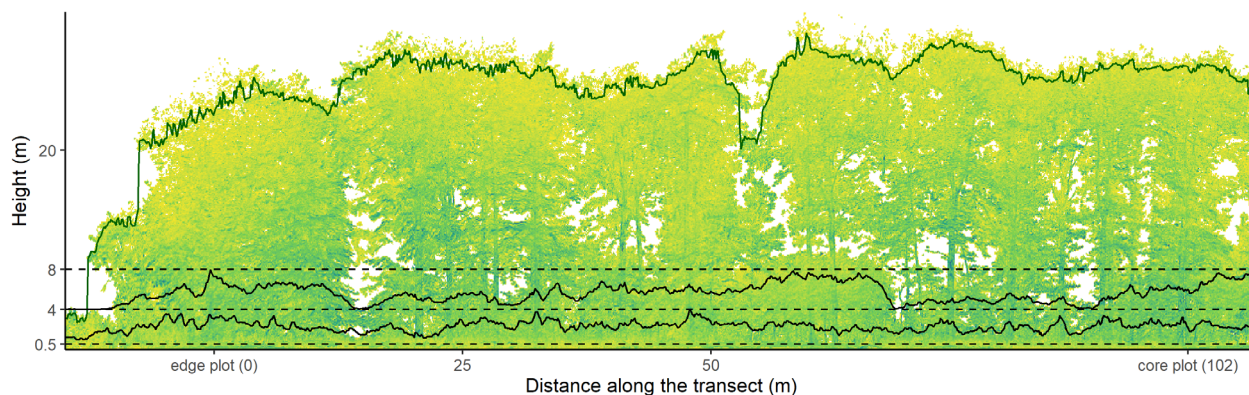


Figure 5. The sideview of the normalised point cloud from the open transect in region 1. Two vegetation layers are indicated on the transect using dashed lines, the high shrub layer (0.5–4 m) and the low arboreal layer (4–8 m). In each of these layers, the corresponding vegetation layer profiles were plotted. The sampling plot where the Audiomoths were installed is indicated in the x-axis for reference. An overview of this plot for every transect can be found in Figure A4.

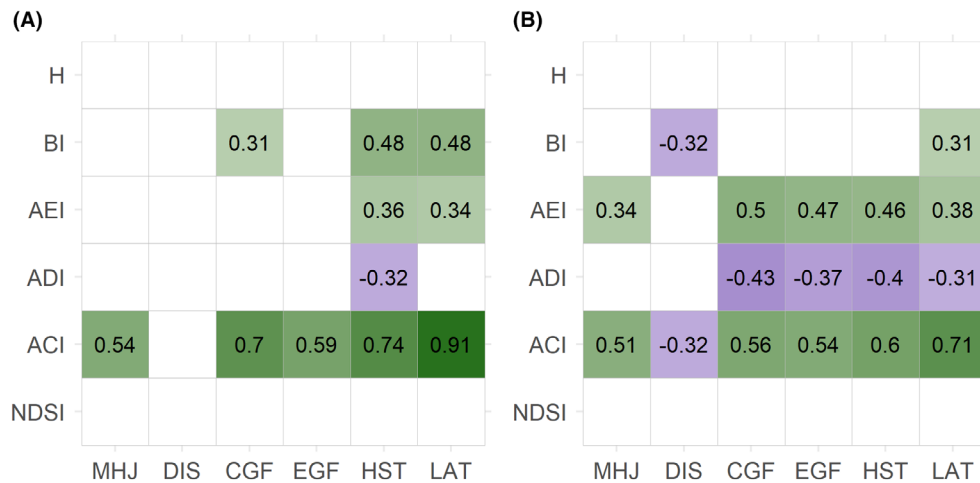


Figure 6. Correlation matrices between the structural metrics and the acoustic indices (AIs) and at the edge and core plot. Only the statistically significant correlation coefficients ($P < 0.05$) are shown. The structural metrics are the maximum height jump (MHJ), rising distance (DIS), canopy gap fraction (CGF), edge gap fraction (EGF), high shrub vegetation trend (HST) and low arboreal vegetation trend (LAT). (A) Edge plot: The acoustic complexity index (ACI) shows the broadest interaction with the forest edge structure and shows moderate to strong correlations with nearly all structural metrics. Very strong correlations with the LAT. (B) Core plot: The ACI is still the most responsive AI to the structural metrics, although the correlations are slightly lower. Correlations between the gap fractions and the evenness indices (AEI, ADI) are now present, whereas they were absent at the forest edge plot. ADI, acoustic diversity index; AEI, acoustic evenness index.

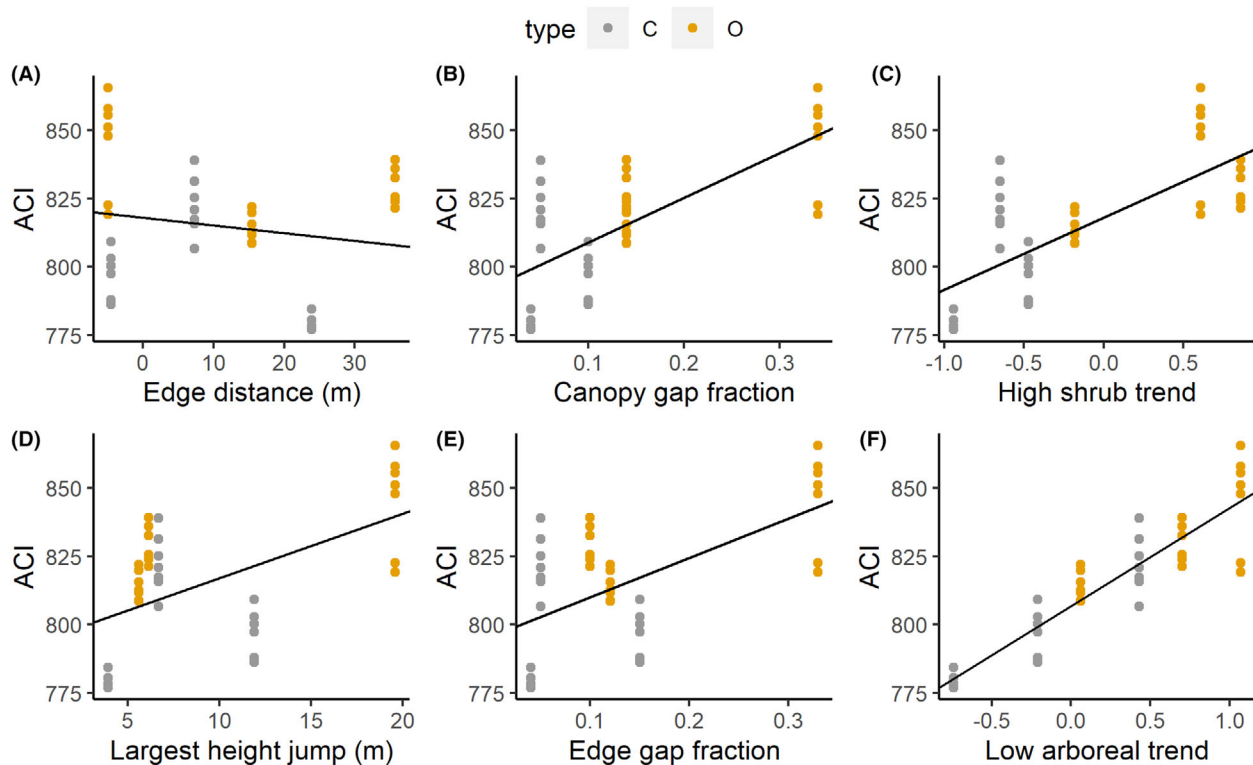


Figure 7. Linear regression of the acoustic complexity index (ACI) values at the forest edge plot in relation to the structural metrics of the corresponding transects. The ACI at the edge plot was chosen as a demonstration because it showed the highest correlations.

computation of all six indices only required a few hours. The R packages *ecoacoustics* and *seewave* were convenient to use and interpretation of AI values does not require substantial knowledge about the recorded species, which is in sharp contrast to the required expertise and large time commitment needed to manually analyse sound recordings. These are both substantial advantages compared to manual species identification, which highlights the potential of AIs in large-scale monitoring.

However, the species analysis on the sample of 60 recordings also highlights the difference in information that is acquired when using AIs compared to actual species identification. At least for this data set, no reliable correlations were found between the AIs and species richness. This is in line with recent findings that reported that effects sizes for AIs as proxies have been decreasing over time (Alcocer et al., 2022). These findings imply that the increased usage of AIs to quantify local biodiversity has revealed some pressing limitations regarding this approach. Real-world recordings are affected by a multitude of confounding factors that can mislead biodiversity estimates via AIs, such as weather, human disturbance or recorder quality. One factor that might be particularly important in this study specifically is the variation the vocal repertoire size that is exhibited by certain bird species. This high variation in vocalisations within the same species may critically influence AI values. As a result, a low-diversity recording containing such species may lead to AI values that normally characterise high acoustic diversity (Mammides et al., 2021).

This can be valuable in long-term monitoring or large-scale studies where manual species identification would be unfeasible. That said, recent development of machine learning programs such as BirdNet (Kahl et al., 2021) creates new opportunities for rapid, large-scale sound monitoring. If these programs can provide fast, reliable and automated species identification, certain AIs could lose some of their advantages, specifically spectral AIs, which can be unintuitive to interpret (Eldridge et al., 2018).

Structural metrics

No consistent patterns were found between the abruptness metrics (rise distance and maximum height jump) and the management type of the forest edges. This indicates that these metrics are not necessarily linked to the openness of the forest edge. The maximum height jumps at every transect were at least higher than six metres because of the presence of overhangs on each transect in this study. Forest edges without any overhang or at least little overhang were thus missing in this study. Applying the other structural metrics on transects in forest edges without overhangs could provide more insights in the

effect of overhangs on the forest edge. For this purpose, the maximal height jump could be a good overhang detector. More complex forest edge overhang metrics could be developed in the future to improve our understanding of this aspect of forest edge structure and its interaction with edge biodiversity.

Both the CGF and EGF were consistently higher in the open transects. The higher CGF is an expected result of the thinning in the open transect and it has been shown that TLS data can be used to quantify these gap fractions (Danson et al., 2007). A similar pattern was observed in the shrub layer trends, which were also consistently higher in the open transects. Furthermore, both the high shrub and low arboreal shrub layer trends were often negative in the closed transects and positive in the open transects. This indicates that there was an overall decrease in undergrowth from edge to core in the closed transects, compared to an increase in the open transects. These two patterns could be linked as the presence of gaps in the canopy promotes the growth of understorey vegetation and tree regeneration. In forest with more tightly closed canopies, on the other hand, the forest floor area tends to be more bare. This was most noticeable in transect R1C, which had both a very closed canopy and a steep decline in undergrowth going along the transect (field observation). This is also reflected in the values of the CGF and shrub layer trends (Table 2).

Effects of forest edge structure on the soundscape

The two abruptness metrics consistently showed the least correlations with the AIs. This could indicate that these components of the forest edge structure might not strongly affect the soundscape. However, the previously discussed issues regarding these metrics could play a part here as well. Because all transects in this study had some type of overhang, no forest edges without overhang were sampled. This could have an impact on the bird communities, for instance because of more exposed nesting grounds, which can negatively impact breeding success (Flaspohler et al., 2001).

The metrics that can be related to the openness of the forest structure did show several moderate to strong correlations with the AI values. At the forest edge plot, most correlations were found between the ACI and BI and the structural metrics, the strongest being with the vegetation trends. These findings suggest that the ACI and BI values at the forest edge increase as the forest structure gets more open. Looking at the BI, this suggests higher activity in the 2–10 kHz frequency range in forest edges with a more open structure. The results for the ACI seem to back this up, as this metric is designed to quantify

irregularity and has been found to increase with bird activity (Bradfer-Lawrence et al., 2019).

In the forest core, one effect clearly stands out. The evenness of the soundscape (AEI, ADI) now shows correlations with the presence of gaps in the forest, which was not the case at the forest edge. This suggests that the forest core soundscapes are more uneven in more open forests. This increased unevenness could be the result of more undergrowth development due to increased light availability, which is supported by the shrub layer trends that were found. The increase in undergrowth provides both food resources and nesting area for bird populations (Snow et al., 1997), leading to higher bird activity. Previous studies, such as Camprodon and Brotons (2006), have similarly found a negative impact of undergrowth clearing on bird biodiversity. The reason why this change in soundscape evenness is more pronounced in at the forest core might be because a low baseline of bird activity in closed canopy forest interior, resulting in a very even soundscape, whereas the baseline of activity is generally higher at the forest edge, regardless of the forest openness. It is important to note that soundscape evenness should be interpreted carefully. During events of very high activity, the soundscape can get fully blanketed by sound, which can result in high evenness. However, the temperate forest interior habitat is likely not acoustically rich enough for this to occur.

Despite the correlations, regressions between the AIs and structural metrics were overall rather weak. One exception is the ACI, which showed several strong regressions with the structure, especially the vegetation trends.

Conclusion

This study serves as a proof of concept for the assessment of bird habitat quality by combining simple, edge level structural metrics with a rapid analysis of sound recordings. Although the specific structural metrics in this paper were simple, a few potential influences of forest edge structure on the soundscape were found, which highlights the potential of the methodologies for upscaling over larger areas. The workflow for acoustic monitoring presented in this study can serve as a useful guideline for such large-scale monitoring programmes in temperate regions. Using a small suite of AIs, large volumes of data can be analysed in very little time. The calculation of these metrics requires little technical knowledge or experience in sound analysis due to publicly available R packages such as *ecoacoustics* and *seewave*, which is a major advantage compared to the manual analysis of soundscapes. While the usage of AIs as direct proxies for biodiversity metrics proved to be unreliable in this study, a large amount of information about the soundscape can be acquired from the AI values. Automatic species recognition software, which is becoming

increasingly available and accurate, could improve how reliably AI values can be interpreted within specific studies. The structural metrics used in this study proved to be effective at demonstrating forest level structural differences between forest edge transects, despite their relatively simple premise. Future research can expand on these metrics. More complex forest edge gradients, such as tree diameter or above-ground biomass gradients, could be valuable for a better quantification of forest edge abruptness. More transects will be required to better develop and test these structural metrics over a wider range of forest (edge) structure. Although this study focuses on forest edges specifically, the concept can be applied on any forest transect, for instance along a gradient from a river up the bank. While some correlations between structural metrics and AIs were found in this study, data on a much larger scale will be needed to provide founded ecological insights on how the soundscape in forest edges is affected by forest edge structure. The addition of different types of biodiversity surveys, such as moth traps, camera traps or vegetation studies, could provide insights on a broader biodiversity level.

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References

- Alcocer, I., Lima, H., Sugai, L.S.M. & Llusia, D. (2022) Acoustic indices as proxies for biodiversity: a meta-analysis. *Biological Reviews*, **97**(6), 2209–2236. Available from: <https://doi.org/10.1111/brv.12890>
- Almond, R. E., Grooten, M., & Peterson, T. (2020). *Living Planet Report 2020-Bending the curve of biodiversity loss*. Switzerland:World Wildlife Fund.
- Boelman, N.T., Asner, G.P., Hart, P.J. & Martin, R.E. (2007) Multi-trophic invasion resistance in Hawaii: bioacoustics, field surveys, and airborne remote sensing. *Ecological Applications*, **17**(8), 2137–2144. Available from: <https://doi.org/10.1890/07-0004.1>
- Bradfer-Lawrence, T., Gardner, N., Bunnefeld, L., Bunnefeld, N., Willis, S.G. & Dent, D.H. (2019) Guidelines for the use of acoustic indices in environmental research. *Methods in Ecology and Evolution*, **10**(10), 1796–1807. Available from: <https://doi.org/10.1111/2041-210X.13254>
- Calders, K., Adams, J., Armston, J., Bartholomeus, H., Bauwens, S., Bentley, L.P. et al. (2020) Terrestrial laser

- scanning in forest ecology: expanding the horizon. *Remote Sensing of Environment*, **251**, 112102. Available from: <https://doi.org/10.1016/j.rse.2020.112102>
- Calders, K., Disney, M.I., Armston, J., Burt, A., Brede, B., Origo, N. et al. (2017) Evaluation of the range accuracy and the radiometric calibration of multiple terrestrial laser scanning instruments for data interoperability. *IEEE Transactions on Geoscience and Remote Sensing*, **55**(5), 2716–2724. Available from: <https://doi.org/10.1109/TGRS.2017.2652721>
- Camprodon, J. & Brotons, L. (2006) Effects of undergrowth clearing on the bird communities of the northwestern Mediterranean coppice holm oak forests. *Forest Ecology and Management*, **221**(1), 72–82. Available from: <https://doi.org/10.1016/j.foreco.2005.10.044>
- CloudCompare. (2022) *CloudCompare* (v2.12). [Computer software]. Available at: <http://www.cloudcompare.org/>
- Danson, F.M., Hetherington, D., Morsdorf, F., Koetz, B. & Allgower, B. (2007) Forest canopy gap fraction from terrestrial laser scanning. *IEEE Geoscience and Remote Sensing Letters*, **4**(1), 157–160. Available from: <https://doi.org/10.1109/LGRS.2006.887064>
- Duelli, P., Obrist, M. & Flückiger, P. (2002) Forest edges are biodiversity hotspots—also for Neuroptera. *Acta Zoologica Academiae Scientiarum Hungaricae*, **48**(Suppl 2), 75–87.
- De Frenne, P., Lenoir, J., Luoto, M., Scheffers, B. R., Zellweger, F., Aalto, J. et al. (2021). Forest microclimates and climate change: Importance, drivers and future research agenda. *Global Change Biology*, **27**(11), 2279–2297. <https://doi.org/10.1111/gcb.15569>
- Eldridge, A., Casey, M., Moscoso, P. & Peck, M. (2016) A new method for ecoacoustics? Toward the extraction and evaluation of ecologically-meaningful soundscape components using sparse coding methods. *PeerJ*, **4**, e2108.
- Eldridge, A., Guyot, P., Moscoso, P., Johnston, A., Eyre-Walker, Y. & Peck, M. (2018) Sounding out ecoacoustic metrics: avian species richness is predicted by acoustic indices in temperate but not tropical habitats. *Ecological Indicators*, **95**, 939–952. Available from: <https://doi.org/10.1016/j.ecolind.2018.06.012>
- Fahrig, L. (2017) Ecological responses to habitat fragmentation per se. *Annual Review of Ecology, Evolution, and Systematics*, **48**(1), 1–23. Available from: <https://doi.org/10.1146/annurev-ecolsys-110316-022612>
- Farina, A. & Gage, S.H. (2017) *Ecoacoustics: the ecological role of sounds*. Hoboken, New Jersey: John Wiley & Sons.
- Farina, A., Pieretti, N. & Piccoli, L. (2011) The soundscape methodology for long-term bird monitoring: a Mediterranean Europe case-study. *Ecological Informatics*, **6**(6), 354–363.
- Flaspohler, D.J., Temple, S.A. & Rosenfield, R.N. (2001) Species-specific edge effects on nest success and breeding bird density in a forested landscape. *Ecological Applications*, **11**(1), 32–46.
- Gage, S.H., Napoletano, B.M. & Cooper, M.C. (2001) Assessment of ecosystem biodiversity by acoustic diversity indices. *The Journal of the Acoustical Society of America*, **109**(5), 2430.
- Govaert, S., Meeussen, C., Vanneste, T., Bollmann, K., Brunet, J., Cousins, S.A. et al. (2020) Edge influence on understorey plant communities depends on forest management. *Journal of Vegetation Science*, **31**(2), 281–292.
- Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D. et al. (2015) Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances*, **1**(2), e1500052.
- Kahl, S., Wood, C.M., Eibl, M. & Klinck, H. (2021) BirdNET: a deep learning solution for avian diversity monitoring. *Ecological Informatics*, **61**, 101236.
- Kasten, E.P., Gage, S.H., Fox, J. & Joo, W. (2012) The remote environmental assessment laboratory's acoustic library: an archive for studying soundscape ecology. *Ecological Informatics*, **12**, 50–67.
- Maeda, E.E., Nunes, M.H., Calders, K., de Moura, Y.M., Raunonen, P., Tuomisto, H. et al. (2022) Shifts in structural diversity of Amazonian forest edges detected using terrestrial laser scanning. *Remote Sensing of Environment*, **271**, 112895. Available from: <https://doi.org/10.1016/j.rse.2022.112895>
- Mammides, C., Goodale, E., Dayananda, S.K., Luo, K. & Chen, J. (2021) On the use of the acoustic evenness index to monitor biodiversity: a comment on “rapid assessment of avian species richness and abundance using acoustic indices” by Bradfer-Lawrence et al. (2020) [ecological indicators, 115, 106400]. *Ecological Indicators*, **126**, 107626. Available from: <https://doi.org/10.1016/j.ecolind.2021.107626>
- Meeussen, C., Govaert, S., Vanneste, T., Bollmann, K., Brunet, J., Calders, K. et al. (2021) Microclimatic edge-to-interior gradients of European deciduous forests. *Agricultural and Forest Meteorology*, **311**, 108699.
- Meeussen, C., Govaert, S., Vanneste, T., Calders, K., Bollmann, K., Brunet, J. et al. (2020) Structural variation of forest edges across Europe. *Forest Ecology and Management*, **462**, 117929.
- Müller, J., Bußler, H., Goßner, M., Gruppe, A., Jarzabek-Müller, A., Preis, M. et al. (2007) Forest edges in the mixed-montane zone of the Bavarian Forest National Park-hot spots of biodiversity. *Silva Gabreta*, **13**(2), 121–148.
- Nunes, M.H., Camargo, J.L.C., Vincent, G., Calders, K., Oliveira, R.S., Huete, A. et al. (2022) Forest fragmentation impacts the seasonality of Amazonian evergreen canopies. *Nature Communications*, **13**(1), 917. Available from: <https://doi.org/10.1038/s41467-022-28490-7>
- Pieretti, N., Farina, A. & Morri, D. (2011) A new methodology to infer the singing activity of an avian community: the acoustic complexity index (ACI). *Ecological Indicators*, **11**(3), 868–873.

- R Core Team. (2021) *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Available from: <http://www.R-project.org/>
- Rappaport, D.I., Royle, J.A. & Morton, D.C. (2020) Acoustic space occupancy: combining ecoacoustics and lidar to model biodiversity variation and detection bias across heterogeneous landscapes. *Ecological Indicators*, **113**, 106172.
- Roussel, J.-R. & Auty, D. (2021) Airborne LiDAR data manipulation and visualization for forestry applications. *R package version 3.1.2*.
- Roussel, J.-R., Auty, D., Coops, N.C., Tompalski, P., Goodbody, T.R., Meador, A.S. et al. (2020) LidR: an R package for analysis of airborne laser scanning (ALS) data. *Remote Sensing of Environment*, **251**, 112061.
- Snow, D.W. & Perrins, C.M. (1997) Handbook of the Birds of Europe, the Middle East and North Africa: The Birds of the Western Palearctic. Concise Edition.
- Sueur, J., Aubin, T. & Simonis, C. (2008) Seewave, a free modular tool for sound analysis and synthesis. *Bioacoustics*, **18**, 213–226. Available from: <https://doi.org/10.1080/09524622.2008.9753600>
- Sueur, J. & Farina, A. (2015) Ecoacoustics: the ecological investigation and interpretation of environmental sound. *Biosemiotics*, **8**(3), 493–502.
- Sueur, J., Pavoine, S., Hamerlynck, O. & Duvail, S. (2008) Rapid acoustic survey for biodiversity appraisal. *PLoS One*, **3** (12), e4065.
- Villanueva-Rivera, L.J. & Pijanowski, B.C. (2018) Soundecology: Soundscape ecology. *R package version*, 1(3), 3.
- Villanueva-Rivera, L.J., Pijanowski, B.C., Doucette, J. & Pekin, B. (2011) A primer of acoustic analysis for landscape ecologists. *Landscape Ecology*, **26**(9), 1233–1246.
- Wermelinger, B., Flückiger, P., Obrist, M. & Duelli, P. (2007) Horizontal and vertical distribution of saproxylic beetles (Col., Buprestidae, Cerambycidae, Scolytinae) across sections of forest edges. *Journal of Applied Entomology*, **131**(2), 104–114.
- Wuyts, K., De Schrijver, A., Vermeiren, F. & Verheyen, K. (2009) Gradual forest edges can mitigate edge effects on throughfall deposition if their size and shape are well considered. *Forest Ecology and Management*, **257**(2), 679–687.

Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure A1. Transformation of a simplified transect height grid into a height profile. The 90% quantile was chosen to create the final height profile because it was less affected by openings in the canopy.

Figure A2. Conceptual overview of a transect height profile and the associated forest edge abruptness metrics.

Figure A3. Overview of the different defined vegetation section based on the location of the edge plot (inner and outer) and the 4 different vegetation layers; low shrub layer (0–0.5), high shrub layer (0.5–4), low arboreal layer (4–8) and the canopy layer (8–max).

Figure A4. High shrub and low arboreal vegetation profiles for all six transects. The profiles are plotted within the corresponding height layer and on a sideview of the transects for visual reference.