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Using acoustics and artificial intelligence to monitor pollination by insects and tree use by woodpeckers

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HIGHLIGHTS

- Monitoring ecosystem functions in situ is a still challenge.
- Ecoacoustics can provide new opportunities to work at large spatio-temporal scales.
- We acoustically tracked pollination by flying insects and wood use by woodpeckers.
- This revealed function phenology and seasonality in relation with weather.
- Pollination might be affected by rainfall increase and wood use by temperature rise.

GRAPHICAL ABSTRACT

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ABSTRACT

The collection and interpretation of field data is a prerequisite for informed conservation in protected environments. Although several techniques, including camera trapping and passive acoustic monitoring, have been developed to estimate the presence of animal species, very few attempts have been made to monitor ecological functions. Pollination by insects and wood use, including tree related foraging and intraspecific communication, by woodpeckers are key functions that need to be assessed in order to better understand and preserve forest ecosystems within the context of climate change. Here, we developed and applied for the first time an acoustic survey to monitor pollination by insects and wood use by woodpeckers in a protected Alpine forest in France. We deployed four autonomous recorders over a year, resulting in 2285 h of recordings. We trained a convolutional neural network (CNN) on spectrographic images to automatically detect the sounds of flying insects' buzzing and woodpeckers' drumming as they forage and call. We used the output of the CNN to estimate the seasonality, diel pattern, climatic breadth and distribution of both functions and their relationships with weather parameters. Our method showed that insects were flying (therefore potentially pollinating flowers) in bright, warm and dry conditions, after dawn and before dusk during spring and summer. Woodpeckers were mainly drumming around March at the time of pair formation in cool and wet conditions. Having considered the role of weather parameters, climate change might have contrasting effects on insect buzzing and woodpecker drumming, with an increase in temperature being favorable to pollination by insects but not to wood use by woodpeckers, and a concomitant increase in relative humidity being favorable to wood use but not to pollination. This study reveals that a systemic facet of biodiversity can be tracked using sound, and that acoustics provide valuable information for the environment description.

1. Introduction

Biodiversity conservation requires the continuous collection of data in order to inform and predict the changes that affect ecosystem populations and communities (Yoccoz et al., 2001; Pereira and David Cooper, 2006; Magurran and Dornelas, 2010). The need to develop reliable indicators in

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order to track biodiversity over time has been recognized by all international authorities involved in preserving nature and defining international conservation targets (Pereira and David Cooper, 2006; Petrou et al., 2015). Biodiversity monitoring is therefore a prerequisite for making appropriate decisions regarding the preservation of ecosystems that face local and short-term (e.g., fires, exploitation) and global and long-term (e.g., climate change, land-use change, invasive species) threats, which are acknowledged as having significant immediate and delayed consequences alike at all scales (Vanbergen and Insect Pollinators Initiative, 2013; Segan et al., 2016; O'Connor et al., 2020; Weiskopf et al., 2020). In particular, climate change is affecting animal behavior (Buchholz et al., 2019), population distribution (Chen et al., 2011), and phenology (Cohen et al., 2018).

Primary information sources on biodiversity can be classified into field observations collected in situ within the ecosystem in question, and remote sensing observations provided ex situ by satellites or airborne imagery (Proença et al., 2017). Although the ex situ option can provide extensive and meaningful data (Anderson, 2018), in situ data still tend to be prioritized of prime importance, because field information (among others) is essential for assessing assemblage composition, documenting functional traits, and understanding fine-scale ecological patterns and processes (Ríos-Saldaña et al., 2018). Field studies mostly work at the species level, hence in situ biodiversity monitoring mainly aims to describe temporal and spatial population properties and estimate species richness and evenness (Carmel et al., 2013). Several in situ monitoring tools, including those based on citizen science programs, have been developed to identify species through direct observations, as well as indirect genetic, image or sound information (Chandler et al., 2017; Kühl et al., 2020; Stephenson, 2020). However, biodiversity monitoring cannot be restricted to species occurrence; it should also include the functions or roles that species play in the ecosystem to which they belong. Indeed, functional diversity is another key facet of biodiversity which has received increasing attention for more than 30 years (Calow, 1987; Irschick et al., 2013). Analyses of functional diversity are necessary to understand how ecosystem functions and services are maintained and to guide conservation efforts (Schwartz et al., 2000; Laureto et al., 2015).

Ecoacoustics is a new discipline that aims to tackle ecological questions through the recording and analysis of the sounds emanating from all or certain parts of ecosystems (Sueur and Farina, 2015). Within this field, several new techniques have been proposed to automatically detect the presence of soniferous species and to globally parameterize the acoustic diversity of a population, a community, an ecosystem or a landscape (Stowell and Sueur, 2020). If ecoacoustics is able to identify species by listening to them, could it also track an ecological function in both time and space? So far, ecoacoustic efforts have been directed to assess species diversity, but very rarely to follow ecological functions, except the indirect tracking of tropical birds' seed dispersion function (Ducrettet et al., 2020), foraging by bats (Kolkert et al., 2020), and crucial coral reef functions (Elise et al., 2019).

Two particular sounds can reveal an important aspect of terrestrial ecosystem functioning: pollination buzzing by flying insects and wood drumming by woodpeckers. The pollination of flowering plants is a significant ecological function of terrestrial ecosystems, as it ensures plant reproduction (Ollerton et al., 2011, Breeze et al., 2016). Pollinator populations, which are regarded as indicators of good ecosystem conditions, are declining (Potts et al., 2010). Climate change is also causing the phenological decoupling of plant–pollinator interactions (Hegland et al., 2009; Settele et al., 2016). Tracking pollination therefore appears to be a major challenge for future biodiversity conservation. Pollination is mainly ensured by flying insects, including Hymenoptera, Diptera, and Coleoptera species, which visit flowers to collect pollen or nectar. Flying insects generate incidental sounds when beating their wings and pollinating (Vallejo-Marín, 2018). These sounds, or buzzing, can be recorded with appropriate recording tools. Woodpeckers are another major ecological provider in forest ecosystems (Virkkala, 2006). By drilling holes in dead tree trunks both to forage and to nest, and by drumming in order to defend their territories, they provide nesting cavities for other bird species (Cockle et al., 2011), disperse wood-rotting fungi (Farris et al., 2004), and help regulate spruce bark beetles (e.g., *Dendroctonus* spp., *Ips* spp.), which attack healthy trees (Fayt et al., 2005). Woodpeckers are therefore considered excellent indicators of forest biodiversity and, more specifically, of bird species richness (Mikusiński et al., 2001).

Here, we hypothesized that these two functions—pollination by flying insects, and wood use by woodpeckers—can be automatically tracked using ecoacoustic methods, enabling information on a forest's ecological state, functions and services to be inferred through listening to their buzzing and drumming. To this end, we used data collected via a long-term ecoacoustic monitoring program in an Alpine protected forest in France. We then applied artificial intelligence (AI) to automatically estimate the seasonality, diel pattern climatic breadth, and spatial distribution of these two important ecological functions, and inferred predictions related to climate change.

2. Material and methods

2.1. Study site and recording

The study site is an Alpine forest called the Risoux, which is mainly composed of a mix of European spruce (*Picea abies*), European beech (*Fagus sylvatica*), and European silver fir (*Abies alba*). At its center, the site is dominated by European spruce. The forest is located in the Parc Naturel Régional du Haut-Jura, a protected area in eastern France, close to the border with Switzerland (46°32′10″ N, 6°52′21″ E, 1230 m a.s.l.). The climate is semi-continental, with cold temperatures (annual average temperature 5.5 °C), large snowfalls (> 2 m), an extended winter period, and a very narrow period between April and October when the forest floor and understory are green. Climate change impacts bird physiology, biotic interactions, conservation and distribution (Scridel et al., 2018). In the specific case of the Alpine Risoux mountain forest, a decline of specialist bird species, an increase of generalist bird species, and shifts in migration and nesting dates has been reported already (Joveniaux and Chevillard, 2014). The loss and the fragmentation of habitats due to anthropogenic pressure have driven the Parc Naturel Régional du Haut-Juras conservation plans, including the implementation of long-term biodiversity monitoring using acoustics.

2.2. Recording

The soundscape of the Risoux was recorded using four automatic recorders (SongMeter 4, Wildlife Acoustics Inc., Concord, MA, USA) installed along a West–East axis in the central zone of the forest. The distance between the recorders was 1.00 ± 0.10 km (Grinfeder et al., 2022). The positioning of the recorders was chosen to (1) cover the forest area, (2) sample a single habitat defined by the dominance of European spruce, (3) avoid pseudo-replication between neighboring recorders, and (4) avoid anthropogenic noise due to car traffic and local activities (hiking, hunting, skiing). The recorders were attached to trees at a height of 2.50 m, and oriented on a 45–315° axis so that the microphones would be parallel to the main West–East circulation axes (Grinfeder et al., 2022). The recorders were programmed to record 1 min every 15 min (1′ on, 14′ off, 96 recordings per day) all year round, with operational maintenance in October and July. The sampling period started on August 1, 2018, and ended on July 31, 2019. Sounds were saved in lossless .wav format with a 44.1 kHz sampling frequency and 16-bit digitization depth. This resulted in a data set of 140,160 sound files (96 × 365 days × 4 sites) for a total of 2336 h of recordings. However, due to some recording failures, the effective database contained 137,087 sound files for a total of 2285 h of recordings.

2.3. Environmental data

Temperature (°C), solar irradiance (lx) and relative humidity (%) were monitored with HOBO MX 2202 and MX 2301 sensors (Onset Computer Corporation, Bourne, MA, USA) using the same spatial and temporal sampling as the audio recorders. Solar irradiance was used to refer to the light intensity per unit area. For data visualization, illuminance was log10 transformed and split into three classes, namely night (<1 lx, i.e., 0 on log10 scale), twilight (between 1 and 400 lx, i.e., between 0 and 2.6 on log10 scale), and day (more than 400 lx, i.e., more than 2.6 on log10 scale). Local sunrise and sunset time were estimated using sunrise-and-sunset.com.

2.4. Supervised sound classification

2.4.1. Dataset organization

The complete dataset contained 137,087 one-minute files. All files were split into successive five-second frames with neither overlap nor tapering leading to 1,645,044 frames. The classification process was trained, validated and tested on a subset of the complete data set containing 1401 one-minute files, i.e., 1% of the complete recording data set. Given that the sounds of interest were expected to be rare, the 1% subsampling consisted in randomly selecting files within the period between April 5, 2019 and July 5, 2019, between 7 am and 7 pm, when woodpeckers and insects are known to be most active. The subset data set was split into three sub-subset data sets: the training data set used to train the classification model (60%), the validation data set used to evaluate the model and refine its hyperparameters (20%), and the test data set used as a reference to assess the model's performance (20%).

2.4.2. Dictionary

The dictionary data set included the reference sounds used to train the classification process. The dictionary covered three distinctive sound classes: “buzzing,” “drumming,” and “background.” The “buzzing” class included all flight sounds produced by insects, including Hymenoptera (e.g., Vespidae, Apidae) and Diptera (e.g., Muscidae, Syrphidae). The “drumming” class included the sounds produced by woodpeckers (black woodpecker *Dryocopus martius*, great spotted woodpecker *Dendrocopos major*, three-toed woodpecker *Picoides tridactylus*) when striking a tree trunk with their beak, when either nesting, foraging, defending a territory, or calling to attract a mate (Garcia et al., 2020). The “background” class included all other sounds coming from other animals or other sources, such as weather sounds (geophony) and anthropogenic sounds (anthropophony). In order to minimize false detections, the “background” class also comprised sounds whose acoustic characteristics are close to the sounds of interest and therefore risked being confused with the latter. These included chainsaw sounds (being close to insects' “buzzing” sounds) and falling tree branches (being close to woodpeckers' “drumming” sounds). The three classes were built with 1000 files from internal and external data that were similarly split into successive five-second frames with neither overlap nor tapering. The internal data were derived from records taken in the Risoux, while the external data came from sound libraries. The sounds of interest were identified by one of the authors (AF) carefully listening and visualizing spectrograms with a custom built Matlab (MathWorks, Natick, MA, USA) program. This annotation process dictionary included 783 “drumming” frames (68 internal, 715 external), 956 “buzzing” frames (406 internal, 550 external), and 2866 “background” frames (2866 internal, 0 external) (Table 1).

Table 1
Number of sound frames used for training the convolutional neural network. The sound frames were extracted from either the Risoux (internal data set) or from the following sound libraries: Soundsnap (https://www.soundsnap.com), the Xeno-Canto collective project (https://www.xeno-canto.org), the Sonothèque of the Muséum national d'Histoire naturelle, Paris (https://sonotheque.mnhn.fr), the Tierstimmenarchivs of the Museum für Naturkunde, Berlin (https://www.tierstimmenarchiv.de), and Fernand Deroussen's private collection (https://naturophonia.jimdo.com).

Sound library	“Buzzing” sounds	“Drumming” sounds	“Background” sounds
Internal data set	406	68	2866
Soundsnap	59	35	0
Xeno-Canto	398	644	0
Sonothèque, Muséum national d'Histoire naturelle, Paris	12	21	0
Tierstimmenarchivs, Museum für Naturkunde, Berlin	30	15	0
Fernand Deroussen's private collection	51	0	0
Total	956	783	2866

2.4.3. Filtering

All files were filtered out in the frequency domain to remove low-frequency noise due to wind and high-frequency sound due to sources other than flying insects and woodpeckers. The filter was a finite impulse response (FIR) bandpass filter between 400 and 2200 Hz.

2.4.4. Image generation and processing

Each sound frame was transformed into a spectrographic image using the short-term Fourier transform (STFT) based on a Fourier window comprising 2048 samples (0.046 s) with a Hamming tapering function and an overlap of 441 samples (= 0.01 s). This resulted in a time precision of 0.036 s and a frequency precision of 21.53 Hz. The initial image obtained with the STFT was then processed to reduce background noise due to distant sound sources and thereby enhance the contrast of the image. A Gaussian filtering (sigma = 1.2) and heuristic thresholding according to Stein's unbiased risk estimate (SURE thresholding) were used to bring out the contour of the foreground sounds (Stander, 2017). To avoid overlearning, that is, to reduce the sensitivity of the neural network differences between the learning and test data sets, each frame of the learning data set was altered by translations and size changes in time and frequency (Ko et al., 2017). The result of the preprocessing was an image of 86 × 498 pixels, hereafter called the enhanced spectrogram image.

2.4.5. Convolutional neural network

A convolutional neural network (CNN) is a deep learning method which is extensively used in image recognition (LeCun et al., 2015). A CNN consists in stacking layers of artificial neurons (also called kernels or filters within the CNN framework) which perform on images a mathematical operation called convolution. Here, a CNN was used as a supervised method to classify the enhanced spectrogram image corresponding to the three sound classes, i.e., “buzzing,” “drumming,” and “background” sounds. This classification was carried out with a single output class. Where “buzzing” and “drumming” both occurred in a five-second frame, the class with the highest output probability was selected. In order to limit the computing power and time required to train the CNN, we chose to build a custom built CNN architecture made of a few successive layers: (1) four convolutional layers with zero padding, one pixel stride and different numbers of convolution kernels with different sizes (layer 1 with ten kernels of size 4 × 4 pixels, layer 2 with five kernels of size 8 × 8, layer 3 with five kernels of size 16 × 16, and layer 4 with three kernels of size 24 × 24); (2) four correction layers with the Rectified Linear Unit (ReLU) activation function after each convolution to introduce non-linearities to the decision function; (3) four layers of maximum pooling, after each ReLU layer, allowing the information to be compressed by halving the size of the intermediate image while preventing overfitting; (4) a fully connected layer, i.e., where the neurons have connections to all the outputs of the previous layer; and (5) a softmax layer associating a probability to each output class. The decision probability threshold for the final classification into one of the three categories was set to 0.95.

2.4.6. Evaluation

The quality of the CNN output was evaluated on the validation data set (“buzzing,” “drumming,” and “background”) by computing the overall accuracy and the average prediction. The overall accuracy was obtained by computing (TP + TN)/(TP + TN + FP + FN), with true positives (TP), true negatives (TN), false positives (FP), and false negatives (FN). The average prediction approximated the area under the curve (AUC) of the precision-recall curve, precision being TP/(TP + FP) and recall being TP/(TP + FN) (Boyd et al., 2013).

2.4.7. Optimization

A first application of the CNN on the complete data set revealed 304 (0.18‰) unexpected detections of “buzzing” sounds at night or during

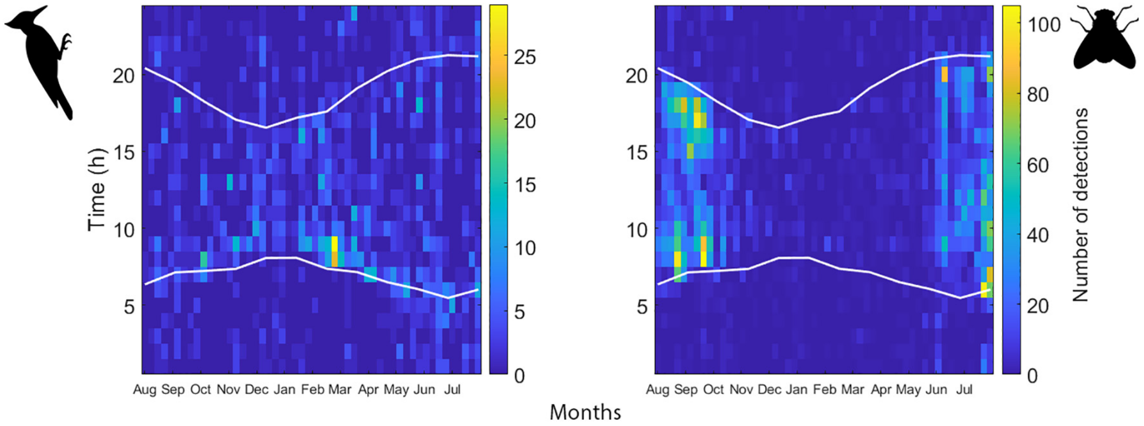

Fig. 1. Annual and diel phenology of "buzzing" and "drumming" sounds. The number of files containing either "drumming" (left) or "buzzing" (right) sounds is depicted according to weeks from the beginning of August to the end of July (*x*-axis) and time of day (*y*-axis). Average sunrise and sunset time are overlaid as gray lines. Note the change in the colour scale for the number of detections.

the winter. These false-positive detections were transferred to the "background" class. There were no unexpected detections for "drumming" sounds.

2.4.8. Implementation

All the supervised classification processes were implemented using the Deep Learning Toolbox of Matlab 2019a on a personal laptop (Intel Core i7 CPU).

2.4.9. Statistics

The medians and the distributions of detections were compared with the medians and the distributions of environmental variables using normalized histograms and non-parametric tests: the Wilcoxon rank test for unpaired samples and the Kolmogorov–Smirnov test, respectively. The proportion of detections according to the four sites was tested using a χ^2 test of conformity. All tests were run with a type I error of 5%.

3. Results

3.1. Annual and diel phenology

The best model obtained with our single CNN had an overall accuracy of 93.9% and an average prediction of 90.5%. "Buzzing" and "drumming" sounds were extremely rare, with only 8196 frames containing the former (0.51%) and 1767 frames containing the latter (0.11%). Most of the "buzzing" sounds were detected between the end of May and the end of October (88% of detections), during the day (86% of detections), with peaks after sunrise and before sunset (Fig. 1). The annual and diel phenology of "drumming" sounds was more dispersed. Nonetheless, most of the activity occurred between the beginning of February and the end of April (43% of detections), during the day (74% of detections), and more specifically just before sunrise and during the subsequent 4 h (47% of detections) (Fig. 1).

3.2. Temperature

The median of "buzzing" detections was 17.29 °C, significantly different from the median annual temperature of 7.55 °C (Wilcoxon test for unpaired samples, $W = 291{,}067{,}117$, $p < 2.2\ 10^{-16}$), with 85.64% of the detections found above the latter. The distribution of "buzzing" detections according to temperature was significantly different from that of the annual temperature (Kolmogorov–Smirnov test, $D = 0.41$, $p < 2.2\ 10^{-16}$). The median of "drumming" detections was 4.16 °C, and thus closer but still significantly different from the median annual temperature (Wilcoxon test, $W = 32{,}708{,}884$, $p < 2.2\ 10^{-16}$), with 35% of the detections found above the latter. The distribution of "drumming" detections according to temperature was also significantly different from the distribution of the annual temperature, but the distance between the distributions was less than for "buzzing" sounds (Kolmogorov–Smirnov test, $D = 0.16$, p-value $<2.2\ 10^{-16}$), indicating a stronger match with local temperature. Overall, "buzzing" sounds occurred at high temperatures which were rare, whereas "drumming" sounds occurred at low temperatures which were abundant (Fig. 2).

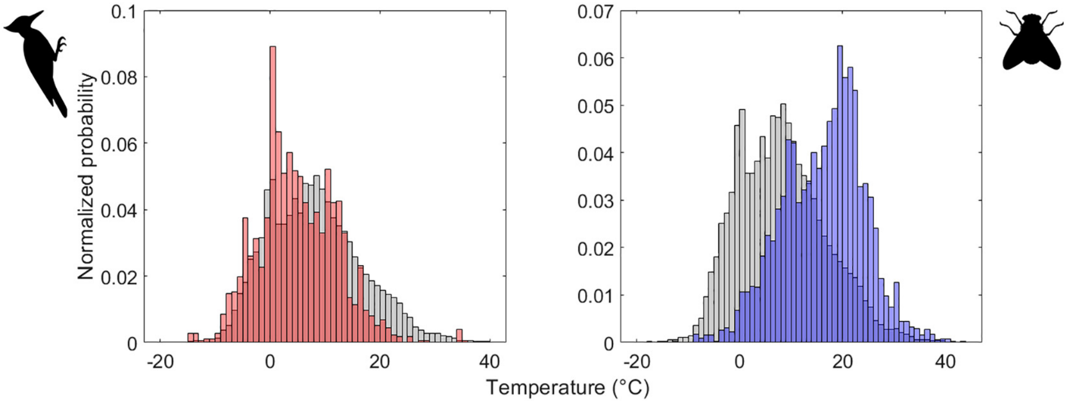

Fig. 2. Temperature breadth of "buzzing" and "drumming" sounds. Histograms of the number of files containing either "drumming" (left, red) or "buzzing" (right, blue) sounds and of the temperature recorded during the year of observations (gray).

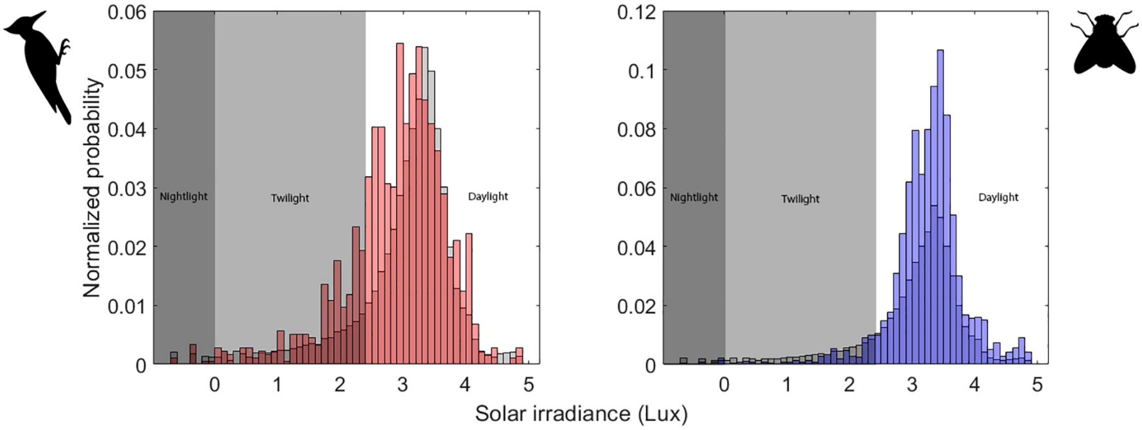

Fig. 3. Light breadth of "buzzing" and "drumming" sounds. Histograms of the number of files containing either "drumming" (left, red) or "buzzing" (right, blue) sounds and of the light measured as illuminance (log10(lx)) recorded during the year of observations (gray).

3.3. Solar irradiance

The median of "buzzing" detections was observed at 1826.6 lx (eq. 3.26 log10(lx)), significantly different from the median annual solar irradiance of 1.9 lx (eq. 0.29 log10(lx)) (Wilcoxon test for unpaired samples, W = 194,466,998, $p < 2.2\ 10^{-16}$), with 92.08% of the detections found above the latter. The distribution of "buzzing" sounds according to solar irradiance was significantly different from that of the annual solar irradiance (Kolmogorov–Smirnov test, D = 0.92, $p < 2.2\ 10^{-16}$). The median of "drumming" detections was observed at 510.72 lx (eq. 2.7 log10(lx)), significantly different from the median annual solar irradiance (Wilcoxon test for unpaired samples, W = 34,677,502, $p < 2.2\ 10^{-16}$), with 76.23% of the detections found above the latter. The distribution of "drumming" sounds according to solar irradiance was also significantly different from the distribution of the annual solar irradiance, but the distance between the distributions was less than for "buzzing" sounds (D = 0.75, *p*-value <2.2e-16), indicating a stronger match with local solar irradiance. Overall, "buzzing" sounds were mostly detected in high light conditions during the day, whereas "drumming" sounds mainly occurred in low light conditions, at twilight or in daylight when overcast (Fig. 3).

A heatmap of the number of detections according to a colour scale in relation to the two environmental variables of temperature and solar irradiance shows that "buzzing" sounds appeared to be restricted to a smaller temperature and light dispersion space, with 75% of the detections found in a smaller rectangle (from 6 °C to 29 °C; from 2.1 log10 lx to 4.1 log10 lx) than was true of "drumming" sounds (from −9 °C to 19 °C; from 0 lx to 4 log10 lx) (Fig. 4).

3.4. Relative humidity

The median of "buzzing" detections was observed at 62.09%, significantly different from the median annual relative humidity of 90% (Wilcoxon test for unpaired samples, W = 37,836,196, $p < 2.2\ 10^{-16}$), with 7.36% of the detections found above the latter. The distribution of "buzzing" sounds according to relative humidity was significantly different from that of the annual relative humidity (Kolmogorov–Smirnov test, D = 0.39, $p < 2.2\ 10^{-16}$). The median of "drumming" detections was observed at 93.5%, significantly different from the median annual relative humidity (Wilcoxon test for unpaired samples, W = 32,064,592, $p < 2.2\ 10^{-16}$), with 50.08% of the detections found above the latter. The distribution of "drumming" detections was also significantly different from that of the annual relative humidity, but the distance between the distributions was less than for "buzzing" sounds ($D = 0.15121, p < 2.2\ 10^{-16}$), indicating a stronger match with local relative humidity. Overall, "buzzing" sounds were recorded in dry but uncommon local conditions, whereas "drumming" sounds were recorded in common wet conditions (Fig. 5).

3.5. Spatial heterogeneity

The number of detections was unevenly distributed among the four recording sites for both "buzzing" (χ^2 test of conformity, $\chi^2 = 1377.3$, d.f. = 3, $p < 2.2\ 10^{-16}$) and "drumming" sounds (χ^2 test of conformity, $\chi^2 = 162.22$, d.f. = 3, $p < 2.2\ 10^{-16}$). The ratios between the maximum and minimum numbers of detections were 2.6 for "buzzing" and 2.1 for "drumming" sounds, respectively (Fig. 6).

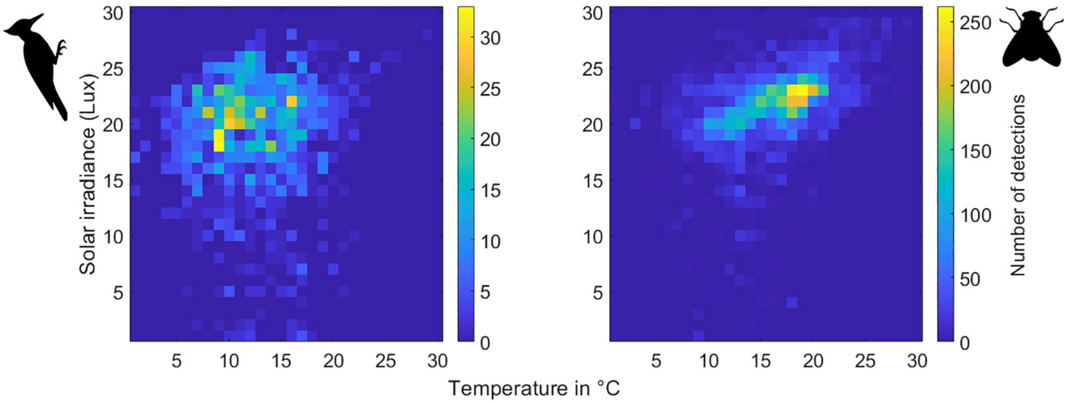

Fig. 4. Temperature and light breadth of "buzzing" and "drumming" sounds. The number of files containing either "drumming" (left) or "buzzing" (right) sounds is depicted according to temperature (°C) and light measured as illuminance (log10(lx)). Note the change in the colour scale for the number of detections.

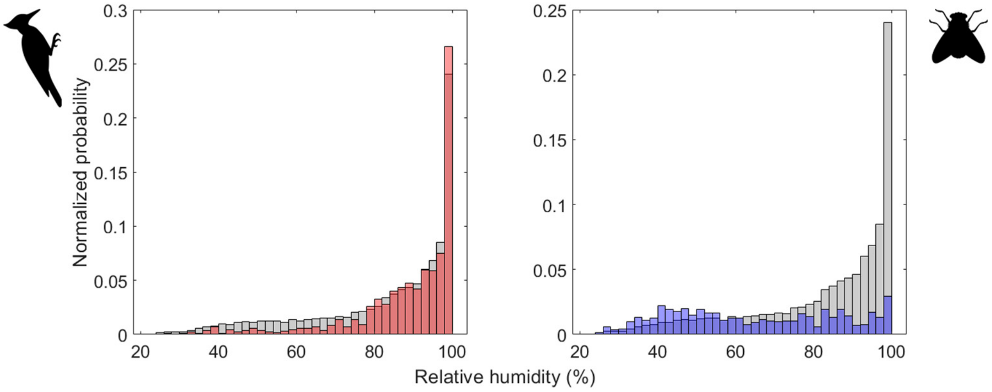

Fig. 5. Relative humidity breadth of "buzzing" and "drumming" sounds. Histograms of the number of files containing either "drumming" (left, red) or "buzzing" (right, blue) sounds and of the light measured as illuminance (log10(lx)) recorded during the year of observations (gray).

4. Discussion

Ecoacoustics is a new discipline that aims to monitor, describe and decipher biodiversity using non-invasive and automatic acoustic methods (Sueur and Farina, 2015). CNNs have been used in a wide range of ecoacoustic applications (Ruff et al., 2021), especially to track marine mammals (Lu et al., 2021), birds (Kahl et al., 2021) and amphibians (LeBien et al., 2020). In this investigation, we demonstrate the novel application of a CNN to track two ecological functions within an Alpine forest which harbors remarkable biodiversity, rather than simply detect the presence of particular species. As a result, we were able to estimate the seasonality, diel pattern, climatic breadth and spatio-temporal distribution of pollination by flying insects and wood use by woodpeckers.

The five-layer CNN selected was trained with only 1401 reference sounds so that the annotation process, as necessary for such a supervised technique, would not be time consuming (indeed, this process took 20 h to complete), and so that the model could be trained on a personal laptop computer with a standard CPU card without any access to specialized computing facilities. The CNN model was then successfully applied to 1,645,044 spectrogram frames with good levels of accuracy (93.9%) and mean prediction (90.5%). In addition, the CNN efficiently detected rare events, as the detection rate was only 0.51% for "buzzing" and 0.11% for "drumming" sounds. All these results suggest that the CNN technique can be used with confidence and without major difficulties for other audio data sets, in particular for those that will be collected over the coming years in the same forest. This also opens the possibility to detect scarce but key acoustic events such as rapid ecological events (e.g., falling tree sounds), sudden threats (e.g., hunters' gunshot blasts) and rare species vocalizations (e.g., gray wolf *Canis lupus*, Eurasian *lynx Lynx lynx*).

The CNN was able to detect the sounds produced by flying insects, including Hymenoptera and Diptera, most of which pollinate flowers. The technique could be transferred to a large number of other applications, including honeybee monitoring, and pollinator activity in crop fields and other habitats. A special case could be the monitoring of hoverflies, a group of Diptera (Syrphidae) which produce distinguishable sound when flying. Hoverflies are regarded as key ecological species, not only as pollinators, but also because their larvae inhabit a large diversity of habitats and microhabitats, from plant roots to tree canopies, and occupy several trophic levels, including saprophagy, microphagy, mycophagy, phytophagy, and entomophagy (Wotton et al., 2019). In the Alpine forest of the Jura

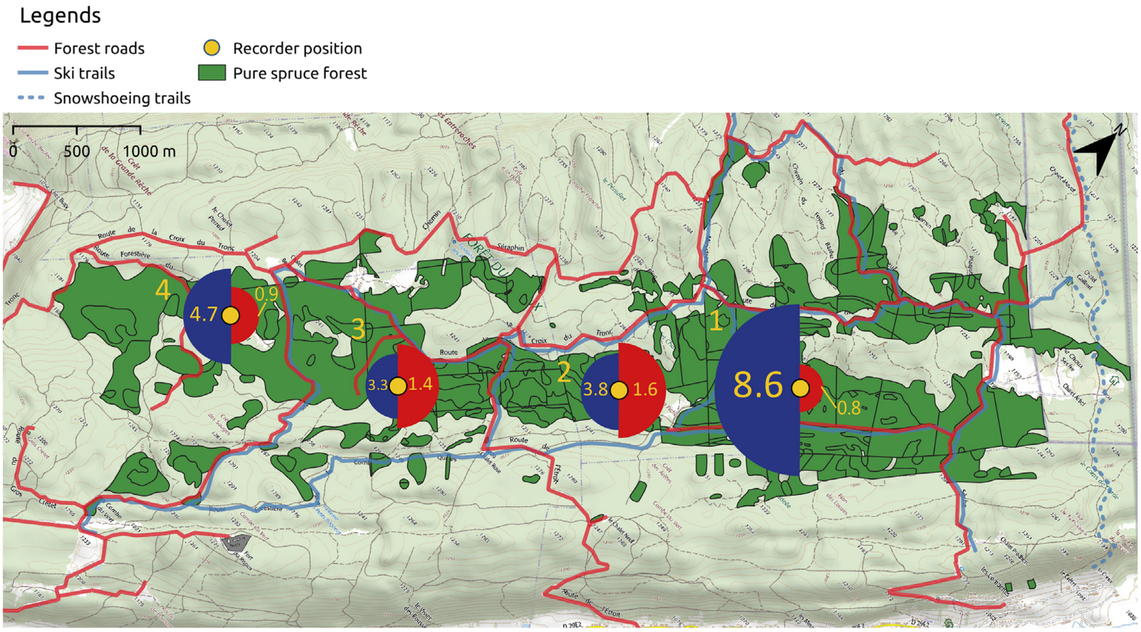

Fig. 6. Spatial distribution of "buzzing" and "drumming" sounds. Relative frequency of 'drumming' (red) and "buzzing" (blue) sounds at each recording site.

Mountains studied here, flying insects were active and were therefore potentially pollinating flowers in bright, warm and dry conditions. These conditions are not very surprising, as pollinators are known to require a minimal ambient temperature for flight muscle activity (Corbet et al., 1993), and tend to prefer warm flowers (Rands and Whitney, 2008). Such environmental conditions restrict the occurrence of buzzing to a period running from May to the end of October, corresponding to spring and summer, again in agreement with currently known pollinator phenology (Duchenne et al., 2020). More specifically, our method revealed two peaks of activity (after dawn and before dusk), a diel pattern that was also apparent when monitoring flower visits by bumble bees in Norway using image-based techniques (Steen, 2017).

Although differences may exist among pollinator species, the general pattern revealed by our monitoring program can still be useful to test for potential shifts in the future. Following the +1.5 °C IPPC climate model (Masson-Delmotte et al., 2021), pollinators might forage over a longer diel period and a longer season, potentially increasing the pollination rate as a result. However, an increase in temperature may be coupled with increases in rainfall and relative humidity, a prediction which holds for the Jura Mountains (Beniston, 2003). Such climatic changes can have detrimental effects on plant-pollinator interactions at individual and population scales, involving, among others, thermoregulatory expense, body overweight, olfactory signal obfuscation for insects, nectar dilution, pollen degradation, and volatile reduction for flowers (Lawson and Rands, 2019). The balance between the possible gain due to increased temperatures and costs due to increased rainfall is difficult to predict in the specific case of the Risoux, although large-scale predictions under a climate change scenario anticipate pollinator declines (Soroye et al., 2020) and possible mismatches between pollinator and plant phenologies (Kudo and Ida, 2013; Renner and Zohner, 2018). The number of automatic detections also revealed differences in the case of “buzzing” sounds between the four sites. This uneven spatial distribution, in particular for the recorder placed on the East side of the forest, may be due to differences in local resources, that is, differences in the number of foraging sites, or micro-climatic differences leading to different pollinator communities associated with different plant communities. Despite the similarity of habitats (i.e., European spruce forest), passive acoustic monitoring also revealed an unanticipated level of diversity within the forest, suggesting the occurrence of local habitat variations. Pollination is intrinsically linked to flower resources, which can differ according to microclimatic and landscape variations. Experts could disentangle these local differences using traditional floristic and entomological surveys.

Woodpeckers are excellent biodiversity indicators of forest ecosystems because their presence indicates complex forests which harbor considerable diversity in terms of forest composition, structure, disturbance and management (Mikusiński et al., 2001). Consequently, woodpeckers have also been deemed good potential proxies of climate change (Walsh et al., 2019). Here, the drumming of the complete woodpecker guild was associated with cool and wet conditions. Thus, a 1.5 °C increase in the ambient temperature may negatively affect woodpeckers, as they would be facing warmer conditions than before. However, at the same time, increased rainfall and relative humidity may favor their populations. Meanwhile, with respect to pollinators, temperature and humidity may have the reverse effect, the former being a negative factor and the latter being a positive factor. As this was the case for the North American woodpecker species, whose populations can expand or contract according to climate change (Walsh et al., 2019), the future population density and phenology of the woodpeckers inhabiting the Risoux forest are also difficult to predict. Future population dynamics will be dependent not only on climate change but also on forest use and management.

We were also able to determine a peak of general woodpecker drumming activity around March at the time of pair formation. Similar seasonality has been estimated for the North American pileated woodpecker (*Dryocopus pileatus*) by experts listening to semi-automated recordings (Tremain et al., 2008). Most of the drumming occurs after sunrise, corresponding to the dawn chorus (Gil and Llusia, 2020). Given that in our study the CNN was not trained to distinguish between territorial and feeding drumming, some detections were found outside of the usual reproduction period. Nevertheless, both types of drumming events revealed the presence of woodpeckers and hence their key ecological function in the forest ecosystem. Differences between the four recording sites might have been due to local population dynamics, discrepancies in resource distribution, or variations in species' nesting preferences.

Similar to our results for pollinators, our monitoring system could not distinguish between the three woodpecker species present in the forest, thus masking potential species differences. Recent studies have shown that there is enough species information encoded in woodpecker drumming (Garcia et al., 2020) to allow the automatic identification of species (Florentin et al., 2016, 2020). In this investigation, we aimed to monitor an ecological function, but a specific assessment of woodpecker populations could be run as a second step if a proper training data set were built for each species inhabiting the forest.

4.1. Concluding remarks

Through an in situ monitoring study based on ecoacoustic recording methods, signal analysis, and AI algorithms, we were able to detect and track two key ecological functions within a forest ecosystem. The two functions showed strikingly different temporal and environmental responses, in part because the species responsible for these functions have markedly different ecological and thermal niches. In particular, flying insects and birds are poikilothermic and homeothermic organisms, respectively, and therefore manifest contrasting degrees of dependence on ambient temperature. The tracking of functions without species identification can be highly valuable for forest monitoring and conservation, but also for other habitats, including crop fields, where pollination is crucial. Moreover, the acoustic monitoring of ecological functions provides a holistic perspective and so it may include some redundant information where species have similar life history traits, or hide heterogeneity where species have distinct biological characteristics.

These results underline the potential of ecoacoustics for not only in monitoring soundscapes or particular vocalizing species, but also in tracking ecological functions through appropriate automatic classification models. The data revealed both the seasonality and the diel pattern of each ecological function, suggesting different (and sometimes opposite) sets of climate pressures in the future. Tracking ecological functions in the long term (i.e., over a period of years) should show how an ecosystem reacts to climatic change. In addition, the monitoring highlighted an unanticipated level of spatial heterogeneity between the recording sites that should be considered for conservation priorities.

CRediT authorship contribution statement

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Writing: all authors.

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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