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Sonic environment and vegetation structure: A methodological approach for a soundscape analysis of a Mediterranean maqui

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ABSTRACT

Herein we present one of the first attempts to couple the complexity of vegetation and topographic features with the sonic environment to understand the distribution of bird species and individuals in their habitat. To achieve this, the sonic features of a bird community were studied during the spring and early summer of 2011 in a Mediterranean maqui located on the western slope of a remote hanging valley that is dominated by *Erica arborea*, *Quercus ilex* and *Arbutus unedo*.

Species composition, height, vertical foliage profile, canopy density and dispersion of vegetation were utilized as probable proxies for the sonic patterns. The acoustic activity of birds was collected through the use of a regular matrix of 20 audio recorders, spaced 25 m apart, which were placed following the topographic isoclines. The sonic complexity of the soundscape was evaluated using the Acoustic Complexity Index (ACI), which is a recently developed metric.

The PCA applied to the vegetation parameters revealed two principal distinguishing factors, which we were able to define as "vegetation density and structure" and "species segregation." Moreover, the results show that, even in the case of sampling sites that are very close together, sonic patterns vary across the season, highlighting the great variability of the soundscape and confirming the adequacy of the sampling scale of 25 m adopted in this study. The topographic features do not seem to be connected to the sonic environment. The main sonic complexity was found where the vegetation was taller and denser, especially where *E. arborea* was the dominant species. Although this proves that acoustic dynamics can be linked to vegetation structure, even on a small scale, a consistent element of sonic variability cannot be explained by vegetation patterns alone, and a soundtope hypothesis must be invoked.

1. Introduction

The recent field of soundscape ecology (Farina et al., 2011a; Pijanowski et al., 2011a,b; Truax and Barrett, 2011) has revealed new perspectives when it comes to investigating the sonic complexity of the environment, which is an important component of the quality of ecosystems. This has produced a powerful and efficient tool to be used for both the short- and long-term monitoring of biological and ecological dynamics (Bardeli et al., 2010; Depraetere et al., 2012).

The acoustic diversity of biophonies (Krause, 2012, p. 68) has been regarded as an indirect estimator with which to evaluate the biodiversity of different habitats (Gasc et al., 2013; Sueur et al., 2008).

Investigations of the sonic complexity of the environment are considered to be useful when it comes to: understanding the relationship between the structure of vegetation and animal dynamics (Pekin et al., 2012); evaluating the complexity of animal assemblages (Gasc et al., 2013); and investigating the relationship between the structure of the landscape and sonic patterns (Bormpoudakis et al., 2013).

In particular, the biophonic components of the sonic environment provide important information about community diversity and the dynamics of vocal animals (Krause, 2012), as well as more generally about the "health" of ecosystems (Carson, 1962). The acquisition of such knowledge is finally possible today thanks to: the use of autonomous recording systems (Blumstein et al., 2011); a powerful methodology with which to process sonic data (Farina et al., 2012); the availability of new sonic indices (Farina et al., 2011b; Sueur et al., 2012; Villanueva-Rivera and Pijanowski, 2012); and automatic identification algorithms for some groups of species (f.i. Ranjard and Ross, 2008; Skowronski and Harris, 2006; Somervuo et al., 2006; Trifa et al., 2008).

Despite the great potential of the soundscape approach, there are very few studies on terrestrial ecosystems in the literature (f.i. Bormpoudakis et al., 2013; Cellis-Murillo et al., 2009; Joo et al., 2011; Mazaris et al., 2009; Pieretti and Farina, 2013; Slabbekoorn, 2004). Moreover, uncertainty persists with respect to field procedures, such as: the selection of types and numbers of recording devices or their calibration (but see Mennill and Fristrup, 2012); the selection of the spatial and temporal scales with which to collect the sonic information according to the habitat investigated (Mennill et al., 2006); and the best indices and software

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with which to efficiently process the sonic data (Farina, 2014, p. 242; Gasc, 2012).

For instance, the choice of one recorder versus an array of recorders is a controversial argument that requires empirical validation, as the few examples of the use of arrays have been used to gauge the best spatial localization of individuals (f.i. Blumstein et al., 2011; Mennill et al., 2006) and not to intercept sonic patterns across a large area.

Moreover, most of the literature regarding the relationships between vocal animals (in particular birds) is based on aural identification carried out during field surveys. This is an approach that is strongly affected by the skill of the observer and influenced by the disturbance created by observer intrusion (Bibby et al., 1992, p. 24; Gibbons et al., 1996, p. 245).

The soundscape approach has the advantage of allowing the researcher to collect information that will be permanently stored in a digital medium. Moreover, the data are processed automatically, and the aural identification can be repeated whenever necessary, reducing the likelihood of disagreements between people with different species identification skills (Hobson et al., 2002). Finally, human disturbance is strictly limited to the period of the placement of the recording devices.

Of course, the relationship between vegetation complexity and the complexity of the sonic environment has only been investigated infrequently, especially from a bioacoustical perspective. In this context, Morton (1975) was one of first authors to emphasize the importance of vegetation structure on the acoustic adaptation of birds. His approach was followed by Marten and Marler (1977), who confirmed the acoustic adaptation hypothesis, while Laiolo et al. (2008) discussed the role of landscape fragmentation for the maintenance of a differentiated song repertoire in the Dupont's Lark (*Chersophilus duponti*). Later, fragmentation was demonstrated by Briefer et al. (2010) to be an important process that influences the composition of elements in skylark songs, although the number and complexity of these elements seem to be more fixed. Krause et al. (2011), meanwhile, have investigated the complexity of the sonic patterns in four habitats in the Sequoia National Park (US), and Pekin et al. (2012) put the emphasis on the relationship between the acoustic diversity and the structure of vegetation by using a LIDAR approach.

There is evidence that vegetation structure affects sound propagation, and the denser the vegetation is, the more the biophonies are degraded by reverberation and attenuation by leaves and branches (f.i. Embleton, 1963; Padgham, 2004). This produces responses with respect to, for instance, the range capacity of territorial birds, as proved by Morton et al. (1986) and Morton (1987) with respect to Carolina wrens.

In addition, the topographic characters of the environment are rarely considered in terms of the relationship with the sonic environment. For instance, Hunter (1989) has observed that singing birds on steep slopes are generally oriented towards the up-slope direction, with an evident advantage for the diffusion of acoustic waves.

Recently, the relationship between the structure of the landscape and the soundscape patterns has been explained by three different models, the first of which considers a patterned distribution of acoustic cues or sonotopes, defined as the result of the overlapping of the geophonies, biophonies and anthrophonies that are coincident with the structure of the landscape (Farina, 2014, p 17). A second model assumes that the sonotopes are broader than the landscape patterns due to an expected active diffusion of sonic cues that go beyond the borders of the vegetation patches. Finally, a third model states that the sonotopes, as described in the previous model, have an internal spatial variability due to the behavioral dynamics of vocal animals, where competition and cooperation mechanisms produce the spatial repartition of individuals (Farina and Pieretti, 2012; Malavasi and Farina, 2013). This further subdivision would create soundtopes, defined as a coordinated aggregation of biophonic sounds (sensu Farina, 2014, p 19; Farina et al., 2011a) inside each sonotope. Soundtopes represent distinct and emerging sonic aggregations with a great temporal variability.

In particular, our principal aims were:

- To test different field methodologies for collecting information on vegetation structure.
- To verify the efficacy of: a tight spatial scale while carrying out sonic investigations in a Mediterranean maqui characterized by dense vegetation in the first 3–4 m of the soil; the application of an array design for placing recording devices.
- To collect the sonic environment characters in general and, in particular, to compare the complexity of the habitats (topography and vegetation).
- To use such results as a basis for a further discussion of the sonotope/soundtope hypothesis.

2. Study area

The study area (Fig. 1), which is 600 m from the Tyrrhenian Sea and stands at an elevation of 300 m, is westerly exposed on the left side of a small hanging valley, with slopes characterized by an inclination of approximately 26°. It is located close to the small town of Deiva Marina, Eastern Liguria, Italy (44°13′27.6″N, 9°30′30.1″E), at the center of a large secondary dense sclerophyll forest dominated by small trees and *Erica arborea*, *Quercus ilex* and *Arbutus unedo* shrubs. The area, which is well away from permanent human settlements and paved roads, is bordered by some paths that are utilized by tourists from late spring to early fall, and occasionally by hunters in fall and early winter.

The area, which was partially terraced and cultivated until the early 1950s, experienced recurrent wild fires (1980s; see also Solans Vila, 2007) that have interrupted the wood recovery and intervened over the course of the process of land abandonment, as testified by the remnants of old scars along the entire study area.

As a result of a previous investigation of the soundscape of this area based on a recording station operating continuously during 2011 (Farina et al., 2013), we are aware that the major contribution to the sonic environment is represented by bird vocalizations and geophonic sources (wind, rain, thunder). Due to the area's remoteness from human settlements, the few anthrophonic disturbances are mainly produced by the engines of fishing and tourist boats, military and rescue helicopters, and civilian aircraft.

3. Methods

Vegetation sampling and sonic recordings were carried out according to a grid of 20 points (4 × 5) regularly spaced at 25 m, covering an area of 175 × 125 m.

In order to test the potential effects of topographic features on the sonic environment, it was decided to divide the analysis of the matrix into five “vertical lines” (following the maximum slope) and four “horizontal lines” (following isocline lines; Fig. 2).

3.1. Vegetation sampling

According to the different sampling techniques proposed for temperate deciduous forests (Blondel and Cuvillier, 1977; Blondel et al., 1973; MacArthur and Horn, 1964; MacArthur and MacArthur, 1961) and Mediterranean scrubs (Cody and Walter, 1976), we tried to detect the complexity of the vegetation by collecting information about the following parameters:

3.1.1. Vegetation height

The height of the shrubs and trees was assessed by direct measures along two perpendicular transects, each of which was: 8 m-long, centered on each recording station, and oriented according to slope inclination. The details of the height of the vegetation were collected

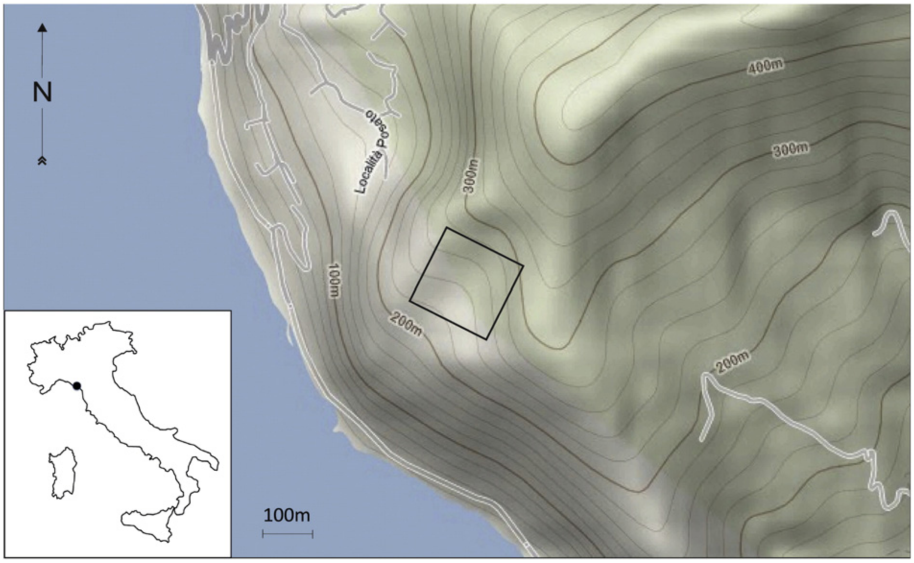

Fig. 1. Location of the study area.

by erecting a metric road every 2 m along the transects and identifying each plant species found (see Fig. 2).

For the successive computations, the heights of the vegetation, expressed in meters, were then resumed for each recording point, indicating only the mean height of the species. This revealed which species were dominant for the entire area.

3.1.2. Foliage profile

A foliage profile was collected every 2 m along a horizontal transect of 12 m centered at each recording station. The stations (1, 6, 11, 16 and 5, 10, 15, 20) located in the extreme vertical lines were sampled only on the internal side of the matrix, and so along a transect of 6 m. A woody board, which was 3.5 cm wide and 4 m tall and painted red and white every 20 cm (Fig. 2), was used to estimate the presence of vegetation at a distance of approximately <10 cm from the board. This totaled 212 counts. The parameters were distinct according to the dominant plants in three main categories: entire profile [(mean) board cover], the lower 2 m [(mean) board cover <2 m] and the higher 2 m [(mean) board cover >2 m].

3.1.3. Canopy density and dispersion

The canopy density and dispersion were measured using digital images of vegetation according to the method, partially modified, described by Goodenough and Goodenough (2012). A Coolpix 990

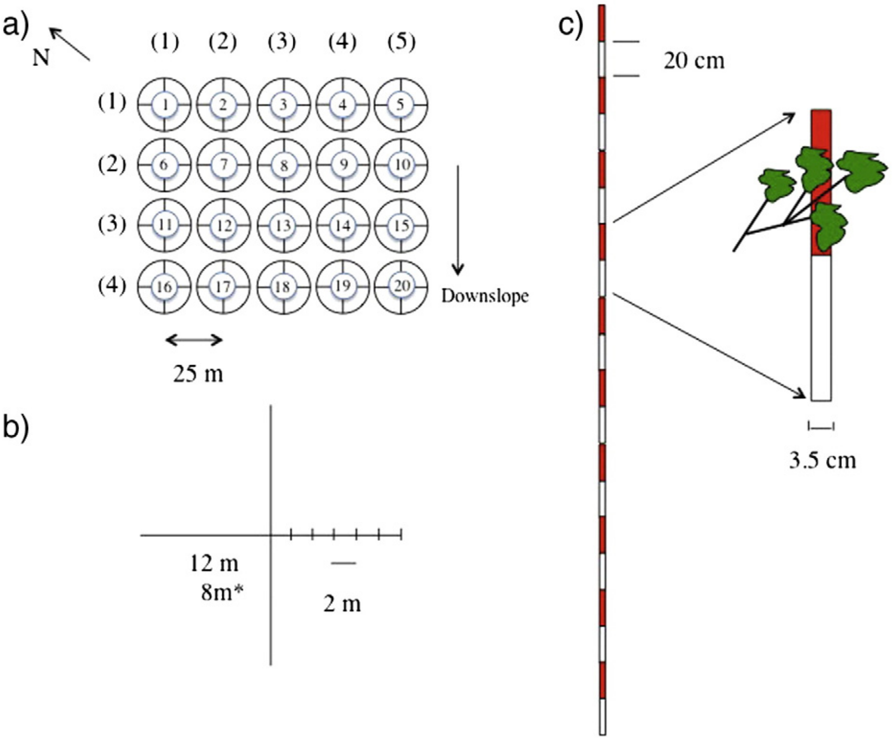

Fig. 2. a) Structure of the recording device array; in brackets, the ordination of vertical and horizontal lines; b) four harm transects utilized to collect information on vegetation structure. The measure indicated with an asterisk refers to the length of the transect used to collect information about vegetation height; c) schematic representation of the vertical board used to collect information on the vegetation profile.

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photo camera, pointed vertically and equipped with a Nikkor 8–24 mm lens zoom, was utilized to take photos of the vegetation strata at soil height (low stratum) and at a height of 140 cm (high stratum; Fig. 3). In order to keep the visual angle of the focal lens constant, it was reduced by a factor of 2× for the shots obtained at soil height. Shots were taken in precisely the place where the digital recorders were located, and were repeated six times every 2 m for each of the four cardinal directions, totaling 25 images at the low stratum (<140 cm) and 25 at the high stratum (>140 cm) for each recording station. A total of 1000 images were obtained across the entire study area.

This method has some advantages, as argued by Goodenough and Goodenough (2012), if compared with, for instance, hemispherical photography (see for instance Rich, 1990) or other intercept methods (f.i. Blondel and Cuvillier, 1977; Blondel et al., 1973; Mueller-Dombois and Ellenberg, 1974, p. 84).

To calculate canopy density and dispersion, monochrome pictures of 640 × 480 pixels were converted into dark and light pixels (representing respectively the canopy and the sky) using the CanopyDig® software proposed by Goodenough and Goodenough (2012). The transformation of a monochrome image into a false color image (blue = vegetation and red = sky) was carried out by choosing between eight images at different threshold values.

The level of the dispersion of the vegetation was calculated by applying the Morisita index of dispersion (Morisita, 1959, 1962) after subdividing each image into 12 sub-images and calculating the number of pixels in each of them using the CanopyDig software according to the procedure suggested by Goodenough and Goodenough (2012).

In more detail, the Morisita index of dispersion is calculated according to the following equation:

$$I_\delta = n\left(\frac{\sum_{i=1}^{n} X_i^2 - N}{N(N-1)}\right)$$

where n = the total number of sub-pictures

X_i = the number of the canopy pixels in each sub-picture *i*
N = the total number of canopy pixels in the entire image.

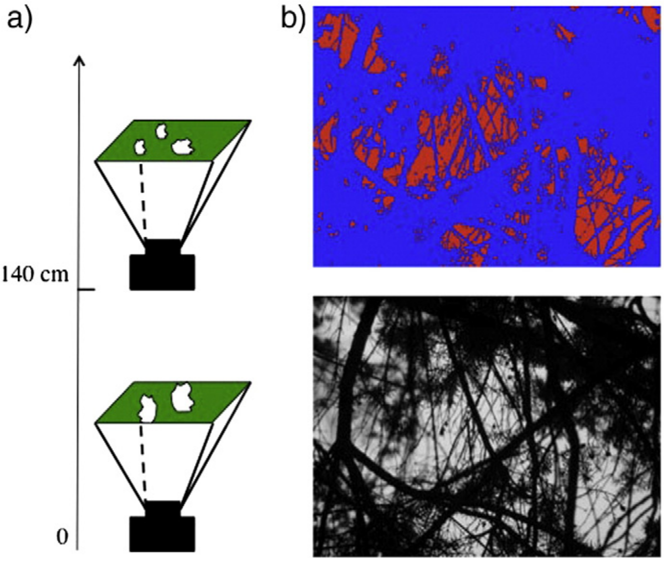

Fig. 3. Representation of the method to collect information on canopy density and dispersion: a) digital camera vertically oriented posed at the soil and at 140 cm from the soil; b) examples of a typical black and white picture and false color transformation with a selected threshold of sky resolution.

This index, which has as its most important property its independence from N, tends to increase with the rise in large gaps in an image.

The Morisita index of dispersion is a robust measure of spatial distribution that is particularly applied to evaluate the dispersion of plants (for an example of the application of this index, see Myers, 1978; Nieder et al., 2000).

3.1.4. Shrub and tree species composition

Shrub and tree species were annotated during the canopy density measurement process and totaled 1000 samplings, of which 500 were for the low stratum (<140 cm) and 500 for the high stratum (>140 cm).

3.2. Methods of recording and processing the sonic environment

The sonic environment was recorded by using 20 audio recording devices (Zoom H4™, Zoom Inc., Japan, System 2.40) during spring and early summer 2011 at the following sessions: 22 February; 6,11,19 and 26 March; 1,8,16,26, and 29 April; 7,13,21, and 28 May; 3,11 and 18 June; 7 and 19 July. The audio recorders were deployed immediately after that the skylight threshold was sufficient to work under the dense vegetation cover. For this technical reason, it was not possible to collect dawn chorus but just the singing activity of the following hours.

Due to the unfavorable (rainy or/and windy) weather conditions, the data collected on 22 February, 16 and 26 April, 3 and 18 June, and 19 July were excluded from the analysis, since the biological sounds risked being masked by rain or wind noise, which probably caused a significant depression in bird acoustic activity or might alter the acoustic signature of the community.

The matrix of recorders was oriented along the slope, with five recorders being placed in four horizontal lines (Fig 2). This orientation, which is coincident with the orientation of the transects utilized to check the vegetation, was used later for the interpretation and discussion of the distribution of the sonic patterns and topographic features. Sounds were sampled at 44,100 Hz at a resolution of 16 bits and stored on 2 GB Secure Digital Cards.

The sound files were synchronized by a post-hoc procedure, and all of the recordings were 120 minute long. The sound analysis was performed using the Acoustic Complexity Index (ACI) (Pieretti et al., 2011)

$$ACI = \frac{\sum_{k=1}^{n} |I_k - I_{k+1}|}{\sum_{k=1}^{n} I_k}$$

where I_k and $I_{(k+1)}$ are two adjacent values of spectral amplitude in a single frequency bin.

The ACI values were obtained by sound data processed by the SoundscapeMeter (Farina et al., 2012), which is a plug-in of the WaveSurfer software (Sjölander, 2002; Sjölander and Beskow, 2000). Frequencies higher than 10 kHz were excluded from the analysis, because they were considered to be not representative of the sonic activity of the bird assemblage investigated. An amplitude threshold value greater than 3000 was adopted to exclude most of the background noise. The sound files were analyzed at a temporal interval of 1 min, enabling us to obtain 120 sub-files of one minute each for each recording station. The ACI was set at a "clumping" resolution of 1 sec (86 data, each at a temporal distance of 0.011 s), totaling 7200 ACI values for each 120 minute session and per recording station.

Once the FFT was settled at 512 points (Hamming windowing, no overlap), the ACI was calculated for each of the 116 classes of frequency (each of 86.20 Hz) in the selected frequency interval of 0–10 kHz. The ACI values were then assigned at an interval of 1 kHz each, creating 10 ACI categories (Fq: [1, 2 … 10] kHz). It was also decided to further split the ACI results into two main groups: 0–1 kHz and 1–10 kHz, which corresponded respectively to background noise (light wind,

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sounds of moving foliage, boats, etc.) and biophonic contributions (mainly birds).

Finally, the ACI index for each recording station was used with the following temporal scale: ACI total = all daily sessions and frequencies combined; ACI monthly (all frequencies combined) for each month = $\text{ACI}_{\text{February}}$ (1), $\text{ACI}_{\text{March}}$ (4), $\text{ACI}_{\text{April}}$ (5), ACI_{May} (4), ACI_{June} (3), and ACI_{July} (2). The numbers in the brackets are the number of recording sessions per month.

3.3. Statistical analysis

All of the statistical tests were performed using Statistica v.8.0 (StatSoft, Inc., Tulsa, OK). A non-parametric approach was used, since the variables could not fit into a normal distribution pattern, even after logarithmic transformation. The Kruskal–Wallis analysis of variance was used to test the significance between multiple independent groups for vegetation along the lines and the columns of the grid. The same statistical analyses were performed for the ACI results, also looking at the differences among days, months and stations.

The Spearman-rho correlation was used to measure the statistical dependence between the parameters of the vegetation and the ACI values.

A Cluster Analysis was performed to classify vegetation data and ACI frequencies by categories using the Euclidean distance and the Ward method. The Mann–Whitney U Test was then used to compare the significant differences between the independent groups highlighted by the results of the Cluster Analyses and for comparing vegetation parameters. This test was also used to assess the significance of the correlations (in terms of ACI values) between the adjacent and the first non-adjacent recording point in order to verify the appropriateness of the spatial scale. This was performed after the exclusion of the March and July sessions to reduce variability due to the migratory habits of some species. Finally, the vegetation variables were oriented using a Principal Component Analysis.

The Surfer9™ (Golden Software, Inc., Golden, Colorado) was adopted to create interpolated maps (Kriging method) to give the spatial orientation of the ACI results. Factor 1 resulting from the PCA analysis of the vegetation was also plotted on an interpolation map.

4. Results

4.1. Vegetation

4.1.1. Composition of the vegetation

Table 1 reports the absolute frequency of the species, revealing that *E. arborea* is the most common followed by *Q. ilex* and *A. unedo*.

Other common species counted were *Smilax aspera*, *Myrtus communis*, *Calycotome spinosa* and *Pinus pinaster*.

4.1.2. Height of the vegetation

A. unedo was the tallest species (3.75 ± 0.76 m), followed by *Q. ilex* (3.32 ± 0.94 m) and *E. arborea* (3.07 ± 0.57 m) (see Table 2 for the mean heights found at each sampling station).

In Table 2 the values obtained by processing all of the 17 variables are summarized.

The height of the vegetation revealed significant differences for *E. arborea* (Kruskal–Wallis: H = 11.17, $p < .01$) and *Q. ilex* (Kruskal–Wallis: H = 8.85, p = .03) when the stations were grouped according to the horizontal lines, but not for *A. unedo* (Kruskal–Wallis: H = 7.39, p = .06). The two central lines presented significant differences for *E. arborea* (Mann–Whitney: U = 22, p = .008) and *A. unedo* (Mann–Whitney: U = 22, p = .03), but not for *Q. ilex* (Mann–Whitney: U = 29, p = .11). The second line had the maximum difference (significant) when compared with the three others: *E. arborea* (Mann–Whitney: U = 1, p.01), *A. unedo* (Mann–Whitney: U = 10, $p < .01$), and *Q. ilex* (Mann–Whitney: U = 4, $p < 01$). No significant differences were found when the heights were compared for the stations along the vertical lines.

4.1.3. Vertical foliage profile

A different distribution of foliage profiles between the three dominant species was evident in the results (see Fig. 4). In particular, the foliage profile of *E. arborea* had a maximum of around 140 cm, while *Q. ilex* has a quite irregular foliage profile, with maximum values ranging from 40 to 180 cm. The foliage profile of *A. unedo*, meanwhile, has a minimum of 180 cm and then increases to 400 cm.

The spatial distribution of the foliage profile according to a gradient from the downslope to the upslope only had a significant difference for *A. unedo* when the horizontal lines are considered (Kruskal–Wallis: H = 8.92, p = .03). The second line in particular is significantly different from the others (Mann–Whitney: U = 11.5, p = .02). A slope effect is not evident for *Q. ilex* (Mann–Whitney: U = 32.5, p = .67), as is also the case for *E. arborea* (Mann–Whitney: U = 26.5, p = .34).

4.1.4. Canopy density

The canopy density presents a significant difference between the four horizontal lines (high stratum, Mann–Whitney: H = 10.62, $p < .01$; low stratum, Mann–Whitney: H = 11.34, $p < .01$). No significant differences were observed between the five different vertical lines (low stratum, Mann–Whitney H = 1.61, p = .80; high stratum, Mann–Whitney: H = 4.58, p = .33).

The two central rows reveal significant differences when compared with the first and last lines (low stratum, Mann–Whitney: U = 7, $p < .001$; high stratum, Mann–Whitney: U = 8, $p < .001$). When compared with all of the other lines, horizontal line n. 3 maintains a significant difference only for the high (Mann–Whitney: U = 6, $p < .005$), but not for the low, stratum (Mann–Whitney: U = 18, $p < .08$) of the vegetation. Horizontal line n. 2 also maintains a significant difference for the low (Mann–Whitney: U = 14, p = .04), but not for the high, stratum (Mann–Whitney: U = 27, p = .35).

A positive correlation exists between the low stratum of the canopy density and the high stratum (Spearman rho: r = 0.81, $p < .01$).

4.1.5. Morisita index of heterogeneity

The Morisita index of the low stratum was significant when the two central lines are compared with lines 1 and 4 (Mann–Whitney U = 20, p = .023), but there are no significant differences for the high stratum (Mann–Whitney U = 31, p = .159). Line n. 2 shows a significant difference for the Morisita high strata (Mann–Whitney U = 10, $p < .01$), but not for the low stratum (Mann–Whitney U = 31, p = .57). Finally, line n. 3 is significantly different from all of the others for the low strata (Mann–Whitney U = 14, p = .04) but not for the high stratum (Mann–Whitney U = 29, p = .45). No differences were found when the Morisita index was tested with respect to the vertical lines.

The Morisita index of the low stratum is not significantly correlated with the high stratum (Spearman-rho r = 0.21, ns).

4.2. The PC analysis of the vegetation variables

Two principal factors explained 62.34% of the variance (respectively: Factor 1 = 40.89%, Factor 2 = 1.45%) among all of the vegetation variables considered. On the basis of the orientation of the variables (Fig. 5) and the position of the recording stations (Fig. 6) on the PCA plot, we were able to interpret these two factors respectively as "vegetation structure" and "species composition." Specifically, the vegetation discriminates according to Factor 1 in terms of canopy height and density, with an increase in homogeneity from left to right (Fig. 9a).

The Cluster Analyses (see Fig. 7) showed that the structure of the vegetation can be distinguished into two main groups: the first group (A) is characterized by more vegetation (tallest plants and highest canopy cover) and the second (B) by less vegetation (shortest plants and lowest canopy cover).

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Table 1
Frequency of main shrub and tree species along the 20 sampling stations (see Methods) below 140 cm (a) and above 140 cm (b), and mean height of the three dominant species (**H-Ea**: *Erica arborea*; **H_Qi**: *Quercus ilex*; **H_Au**: *Arbutus unedo*) for each sampling station (**SS**).
Nv: absence of vegetation; **Ea**: *Erica arborea*; **Qi**: *Quercus ilex*; **Au**: *Arbutus unedo*; **Cs**: *Calycotome spinosa*; **Mc**: *Myrtus communis*; **Csp**: *Cistus* sp.; **Sa**: *Smilax aspera*; **Cv**: *Calluna vulgaris*; **Lsp**: *Lonicera* sp.; **Pp**: *Pinus pinaster*; **Gsp**: *Genista* sp.; **Rsp**: *Rosa* sp.; **Bp**: *Brachypodium pinnatum*; **Esp**: *Euphorbia* sp.; **Dv**: dead vegetation.

Ss	Nv		Ea		Qi		Au		Cs		Mc		Csp		Sa		Cv		Lsp		Pp		Gsp		Rsp.		Bp		Esp		Dv	
	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	a	a	b
1	0	3	18	22	5	5	2	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	1	0	1	0	1	0	7	2
2	3	1	12	18	5	9	7	0	0	1	0	2	0	0	0	2	0	1	0	0	1	1	1	1	1	1	1	1	1	1	5	1
3	15	2	3	13	7	12	2	2	0	2	0	3	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	0
4	7	4	8	12	9	7	3	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
5	12	3	8	11	4	11	3	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
6	1	3	22	3	9	7	16	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	17
7	0	1	22	9	9	5	9	0	0	0	0	0	0	1	0	6	0	0	0	0	2	0	2	0	2	0	2	0	2	0	1	11
8	3	2	20	16	4	9	9	1	1	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	6
9	1	1	14	5	9	3	7	1	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	1	0	1	0	1	0	1	0	12
10	0	4	16	7	9	10	12	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9
11	1	1	17	13	8	8	4	0	0	0	1	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	14
12	3	0	17	6	14	10	4	2	0	0	1	3	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	12
13	6	1	12	11	9	11	3	1	0	0	0	0	0	1	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	4
14	0	0	21	13	14	8	9	1	0	0	0	0	0	0	3	6	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	15
15	1	0	16	12	8	7	9	1	0	0	0	0	0	0	2	9	0	1	0	0	2	0	0	0	0	0	0	0	0	1	5	9
16	2	7	12	5	18	8	3	0	0	3	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	1	0	12
17	0	3	16	9	9	8	8	0	0	6	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	8
18	1	3	22	3	9	7	16	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	17
19	0	4	21	14	13	6	11	0	1	4	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	12
20	0	4	20	15	9	7	8	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	3	16
Sum	56	47	317	217	181	158	145	13	2	19	3	12	0	3	6	46	0	6	1	2	9	1	4	2	4	3	4	4	4	6	28	178
Sum (a + b)		103		534		339		158		21		15		3		52		6		3		10		6		7		8		10		206

According to Table 1, station n. 10 on the extreme left of the plot (Fig. 6) is characterized by very low canopy cover and a low height for each species. On the opposite side, station n. 1 is characterized by the highest canopy density and by the greatest height for *E. arborea*, *A. unedo* and *Q. ilex*.

Factor 2 probably discriminates for species composition, where *E. arborea* occupies the upper and *Q. ilex* and *A. unedo* the lowest positions. Station n. 15, for instance, is characterized only by the presence of *E. arborea*; in contrast, stations n. 18 and n. 3 are characterized by low numbers of *E. arborea* and the presence of *Q. ilex* (station n. 18) and *A. unedo* (station n. 3).

4.3. Acoustic Complexity Index

The ACI values detailed for each session and every station are reported in Fig. 8, and the interpolated spatial distribution of the total ACI is set out in Fig. 9b. Table 3 contains the ACI values for the frequency categories and months. The spatial distribution of the ACI for every session and

Table 2
Structure of vegetation along the 20 sampling stations (**SS**). The stations were labeled (A and B) according to the first two PCA factors. A (mean) and B (mean): mean value of each variable according to the PCA ordination.
CD_L: canopy density <140 cm; **CD_H**: canopy density >140 cm; **Iδ_L**: Morisita index <140 cm; **Iδ_H**: Morisita index >140 cm; **Height_Au**: (mean) Height of *Arbutus unedo*; **Height_Qi**: (mean) Height of *Quercus ilex*; **Height-Ea**: (mean) Height of *Erica arborea*; **Au**: (mean) foliage profile of *Arbutus unedo*; **Au_H**: (mean) foliage profile of *Arbutus unedo* <2 m; **Au_L**: (mean) foliage profile of *Arbutus unedo* >2 m; **Qi**: (mean) foliage profile of *Quercus ilex*; **Qi_H**: (mean) foliage profile of *Quercus ilex* <2 m; **Qi**_L: (mean) foliage profile of *Quercus ilex* >2 m; **Ea**: (mean) foliage profile of *Erica arborea*; **Ea_H**: (mean) foliage profile of *Erica arborea* <2 m; **Ea_L**: (mean) foliage profile of *Erica arborea* >2 m; **All veg**: Ea + Qi + Au.

SS	CD_L	CD_H	iδ_L	iδ_H	Height_Au	Height_Qi	Height_Ea	Au	Au_H	Au_L	Qi	Qi_H	Qi_L	Ea	Ea_H	Ea_L	All veg	A/B
1	1973	1949	28.28	30.58	5.04	4.82	4.09	0.29	0.29	0	0.57	0.57	0	6.29	4.86	1.43	7.14	A
2	1993	1793	27.58	32.50	4.10	2.89	2.70	1.46	1.46	0	1.38	0.08	1.31	2.85	1.46	1.38	5.69	A
3	2015	1602	26.90	32.79	3.58	2.30	2.40	3.62	3.00	0.62	2.77	0.69	2.08	1.92	0.62	1.31	8.31	A
4	2023	1880	27.10	34.66	4.00	2.96	2.83	1.77	1.62	0.15	1.62	1.08	0.54	4.46	2.38	2.08	7.85	A
5	1961	1778	29.20	34.67	3.52	2.35	2.41	1.29	1.29	0	1.86	0.71	1.14	4.43	2.29	2.14	7.57	A
6	1909	1323	27.30	32.32	3.70	2.52	2.18	0	0	0	1.00	0.00	1.00	4.43	0.29	4.14	5.43	B
7	1962	1555	27.46	38.63	3.83	1.59	2.07	0.23	0.23	0	1.62	0.15	1.46	3.23	0.08	3.15	5.08	B
8	1885	708	36.41	55.51	2.38	1.88	1.81	0.46	0.46	0	2.38	0.31	2.08	2.23	0.00	2.23	5.08	B
9	1706	825	30.03	46.17	2.75	1.94	1.87	0.54	0.38	0.15	1.85	0.31	1.54	2.54	0.08	2.46	4.92	B
10	1831	594	37.29	66.31	2.19	1.77	1.72	0.57	0.14	0.43	3.00	0.00	3.00	2.86	0.57	2.29	6.43	B
11	1710	1385	44.42	36.89	4.50	3.22	2.53	1.57	1.57	0	1.71	0	1.71	4.14	0.71	3.43	7.43	A
12	1900	1543	42.19	21.70	2.88	2.64	2.35	0.23	0.23	0.00	1.92	0.62	1.31	2.69	0	2.69	4.85	B
13	1796	1009	32.36	62.06	3.14	2.50	2.16	1.08	0.38	0.69	0.54	0.00	0.54	3.31	0.23	3.08	4.92	B
14	1949	1801	27.55	27.56	4.50	4.09	3.14	0.77	0.69	0.08	1.31	0.38	0.92	6.46	2.46	4.00	8.54	A
15	1869	1539	30.34	28.87	3.67	3.34	2.56	0.00	0.00	0	0	0.00	0	3.00	0.00	3.00	3.00	B
16	2003	1926	27.97	33.49	4.06	4.48	3.00	1.86	0.86	1.00	2.57	2.00	0.57	2.86	0.71	2.14	7.29	A
17	2005	1832	27.35	31.44	4.13	2.54	2.66	3.38	3.23	0.15	1.46	0.54	0.92	4.38	1.15	3.23	9.23	A
18	1847	1479	36.46	25.13	4.06	2.19	2.29	2.54	2.15	0.38	3.54	1.23	2.31	1.69	0.15	1.54	7.77	A
19	2080	2013	26.40	27.12	4.77	4.28	3.39	1.46	1.46	0.00	3.23	2.38	0.85	4.54	1.62	2.92	9.23	A
20	2058	1738	26.33	31.71	4.32	3.70	2.93	4.24	4.00	0.24	0.60	0.08	0.52	4.00	1.56	2.44	8.84	A
A (mean)	1968	1765	29.63	31.55	4.22	3.32	2.87	2.02	1.80	0.22	1.89	0.81	1.07	4.00	1.66	2.34	7.91	
B (mean)	1857	1137	32.92	43.94	3.07	2.27	2.09	0.39	0.23	0.16	1.54	0.17	1.37	3.04	0.16	2.88	4.96	

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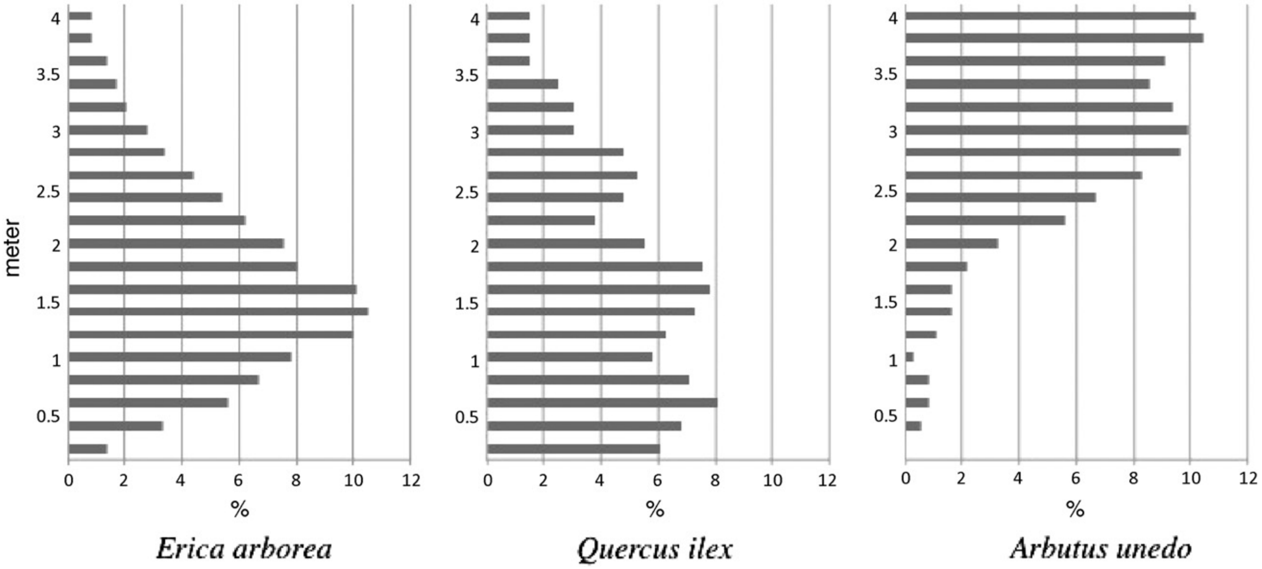

Fig. 4. *Erica arborea*, *Quercus ilex* and *Arbutus unedo* vertical profiles (20 intervals of 20 cm on a height of 4 m) expressed as a %.

for each recording station is available in the Supplementary materials (SM1). The acoustic footprint, intended as the distribution of frequencies after the exclusion of the first seven bins (602 Hz), which were principally attributed to the geophonies and anthrophonies and regarded as background noise, is summarized for each station (see Supplementary materials, SM2).

A Cluster Analysis of how the frequency categories are distributed in the different recording stations is represented in Fig. 10, where four groups are distinct: the first group is represented by background noise (Fq: 1 kHz), the second by rare frequencies (Fq: 2 kHz and Fq: 10 kHz), the third by intermediate values (Fq: 6 kHz Fq: 7 kHz, Fq: 8 kHz and Fq: 9 kHz) and the fourth by the highest ACI values (Fq: 3 kHz, Fq: 4 kHz and Fq: 5 kHz; mainly attributed to three songbirds (*Turdus merula*, *Erithacus rubecula* and *Leiothrix lutea*) by one of us, AF, and following a previous investigation, Farina et al., 2013).

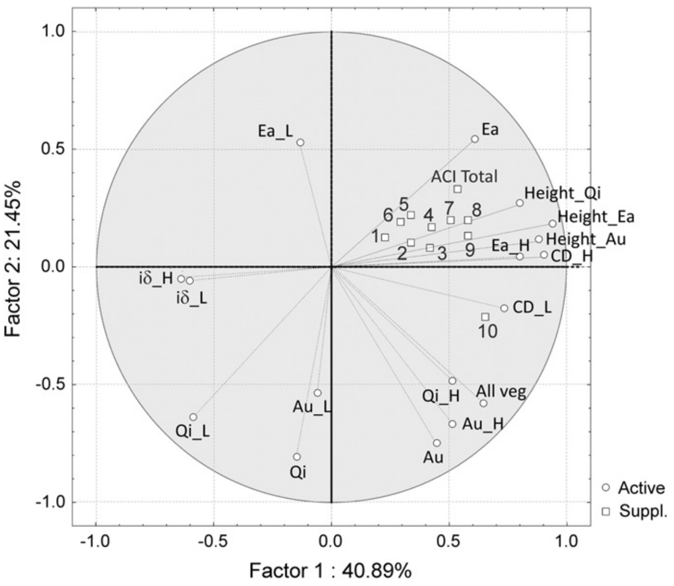

Fig. 5. Ordination of the recording stations according to the first two factors of a Principal Component Analysis. **CD_L**: canopy density <140 cm; **CD_H**: canopy density >140 cm; **Iδ_L**: Morisita index <140 cm; **Iδ_H**: Morisita index >140 cm; **Height-Ea**: (mean) height of *Erica arborea*; **Height_Qi**: (mean) height of *Quercus ilex*; **Height_Au**: (mean) height of *Arbutus unedo*; **Au**: (mean) foliage profile of *Arbutus unedo*; **Au_H**: (mean) foliage profile of *Arbutus unedo* <2 m; **Au_L**: (mean) foliage profile of *Arbutus unedo* >2 m; **Qi**: (mean) foliage profile of *Quercus ilex*; **Qi_H**: (mean) foliage profile of *Quercus ilex* <2 m; **Qi_L**: (mean) foliage profile of *Quercus ilex* >2 m; **Ea**: (mean) foliage profile of *Erica arborea*; **Ea_H**: (mean) foliage profile of *Erica arborea* <2 m; **Ea_L**: (mean) foliage profile of *Erica arborea* >2 m; **All veg**: Ea + Qi + Au; from 1 to 10 the ACI values of the different categories of frequency of each 1 kHz band; **ACI Total**: the sum of all ACI values.

The background noise levels (Fq: 1 kHz) varied significantly during the different sessions (Kruskal–Wallis: $H = 119.31$, $p < .01$). In particular, they were generally higher in the first half of the season (March and April; Kruskal–Wallis: $H = 7.69$, $p = .01$), and were differently distributed along the months (lower in March, May and July; Kruskal–Wallis: $H = 62.46$, $p < .01$). A significantly different distribution among the 20 stations was also observed for this frequency band (Kruskal–Wallis: $H = 118.26$, $p < .01$), as was also the case when the stations were grouped according to the horizontal (Kruskal–Wallis: $H = 69.72$, $p < .01$) or vertical (Kruskal–Wallis: $H = 17.25$, $p < .01$) lines. In particular, the higher two horizontal lines were less "noisy" than the lower ones, while along the vertical lines, 1 and 3 were the quietest.

The ACI values of each of the 10 frequency intervals were significantly different along the 14 recording sessions (Kruskal–Wallis: $H = 134.52$, $p < .01$), but were preferentially distributed in the late part of the season (Kruskal–Wallis: $H = 45.05$, $p < .01$), demonstrating the typical trend of a bird breeding community: ascendant from March to May and descendent thereafter (Kruskal–Wallis $H = 102.66$, $p < .01$), with a peak of singing activity in April, May and June. When looking at the different placement of the stations, there was a precise difference between them (Kruskal–Wallis: $H = 68.53$, $p < .01$), as well as along the horizontal (with a very low third line, Kruskal–Wallis: $H = 16.69$, $p < .01$) and vertical lines (indicating a high first and low second vertical line, Kruskal–Wallis: $H = 13.29$, $p < .01$).

When focused on the central breeding months (April, May and June), Fq: 1 kHz was significantly different because of a very low value in May (Kruskal–Wallis: $H = 49.05$, $p < .01$), while in the Fq: 2–10 kHz frequency interval, the values were more similar (Kruskal–Wallis: $H = 7.71$, $p < .02$).

Both noise (Fq: 1 kHz) and biophony (Fq: 2–10 kHz) levels were significantly different along the five months of recordings.

Along the season, the comparisons between the ACI of the horizontal adjacent stations and the first horizontal non-adjacent stations were not significant (Mann–Whitney: $U = 99.50$, $p = .41$), as was also the case between the vertical adjacent stations and the first vertical non-adjacent stations (Mann–Whitney: $U = 39.50$, $p = .17$).

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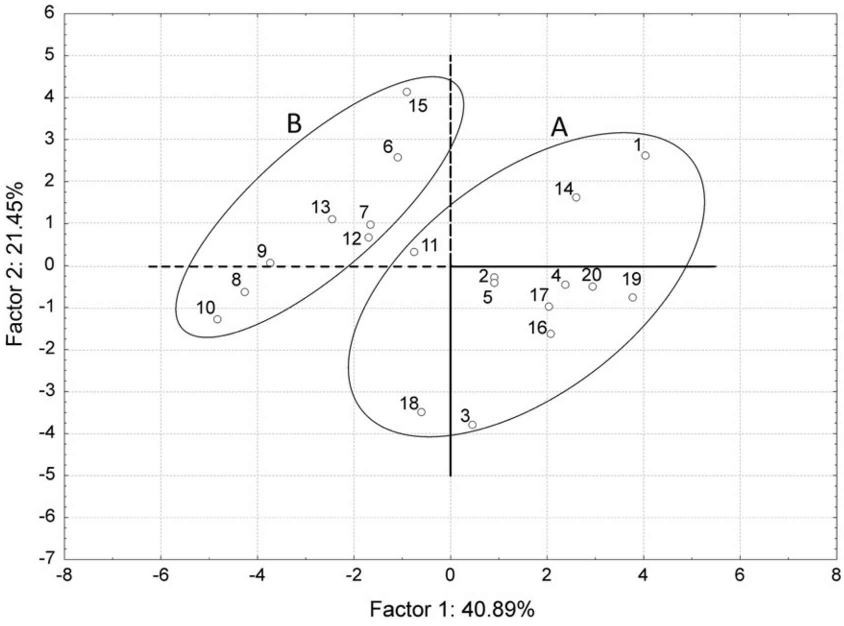

Fig. 6. Distribution of recording stations according to the PCA of the vegetation variables. A and B the two major aggregations according the Cluster Analysis (A: vegetation structure; B: species composition).

4.4. ACI and vegetation variables

The relationship between vegetation variables and the ACI at different aggregation levels is represented in Table 4. When considering the sum of all the ACI frequency categories (ACI Total) and the vegetation variables, no significant correlation is observable. Likewise, no significant correlation between vegetation variables was found for ACI$_{\mathrm{Fq:\ 1\ kHz}}$ and ACI$_{\mathrm{Fq:\ 2\text{–}10\ kHz}}$.

Among the variables used to describe the structure of the vegetation, Height_Au was the variable with the most significant relationships with the ACI aggregations (nine significant relationships), followed by Ea (five cases) and Height_Ea (five cases). Au_L and Qi had no cases that were correlated with ACI aggregations.

Among the 10 categories of ACI_frequencies, the categories that were more related to the vegetation resulted ACI$_{\mathrm{Fq:\ 10\ kHz}}$ (9), followed by ACI$_{\mathrm{Fq:\ 9\ kHz}}$ (6). ACI$_{\mathrm{Fq:\ 8\ kHz}}$, ACI$_{\mathrm{Fq:\ 1\ kHz}}$, and ACI$_{\mathrm{Fq:\ 4,\ 5,\ 6\ kHz}}$ had no significant relationships with the vegetation variables. ACI$_{\mathrm{Fq:\ 2,\ 3,\ 8\ kHz}}$ had an intermediate number of relationships with the variables (2, 1 and 3 respectively).

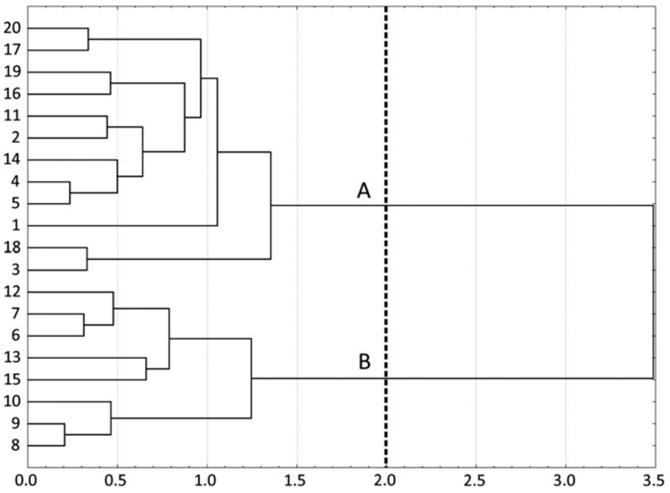

Fig. 7. The sampling stations clustered according to the vegetation variables.

According to the PCA and the two separate groups of vegetation variables (A and B), the ACI tends to be higher in the stations where the structure of the vegetation is denser and where there is the presence of *E. arborea* (Group A).

The ACI values, according the different categories of frequencies, were not significantly different between A and B. Only ACI$_{\mathrm{Fq:\ 9\ kHz}}$ (Mann–Whitney: $U = 22$, $p < .04$) and ACI$_{\mathrm{Fq:\ 10\ kHz}}$ (Mann–Whitney: $U = 12$, $p < .005$) revealed a significant difference.

The ACI values of each category of frequencies averaged for all of the stations were always higher in Group A but in May, the ACI was similar in the two groups (Table 3).

5. Discussion

5.1. Methodological aspects

The field procedure to place an array of recording devices has demonstrated great potential when it comes to obtaining synchronized information about the acoustic activity of birds (biophonies) and describing the variability of the sonic context assigned to geophonies and anthrophonies. The “array method” enables sonic patterns along the seasons to be described and relationships with vegetation patterns to be ascertained.

According to the aims of this investigation, the scale at which we have conducted the field survey (25 m) was confirmed as an adaptable resolution to ascertain both vegetation and sonic complexity. Yet this scale is habitat dependent, and has been expanded in other studies when we have operated in different conditions. For instance, in a young beech woodland (50–60 years old) without low canopy vegetation, we chose a scale of 100 m (Farina personal comment, Pieretti, 2008, Master's Thesis), while in a mountain ecotone with a sparse underground the scale was set at 80 m (Farina personal comment). In fact, in temperate biomes, the density of the vegetation in the first few meters strongly affects the diffusion of sound, as proved by the playback experiments conducted by Naguib et al. (2000) on chaffinches (*Fringilla coelebs*).

The lack of significance found in the comparison between the horizontal adjacent stations along the season and the first horizontal non-adjacent stations, and between the vertical adjacent stations and the

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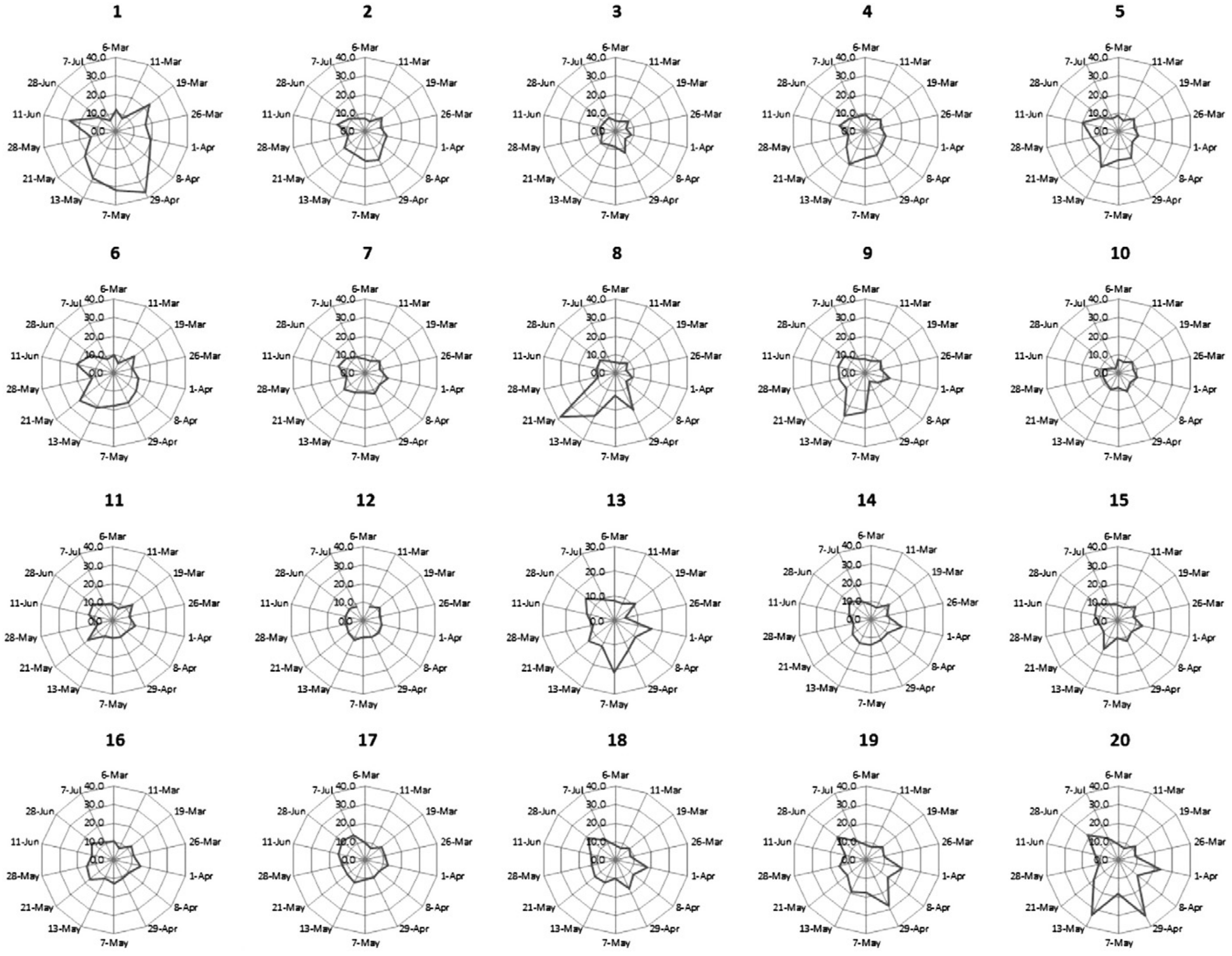

Fig. 8. Distribution of ACI values along the season from March to July for each recording station.

first vertical non-adjacent stations, confirmed the appropriateness of the selected distance for the placement of the recording devices.

5.2. Vegetation patterns

The vegetation has a complex pattern. This is probably due to: different soil composition and the depth of the soil, with rock outcrops in the middle part of the area; and the recent history of repeated fires, which is a disturbance that is common to the entire Mediterranean basin (Blondel and Aronson, 1999; Grove and Rackham, 2001; Naveh, 1974).

The intersection of different techniques of vegetation sampling was important, confirming that, at least in a Mediterranean maqui, the description of the vegetation patterns must be studied from different angles. In the study area, the maqui looks to be so dense that it would not be possible to find spatial discontinuities or patterned ecotones.

When investigated at the high resolution, the apparent homogenous structure of the maqui is revealed to have a fine-scale heterogeneity, which is also verified in other Mediterranean contexts (f.i. Sardinia Island by Cody and Walter, 1976). Indeed, after a Cluster Analysis, it is possible to clearly distinguish two separate aggregations (indicated as A and B, see Fig. 7) that are useful for interpreting sonotope patterns.

Among the 17 variables utilized to describe the complexity of the vegetation, the height and foliage profiles were the best predictors of acoustic complexity, concurring with the spatial classification of the sampling stations into groups A and B.

The Morisita index did not contribute as expected to establishing a significant relationship with the ACI, but until now was mainly experimented with in either homogeneous or heterogeneous (Goodenough and Goodenough, 2012) adult forests (f.i. Stewart, 1986), and never in a dense maqui of a few meters in height. Likewise, has never been compared with sonic complexity.

The use of different techniques to sample the vegetation helped to deal with the uncertainty of adopting only one methodology in such a condition. The moderate slope of the study area created further difficulties when it came to measuring the height of the vegetation and using indirect methods to evaluate the height of the plants, forcing us to directly measure individual plants per individual plant.

5.3. Sonic patterns

The variability of the sonic patterns can be explained only in part by the vegetation proxies. The emergence of temporary sonic aggregations or soundtopes (sensu Farina et al., 2011a) is probably the result of the acoustic interaction of the birds. Soundtopes emerge when the ACI is analyzed daily and monthly, and are proved by the presence of a great variability in the spatial distribution of the different classes of frequencies and in the frequency footprint.

The statistical analysis conducted at different levels of the ACI aggregation (per daily session, month, frequency categories, etc.) proved the great spatial and temporal variability of the sonic environment found among the stations, despite their closeness (only 25 m).

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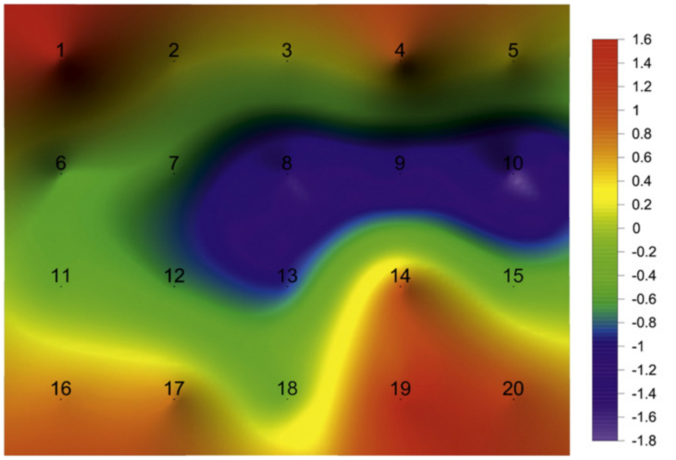
a) Factor 1



b) ACI

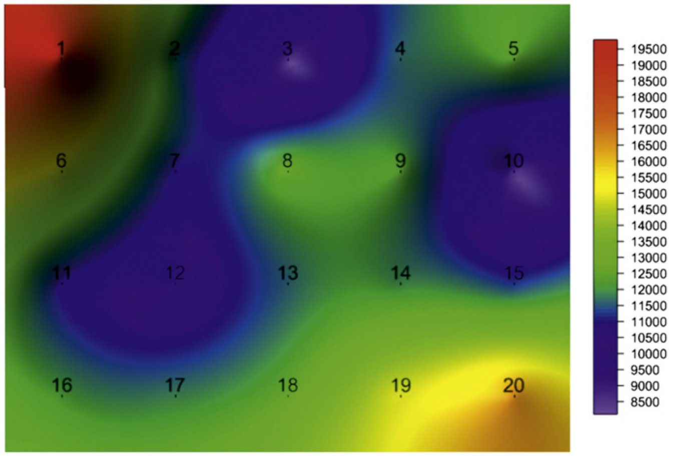


Fig. 9. Spatial representation of Factor 1 resulting from the PCA of the vegetation and spatial interpolation of the ACI when all of the sessions are averaged.

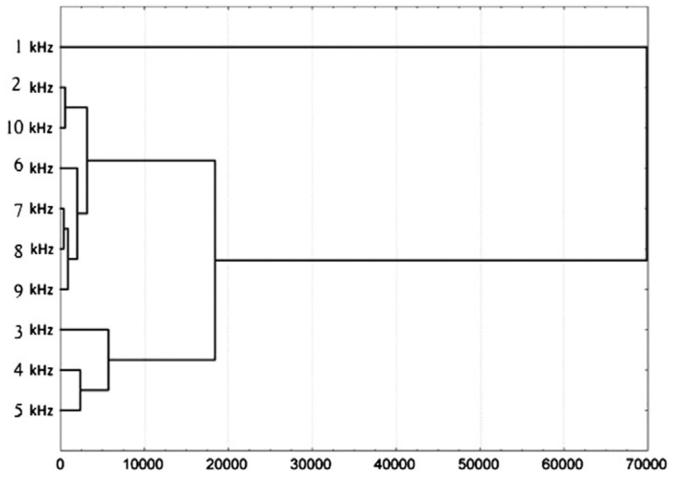


Fig. 10. Cluster Analysis of the ACI values according to the different frequency classes.

The similarity in May of the ACI values observed between the two groups found by the Cluster Analysis (A and B) could depend on the presence of a migratory bird species (*Sylvia cantillans*) that prefers edges and low shrubs and has been observed to display acoustic activity (starting in May) in the station classified by the PCA as B.

5.4. Some caveats

A high ACI value can be discussed for a single frequency bin or in terms of the entire set of frequencies. In this specific case, stations with a high $\mathrm{ACI}_{\mathrm{total}}$ can indicate an even distribution of information among the entire set of frequencies. Biologically speaking, this could mean the presence of many species (high α diversity sensu Whittaker, 1972) or complex acoustic patterns. For instance, in the case of a frequency modulated song like in the robin (*E. rubecula*), the closeness of a microphone to a singer allows an acoustic spectrum that is richer in information from a broader range of frequencies to be recorded. This is unlike the case with a distant song that is degraded, especially in the

Table 3
Distribution of the ACI according to the frequency classes and months for each sampling station (SS); labeled A and B according to the PCA factors, and averaged values of the ACI categories according to A and B.

SS	1 kHz	2 kHz	3 kHz	4 kHz	5 kHz	6 kHz	7 kHz	8 kHz	9 kHz	10 kHz	Total	2–10 kHz	March	April	May	June	July	A/B
1	7763	97	1523	5043	4549	1734	1253	1551	872	28	24,413	16,650	14,874	26,536	23,778	18,563	6526	A
2	8571	55	696	2440	1692	435	293	273	66	3	14,525	5954	8390	13,871	13,402	13,240	7785	A
3	8049	60	533	814	457	126	55	64	60	10	10,229	2180	6689	9494	8440	8193	8269	A
4	10,594	71	578	1097	1181	416	195	246	214	7	14,600	4005	8668	12,322	14,119	12,736	9063	A
5	9712	64	691	1841	1514	553	375	555	372	14	15,691	5979	8658	12,067	16,290	16,008	7989	A
6	9009	131	1699	3540	2540	575	355	334	125	6	18,315	9306	10,053	15,610	18,585	18,182	8427	B
7	9667	99	886	1252	919	305	223	201	103	9	13,664	3997	8151	11,548	11,862	14,068	9440	B
8	8020	99	1196	2572	2690	1086	167	75	41	2	15,950	7930	6513	13,057	21,448	10,495	7319	B
9	9088	88	937	2097	1786	672	279	331	213	4	15,495	6407	8425	9118	18,543	15,016	8583	B
10	8569	43	340	588	343	87	52	88	59	2	10,170	1602	7850	10,154	8735	6559	2819	B
11	10,738	120	817	867	612	157	101	125	99	7	13,642	2905	9690	10,614	11,073	13,583	9379	A
12	10,385	29	199	380	309	133	46	49	33	3	11,567	1182	9418	10,356	10,086	9950	8300	B
13	10,190	227	1031	1212	1111	547	102	46	26	2	14,493	4303	7751	13,349	13,680	13,078	9558	B
14	10,037	267	1493	1634	892	256	108	142	75	3	14,906	4869	9117	13,870	12,708	13,448	10,532	A
15	10,952	80	659	1166	782	160	73	107	62	1	14,043	3090	9384	12,019	11,471	13,432	9704	B
16	9927	115	1646	1867	1068	265	139	159	77	6	15,270	5343	10,101	12,410	13,893	13,388	10,480	A
17	10,453	125	1479	1420	704	281	188	148	90	9	14,897	4444	9694	10,757	12,220	15,466	15,086	A
18	10,192	160	1352	1993	1346	344	156	161	77	8	15,789	5597	8357	15,825	12,718	16,241	12,169	A
19	10,683	158	1183	2713	2084	637	335	398	235	10	18,436	7753	9163	20,681	16,334	15,811	11,292	A
20	10,322	219	1805	3542	2856	1078	726	725	372	18	21,662	11,340	9183	23,424	19,780	17,313	13,283	A
A (mean)	9753	126	1150	2106	1580	523	327	379	217	10	16,172	6418	9382	15,156	14,563	14,499	10,154	
B (mean)	9485	99	868	1601	1310	446	162	154	83	4	14,212	4727	8443	11,901	14,301	12,597	8019	

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Table 4
Correlation matrix between the vegetation parameters and the ACI values aggregated according the different frequency categories and months. N1: number of significant correlations of the ACI categories; N2: number of significant correlations of the vegetation parameters. Significant correlations are reported in bold.

	CD_L	CD_H	Id_L	Id_H	Height_Ea	Height_Qi	Height_Au	Au	Au_H	Au_L	Qi	Qi_H	Qi_L	Ea	Ea_H	Ea_L	N1
ACI_Fq: 1 kHz	0.063	0.209	−0.005	−0.385	0.325	0.388	0.314	0.218	0.257	−0.047	−0.106	0.081	−0.363	0.261	0.015	0.429	0
ACI_Fq: 2 kHz	0.026	0.084	−0.236	−0.180	0.238	0.272	**0.483**	0.230	0.249	0.198	−0.238	−0.027	−0.291	0.357	0.177	**0.496**	2
ACI_Fq: 3 kHz	0.208	0.242	−0.349	−0.212	0.352	0.376	**0.519**	0.147	0.160	0.101	−0.279	0.055	−0.366	0.324	0.274	0.236	1
ACI_Fq: 4 kHz	0.274	0.256	−0.380	−0.191	0.317	0.284	0.409	−0.005	0.092	−0.224	−0.192	0.118	−0.295	0.234	0.292	−0.106	0
ACI_Fq: 5 kHz	0.224	0.162	−0.340	−0.017	0.211	0.185	0.251	−0.050	0.067	−0.236	−0.219	0.098	−0.316	0.229	0.268	−0.209	0
ACI_Fq: 6 kHz	0.168	0.123	−0.286	0.056	0.132	0.108	0.171	−0.089	0.053	−0.253	−0.253	0.089	−0.329	0.246	0.212	−0.127	0
ACI_Fq: 7 kHz	0.426	0.400	**−0.529**	−0.069	0.341	0.208	0.413	0.036	0.167	−0.324	−0.264	0.161	−0.361	**0.451**	**0.490**	−0.122	3
ACI_Fq: 8 kHz	0.427	**0.478**	**−0.502**	−0.198	**0.451**	0.320	**0.501**	0.079	0.168	−0.288	−0.154	0.242	−0.344	**0.473**	**0.564**	−0.156	6
ACI_Fq: 9 kHz	0.423	**0.510**	**−0.492**	−0.135	**0.474**	0.344	**0.532**	0.147	0.243	−0.255	−0.124	0.303	−0.367	**0.588**	**0.604**	−0.044	6
ACI_Fq: 10 kHz	**0.624**	**0.595**	**−0.550**	−0.242	**0.457**	0.233	**0.549**	**0.463**	**0.541**	−0.046	0.096	**0.513**	−0.193	0.333	**0.558**	−0.275	9
ACI_Total	0.292	0.319	−0.355	−0.283	0.379	0.347	0.406	0.055	0.163	−0.171	−0.119	0.310	−0.377	0.351	0.359	−0.080	0
ACI_Fq: 2–10 kHz	0.247	0.227	−0.361	−0.119	0.286	0.253	0.333	0.005	0.111	−0.206	−0.195	0.142	−0.307	0.281	0.335	−0.121	0
ACI_March	0.223	**0.487**	−0.129	**−0.505**	**0.614**	**0.735**	**0.566**	−0.065	−0.059	−0.247	−0.327	0.101	**−0.563**	**0.519**	0.333	0.289	7
ACI_April	0.359	0.402	−0.335	−0.409	**0.522**	**0.504**	**0.588**	0.077	0.137	−0.148	−0.287	0.142	**−0.487**	0.413	0.439	−0.093	4
ACI_May	0.205	0.186	−0.298	0.035	0.227	0.242	0.192	−0.074	0.026	−0.181	−0.228	0.155	−0.400	0.317	0.289	−0.125	0
ACI_June	0.153	0.290	−0.301	−0.367	0.344	0.289	**0.563**	0.014	0.119	−0.277	−0.275	0.102	−0.336	**0.457**	0.339	0.194	2
ACI_July	0.242	0.302	−0.332	−0.427	0.362	0.326	**0.476**	0.435	0.434	0.289	−0.105	0.200	−0.353	0.187	0.076	0.420	1
N2	1	4	4	1	5	2	9	1	1	0	0	1	2	5	4	1	

higher frequencies, by vegetation and atmospheric conditions. This effect is well known in the literature (f.i. Padgham, 2004; Slabbekoorn et al., 2002).

5.5. Relationship between topography and the sonic environment

The non-significant differences between the horizontal and vertical stations when every station is compared with the first adjacent one, despite the presence of slopes with a steepness of 26°, seems to rule out an expected topographic effect with more interactions between species and individuals along a horizontal plane, and fewer interactions between individuals and species along the line of maximum slope for more sound dispersion.

5.6. Relationship between vegetation and the sonic environment

All of the different variables that describe the vegetation were important for depicting the complexity of the vegetation cover, but only the Height_Au (height of *A. unedo*) contributed to explaining nine of 17 ACI categories, followed by Ea (average foliage profile of *E. arborea*) and Height_Ea (Height of *E. arborea*) both of which were correlated with five ACI categories.

The best correlation between the ACI and the vegetation parameters was found with the frequency categories 7, 8, 9 and 10. This result can be attributed to birds that sing at these frequencies, like, for instance, *Regulus ignicapillus* and *S. cantillans* (Farina et al., 2013). But this concordance could also be an indicator of the proximity to the microphones of species such as *E. rubecula* and *T. merula* which, when their song is not degraded by distance, exhibit some components of the acoustic performance placed on the highest frequencies. This point is quite important, because the ACI cannot discriminate between the species considered (see Farina et al., 2012), but can separate the different frequency components of a bird song captured by microphones.

The structure of the vegetation has two evident patterns: higher vegetation on the border of the area and lower vegetation in the center, where *E. arborea* is dominant. This ordination is only partially related to the distribution of the sonic frequencies that were heterogeneous in space and time, confirming indirectly the presence of different sonotopes, and the presence of several soundtopes that are highly variable in space along the season according to the breeding phenologies of the different species (see Supplementary materials, SM1). A reasonable concordance between the ACI of the entire season and the spatial representation of the Factor 1 can also be seen in Fig. 9. This demonstrates how important the structure of vegetation is when it comes to affecting the soundscape, structuring well recognizable sonotopes. At the same time, the presence of soundtopes that are the result of acoustic habits is confirmed.

6. Conclusions

The different methods of vegetation sampling have demonstrated their capacity to explain some of the sonic environment characteristics. In particular, the use of vegetation height and the vertical foliage profile seem to be two of the best proxies for matching bird biophonies, as previously outlined in a pioneering piece of work by MacArthur and MacArthur (1961).

The ACI has demonstrated great operational flexibility when it comes to adapting the index to the sonic context, for instance in terms of background noise removal and its capacity to describe the fine structure of the sonic environment, analyzing every frequency at a particular time.

The ACI application requires a change in the ecological paradigms, which were until now based on the matching between individual species and environmental variables. The ACI approach considers not only the species, but also the acoustic information that species collectively produce during their activity, allowing a more informative dimension of living habits to be explored. This enables important components of behavioral habits that would otherwise be neglected by different approaches to be examined. It has been proved how informative the acoustic signals uttered by species may be for communicating their physical condition (Gil and Gahr, 2002) or their relationship with the climate (Snell-Rood, 2012) and weather (Moller, 2010).

The displacement of several microphones resolves the uncertainty about the number of species present in an area and their distribution.

In spite of an intensive effort to sample vegetation and the sonic environment, uncertainty emerges from this analysis about the relationship between vegetation and birds' biophonies if we do not adopt the sonotope/soundtope model. Although other communication models could be invoked to explain the sonic complexity observed (f.i. Heterospecific attraction and competition, Mönkkönen et al., 1990, or the Network models, Burt and Vehrencamp, 2005; Naguib, 2005, to mention just a few), this model allows us to: explain the partial correlation between vegetation and acoustic patterns that create distinct sonotopes, and attribute the residual variability to the intrinsic dynamics of birds during the breeding period (soundtope patterns). In fact, the variability that emerges when sessions are confronted with each other, and cannot be explained by vegetation patterns, may represent the dynamic connected to the "soundtope." This seems to be one of the most relevant conclusions that we can reach from this investigation. This result is an important starting point for the application of the automated

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sampling of acoustic diversity technique, and indicates that every environment requires a specific spatial resolution to sample sonic components.

In conclusion, soundscape ecology is an innovative approach to studying the sonic complexity of the environment at different spatial and temporal scales. Although under experimentation, appropriate field methods for collecting geophonic, biophonic and anthrophonic sources, and efficient metrics to process the huge quantity of acoustic data, provide a great opportunity to investigate the contribution of sonic processes to environmental complexity.

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