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Spatial and temporal variation of bird dawn chorus and successive acoustic morning activity in a Mediterranean landscape

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Ecoacoustic techniques using multiple acoustic sensors and two metrics of the acoustic community – the acoustic complexity index (ACI) and the chorus ratio (CR) – were successfully used to describe and characterize the morning acoustic activity of birds according to three equal temporal intervals during spring 2013: Dawn Chorus, Post Chorus 1, and Post Chorus 2. The metrics were applied across five Italian Mediterranean locations (Valenza, Madonna dei Colli, Monte Curto, Virolo, Croce di Tergagliana) that differed by land-cover typologies. Results from the ACI metrics showed a peak during the Dawn Chorus and a visible lull close to sunrise between Dawn Chorus and Post Chorus 1. The lull was evident in all localities except Valenza, where singing activity was relatively constant across the successive morning intervals. Temperature and vegetation structure were confirmed as important factors associated with morning acoustic activities. Vegetation evenness and temperature across the season was negatively correlated with ACI, whereas CR was positively correlated with temperature and vegetation diversity. Of the 33 species of birds identified during the maximum dawn chorus activity, Blackcap, Blackbird, European Robin, and Great Tit were acoustically dominant and their activity was significantly higher before sunrise except for Blackcap, whose acoustic activity showed no significant differences across time intervals. The dawn chorus is one of the most conspicuous behaviours of birds, engendering much speculation but no definitive, univocal explanations. The ecoacoustic approach opens a new perspective for investigating this complex phenomenon.

Keywords: acoustic community; acoustic complexity index; acoustic signature; birds; chorus ratio; dawn choruses

Introduction

Choruses are one of the most spectacular events of nature, generated by the contemporaneous vocalization of several individuals and species in terrestrial, freshwater, and marine habitats. The majority of research on choruses has focused on the origins, patterns, and functions of chorusing activities produced by birds at dawn. For instance, Staicer et al. (1996) reviewed major hypotheses to explain the chorusing behaviour of individuals, populations, and communities by grouping the causal factors into three categories: intrinsic, environmental, and social.

The intrinsic factors have been assigned to the circadian cycles of testosterone and physiological needs of individuals (Cuthill and MacDonald 1990; Thomas 1999; Thomas

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and Cuthill 2002; Thomas et al. 2002; Barnett and Briskie 2007). Environmental factors are mainly represented by light intensity (Kacelnik 1979; Berg et al. 2006), air motion (Wiley and Richards 1978; Henwood and Fabric 1979; Wiley 1991; Dabelsteen and Mathevon 2002), and habitat structure (Brown and Handford 2003). The social factors influencing choruses are based on mate attraction, territory defence, and the resolution of social dynamics (e.g. Morse 1989; Greenfield 1994; Hoi-Leitner et al. 1995; Burt and Vehrencamp 2005; Tobias et al. 2014).

Despite consistent and robust literature based on observations and experimentation on individual species' behaviour, dawn choruses remain controversial because of the complexity and uncertainty associated with studying acoustic communities and their interactions with environmental factors that are heterogeneously distributed in space and time (Staicer et al. 1996; Farina 2014). In particular, less research has been devoted to understanding the influence of environmental conditions on spatial and temporal patterns of choruses at the community level (e.g. Wright 1912, 1913; Allen 1913; Allard 1930; Leopold and Eynon 1961). For this, many aspects of choruses, such as the relationship between dawn acoustic activity and the successive morning singing routine in relation to habitat typology and climatic conditions, remain insufficiently known. Even fewer studies have specifically compared singing activities in the morning across different habitats, along seasons, and the role of different species that contribute to choruses (Keast 1994; Hasan 2011). Among these, Lindenmayer et al. (2004) observed in south-eastern Australia the decline of bird song activity moving from eucalyptus forest to a pine plantation, while Berg et al. (2006) analysed the temporal trend of the chorus for neo-tropical passerines.

The complex investigative scenario that is required to address chorus phenomena is currently facilitated by the new theoretical and methodological approaches offered by ecoacoustics (Sueur and Farina, submitted), in conjunction with the availability of a new generation of digital automatic acoustic sensors (Farina et al. 2014). Additionally, new metrics derived from information gathered by passive remote sensing technologies have been used to effectively evaluate the complexity of acoustic communities by numerically describing their acoustic signature across different landscapes (e.g. Sueur et al. 2008; Depraetere et al. 2012; Gage and Axel 2014). Specifically, the acoustic complexity index (ACI: Pieretti et al. 2011) was tested in terrestrial (Farina et al. 2011; Farina 2014) and marine environments (e.g. McWilliam and Hawkins 2013) and was suggested to be a very effective index to describe spatio-temporal and spectral characteristics (acoustic signature) of community activities (Towsey et al. 2014; Pieretti et al. 2015). An additional metric called the chorus ratio (CR) was used for the first time in order to evaluate the ratio between the ACI value before and after sunrise.

The purpose of this investigation was

- To test a sampling design of multi sensors to collect information on the activity of acoustic communities of birds from selected locations, process acoustic information using the ACI, and test the new CR metric.
- To compare the acoustic patterns that emerge during the dawn choruses and in the successive morning singing routines.
- To describe acoustic patterns that emerge during the morning acoustic activity of different communities during the breeding season within diversified locations across the Mediterranean landscape.
- To better understand the acoustic contributions from different species during the dawn chorus and during the successive morning singing routines by integrating

automated ecoacoustic methodologies with aural procedures of species identification and counting.

Study area

Geographical locations

This investigation was performed at five different locations in the Northern Apennines (Italy): Croce di Tergagliana (44°14′56.19″N, 10°05′33.31″E, 625 m a.s.l.), Virolo (44°13′59.98″N, 10°06′01.29″E, 349 m a.s.l.), Monte Curto (44°14′01.02″N, 10°04′03.69″E, 222 m a.s.l.), Madonna dei Colli (44°12′37.85″N, 10°03′27.12″E, 217 m a.s.l.), and Valenza (44°13′01.91″N, 10°00′36.04″E, 129 m a.s.l.). These locations were selected for the investigation because they are representative of different land-use mosaic configurations and vegetation structures (Figure 1).

Weather conditions

The temperature for the five locations was calculated by averaging the data collected at three meteorological stations (Associazione Meteo Apuane – MeteoApuane.it © 2007–2013) closest to the sampling areas: Aulla (44°12′45″N 09°58′01″E, 72 m s.l.m.), Moncigoli (44°13′31″N 10°05′42″E, 231 m s.l.m.), and Fivizzano (44°13′47″N 10°07′12″E, 328 m s.l.m.) (Figure 1). The temperature consistently fluctuated in May with the lowest values recorded midway through the month and the greatest temperature at the end (Table 1 suppl.). In this month, precipitation was recorded for 22 days. Another consistent fluctuation of temperature was observed during the second half of June. The wind speed was an average of 3.2 km/h for the entire period. It should be noted, however, that the morphological complexity of the area recommends a cautious assessment of weather data.
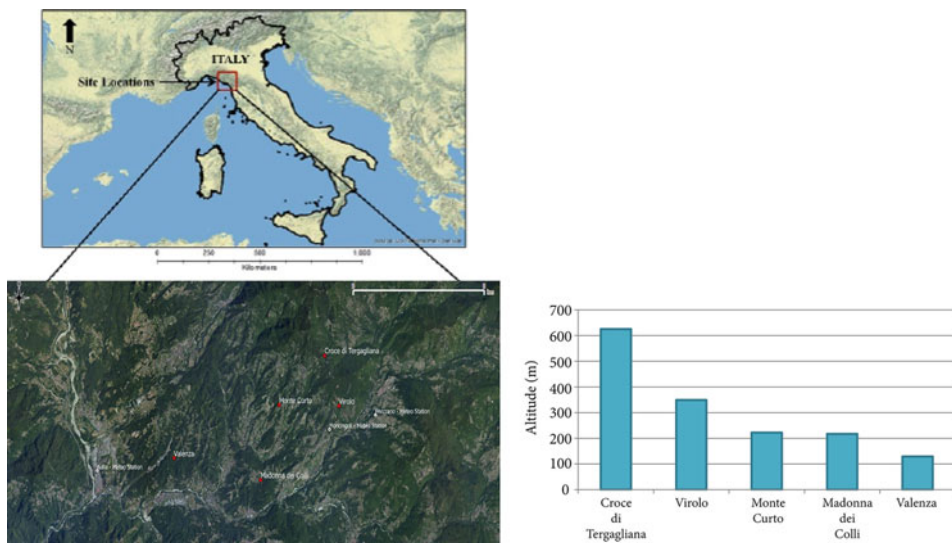

Figure 1.   Study area with the distribution of the five investigated locations and the meteorological stations. Histogram of locations' altitude in meters above sea level.

Vegetation

Patterns of land cover, ground vegetation richness, canopy density, and dispersion were used to characterize the structure of the vegetation around each audio digital recorder by using satellite images and ground transects. Details on the methods utilized are reported in Appendix 1 of the Supplementary Materials. Data are summarized in Table 2 suppl. Fifty-seven species of plants were found along line transects established on the ground across each recording site. The most diverse vegetation cover was found in Croce di Tergagliana (Table 1), where the high diversity was due to the effects of moderate livestock grazing. An increase in vegetation diversity is a well-known effect when the grazing pressure is modest (Fuhlendorf and Engle 2001).

Vegetation cover across all sites was classified using satellite images and was generally dominated by broadleaf woodlands mixed with cultivation under a regime of diffuse land abandonment. Ten types of land cover were observed in Valenza, Virolo, Croce di Tergagliana, and Madonna dei Colli, all with dominant woodlands. The woodland cover was approximately 50% of the land in Monte Curto. The landscape shape index, which measures the complexity of the mosaic (MacGarigal et al. 2012), increased with proximity to lowlands and the area of cultivated land. Areas defined as abandoned land were more prevalent in Croce di Tergagliana than any of the other sites. The greatest canopy density was quantified at Valenza and Virolo, which reflected the distribution of tree cover. In Valenza, the woodland was dominated by cohorts of mature trees, whereas in Virolo young trees prevailed, although both areas had a closed canopy. On the other hand, Madonna dei Colli and Monte Curto had a greater amount of open spaces, while Croce di Tergagliana had an intermediate level of tree cover (Table 2 suppl.).

Materials and methods

Methods for recording and processing acoustic data

Recording

Four digital recorders were deployed at a distance of 100 m from each other in each location in order to create a robust sampling design. Bird vocalizations were recorded using Zoom H4 recorders (Zoom H4™, Zoom Inc., Chiyoda-Ku, Tokyo, Japan, System 2.40). The Zoom H4 is a commercial digital recorder with two built-in unidirectional condenser microphones with good acoustic reliability, and has been successfully used in other ecoacoustic studies (Farina et al. 2013, 2014). Sounds were recorded at a sampling frequency of 44.1 kHz and at a resolution of 16 bits in stereo mode. The microphones were set in outdoor recording mode with a gain of -12 dB. The recorders were fixed at a height of 1.50 m on the trunk of the nearest tree.

The Zoom H4s were activated at the solar time of 3.30 a.m. (CET) using an external timer (ZYT16G-2a/3a microcomputer timer switch, Toone®, Shanghai Zhuoyi Electronic Co., Ltd., Shanghai, China) and powered by a 12-V, 2-A·h rechargeable battery (MKC, Melchioni, Milano, Italy). Each Zoom H4 recorded for 3 h 23 m in each of the seven sessions conducted between May and July 2013: 9, 17, 31 May; 9, 12, 18 June; 2 July. Recording sessions were made only in good weather; adverse weather conditions, especially in May, prevented the selection of recording sessions with more favourable daily scheduling. The data were synchronized with the solar time using ephemeris tables (http://www.eurometeo.com/italian/ephem).

The Dawn Chorus was empirically comprised between the first song and the sunrise moment, which varied according to the day of the season. The morning acoustic activity

Table 1. Vegetation richness and canopy parameters at the five localities.

| | Vegetation richness | | | | | | | | | Canopy parameters | | | |
| | H' | | Exp H' | | Evenness | | Total | | Number of species | | Canopy density | | Morisita index | |
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Croce Tergagliana	2.73	0.21	15.64	3.31	0.86	0	234.3	42.5	24.75	6.4	63.1	13.4	1.0	0.0
Virolo	2.55	0.24	13.09	3.38	0.84	0	251.3	40.8	21	4.24	69.7	6.1	1.1	0.4
Monte Curto	2.61	0.22	13.8	2.81	0.86	0	226.3	45.0	21.25	3.5	47.3	16.0	1.9	0.4
Madonna dei Colli	2.26	0.23	9.79	2.26	0.75	0.1	245.0	104.0	21	5	50.0	9.8	1.2	0.3
Valenza	2.33	0.41	10.88	4.28	0.75	0.1	264.3	80.2	22	4.69	75.0	8.0	1.0	0.1

was divided into three periods of equal length: Dawn Chorus (DC), Post Chorus 1 (PC1), and Post Chorus 2 (PC2) (Figure 2). This unbiased distinction was used to effectively study chorus phenomena based on the time of day, which was changing with the season, and with the aim of evaluating the expected reduction in the singing activity of birds after sunrise.

Automatic sound analysis

The morning acoustic activity was analysed using the ACI, which was based on the measurement of the differences in amplitude between successive temporal steps along each frequency bin (Pieretti et al. 2011).

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

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

The ACI values were obtained by processing the acoustic recordings (wav files) using SoundscapeMeter (Farina et al. 2012), which is a plug-in application to the WaveSurfer software (Sjölander and Beskow 2000; Sjölander 2002). In order to eliminate instrumental noise and guided by empirical evidence, a power spectral density of the minor digital signal (less than 3000 mV^2/Hz) was adopted in order to filter most of the background noise across the entire spectrogram. To calculate the ACI, we set the following parameters: FFT 512 points, Hamming window, no overlap, and clumping of 1 s. The lowest 100 Hz were excluded from the successive computation, producing 250 instead of 256 frequency bins.

The frequency evenness ($J'f$) of the distribution of the ACI values along the frequency bins were calculated according to the following equation:

$$J'f = \frac{H'}{H'_{max}} \quad \text{(Hill 1973)} \tag{2}$$

This index has been extensively used by ecologists to measure the distribution of individuals in a collection of species (Pielou 1966; Peet 1975). We replaced the number of species with the number of frequency bins where there could be a maximum of 250.
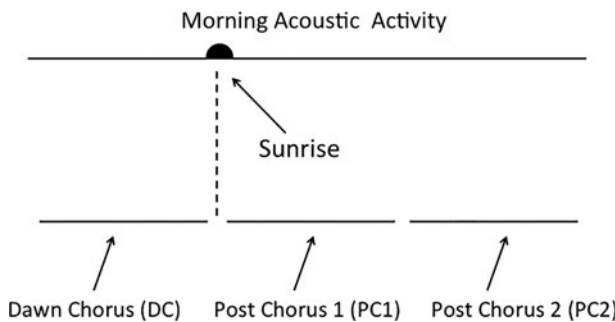

Figure 2.   Model of the temporal repartition of the morning acoustic activity. The Dawn Chorus (DC), Post Chorus 1 (PC1), and Post Chorus 2 (PC2) are the intervals at which the morning acoustic activity was investigated.

Therefore, H' is the Shannon function (Shannon and Weaver 1949) calculated as

$$H' = -\sum_{1}^{250} p_i \ln p_i \qquad (3)$$

where p_i is the abundance of each frequency bins. Additionally, H'_{max} used in Equation (2) is defined as the maximum diversity when all of the frequency bins ($S = 250$) are present in the same abundance. H'_{max} was calculated using Equation (4):

$$H'_{max} = \ln S \qquad (4)$$

The frequency evenness ($J'f$) distribution was considered as a good indicator of the degree of occupancy of frequency bins and, consequently, of the complexity of the vocalizations.

To determine the effect of sunrise on acoustic performance, which was represented by an abrupt reduction of the Dawn Chorus, we selected a temporal window of 17.5 min before and after sunrise. This temporal window was subdivided into 5 min steps (three for each "side" of sunrise and one centred on sunrise moments: -15, -10, -5, 0, $+5$, $+10$, $+15$) in order to observe where and how many times the minimum acoustic activity occurred.

Chorus ratio

To evaluate the variation of the singing activity before and after sunrise, we calculated a chorus ratio (CR) between the averaged ACI at Dawn Chorus and the averaged ACI at Post Chorus 1 and Post Chorus 2 intervals for each recorder during each day of sampling according the equation

$$CR = \frac{2^* DC}{PC1 + PC2}. \qquad (5)$$

CR values approaching unity indicate similar distributions of singing activities along DC, PC1, and PC2; greater than unity when Dawn Chorus prevails; and less than unity when Post Chorus 1 and Post Chorus 2 are more important.

Aural sound analysis

With the aim of empirically verifying whether the singing community during Dawn Chorus and Post Chorus 1 and 2 was composed of the same species, we selected two 10-min periods before and after sunrise where the highest ACI value occurred. Successively, each of these two temporal periods were sub-sampled in 10 one-minute files, and the 2nd, 4th, and 8th min were aurally checked in order to identify the vocalizing bird species by annotating the number of singing events per species every 6 s.

Statistical analysis

The ACI, $J'f$, and CR values were averaged for each recorder across all days and averages were also computed for each locality based on the three periods of morning. In order to test our sampling design, a linear mixed model (LMM; Bates et al. 2014) was performed to evaluate the conditional mean of the chorus phenomenon by understanding the differences in the ACI across the recorders during the entire morning period. The recorders were used

in the LMM as fixed effects while location and date were used as the random-effect term. An analysis of variance (ANOVA) and post-hoc Tukey test (Tukey 1949) was performed for different levels of random effects.

An additional LMM was applied in order to test the differences between the mean of the ACI and the mean of frequency evenness of the ACI ($J'f$) among Dawn Chorus, Post Chorus 1, and Post Chorus 2. Location and date were also included as random factors.

A linear model was also applied on ACI and CR values to determine if vegetation characteristics (H', evenness, canopy density, and Morisita index), date, and temperature affect the vocalizations of the community. The best-fit model was selected by means of model averaging based on the information criterion and performed on a subset of the full model, excluding collinear variables from a Pearson correlation matrix with coefficients larger than $r = 0.5$. Validation graphs (e.g. residuals versus fitted values, Q–Q plots, and residuals versus the original explanatory variables) were then analysed in order to control possible model misspecification and the presence of outliers. The morning periods were included in the final model to assess if time could contribute significantly in explaining the variability of the ACI. Finally, the same procedure was applied in order to test possible effects of vegetation features in the locations on the CR.

A general linear mixed model (GLMM: Breslow and Clayton 1993) was used to determine if the composition of the singing community was different between DC, PC1, and PC2. The GLMM of the Dawn Chorus, Post Chorus 1, and Post Chorus 2 was applied to the number of singing species and morning periods using a Poisson distribution and log–link function. The random intercept in the model was adjusted for different locations and different data. The same model was performed on the total number of singing events by each species in order to test the differences between Dawn Chorus and Post Chorus 1 & 2 activity, including the location and data terms as random effect.

Results

Acoustic information

Intra-location acoustic information

The validity of the sampling design was confirmed based on the different ACI values that emerged from the use of four recorders in the same location, which ultimately did not influence the comparisons among locations. In fact, the LMM showed that the ACI results were not significantly different among recorders or same location and dates ($F_{(19,357)} = 0.086$, p-value > 0.05 and $F_{(19,357)} = 0.40$, p-value > 0.05). Instead the random effect of location significantly affected acoustic information (location: $\chi^2_{(1)} = 18.5$, p-value < 0.05) while the random effect of dates did not (dates: $\chi^2_{(1)} = 0.949$, p-value > 0.05).

Inter-location acoustic information

The five locations were significantly different in ACI values along the morning acoustic activity (ANOVA: $F_{(4376)} = 7.90$; p-value < 0.05) (Figure 3). The results of the Tukey HSD post-hoc test are reported in Table 2. The average ACI for all recorders and temporal sessions at each location illustrated a distinct peak during Dawn Chorus (Figure 4(a)). After sunrise, however, ACI steadily decreased in all locations except Valenza, where peaks in chorus activity persisted (Table 3). The Dawn Chorus was separated from the Post Chorus 1 by a visible lull in song emission, which more frequently occurred around sunrise; specifically, 5 min before sunrise and ± 2.5 min around sunrise (Figure 4(b)). The
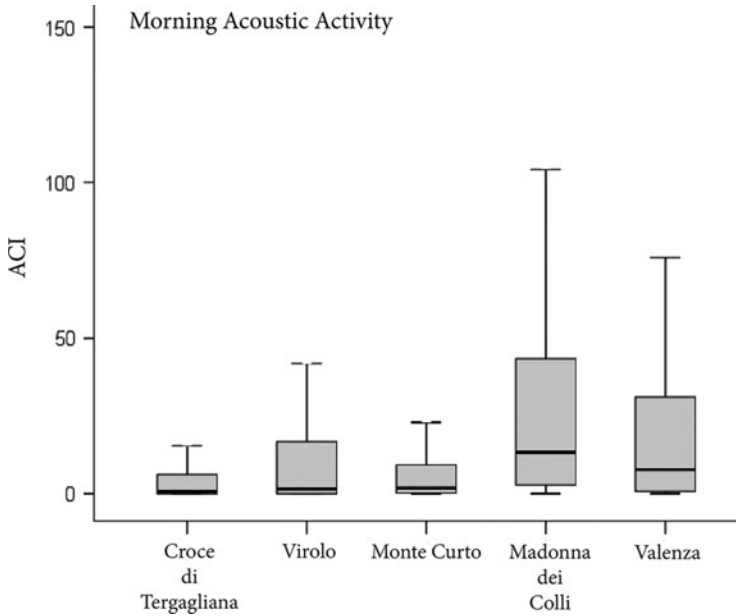
Figure 3. Morning acoustic activity (median ± 25th–75th percentiles; whiskers minimum and maximum values) at the different locations that resulted in significantly different ACI values.

average Dawn Chorus length was 53.4 min for all of the localities and temporal sessions (Table 3). The LMM of ACI and $J'f$ during DC, PC1, and PC2, with the aforementioned fixed and random variables, showed significant differences in ACI $J'f$ values among the three periods ($F_{(2371)} = 9.15$, $p < 0.05$; $F_{(2374)} = 9.41$, $p < 0.01$). The estimated reduction of ACI and $J'f$ during Post Chorus 1 and Post Chorus 2 compared to Dawn Chorus is reported in Table 4.

Seasonal and environmental effects on morning acoustic activity
Seasonally, the ACI of the acoustic morning activity peaked on 17 May and then had an abrupt fall on 31 May. A second minor peak was observed on 2 July (Figure 5). The

Table 2.   Tukey HSD post-hoc test of ACI among different locations.

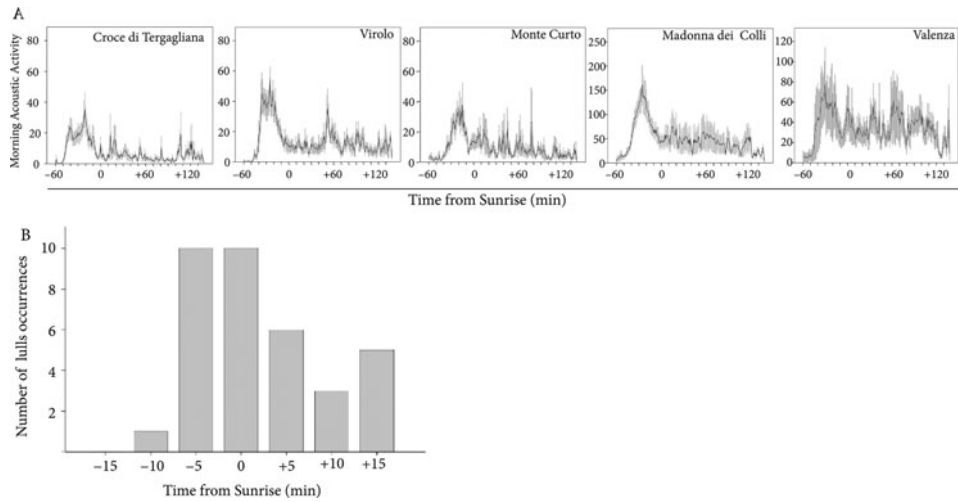|	Croce di Tergagliana	Virolo	Monte Curto	Madonna dei Colli	Valenza
Croce di Tergagliana					
Virolo	7.67 (p-value = 0.91)				
Monte Curto	2.23 (p-value = 0.99)	5.44 (p-value = 0.97)			
Madonna dei Colli	39.93 (p-value < 0.01)	− 32.26 (p-value < 0.01)	− 37.69 (p-value < 0.01)		
Valenza	27.048 (p-value < 0.01)	− 20.37 (p-value = 0.19)	25.81 (p-value < 0.01)	− 11.88 (p-value = 0.69)	

Figure 4.   (a) The ACI value along the localities when all the temporal sessions are plotted together, which makes it possible to distinguish a lull around sunrise (0). (b) Mean value of occurrences of a lull in intervals of 5 min (17.5 min before and 17.5 min after sunrise) considering all localities and sessions. The zero point represents sunrise.

acoustic signature (all localities plotted together), namely the result of the abundance of the different frequency bins, exhibited a more complex shape represented by the presence of distinct peaks on 17 May and 18 June. A simplified shape of the morning acoustic activity was apparent on 2 July close to the end of the breeding season (Figure 6). The evenness of vegetation and temperature of the recording session improved the LMM for ACI (Table 5), where the ACI was significantly higher at lower temperatures and vegetation evenness (Figure 7(a),(c)).

Seasonal and environmental effects on Chorus ratio

The LMM applied to CR included significant explicative variables H', canopy parameters, and temperature (Table 5). Greater CR values were correlated with increasing temperatures and vegetation richness (Figure 7(b),(d)).

Table 3.   Mean duration of the dawn chorus from the aural count in each locality and the mean amount of the ACI for each temporal period (DC, PC1, PC2).

	DC duration (min)	ACI_{DC}	ACI_{PC1}	ACI_{PC2}
Croce di Tergagliana	51.7 (6.34)	15.9 (4.71)	6.8 (6.28)	3.7 (1.93)
Virolo	50.3 (5.59)	27 (20.57)	12.5 (8.38)	14.2 (11.25)
Monte Curto	52.9 (11.29)	14.5 (5.19)	8.9 (4.12)	7.9 (3.65)
Madonna dei Colli	62.3 (16.38)	65.9 (44.46)	56.6 (74)	33.4 (37.51)
Valenza	49.9 (5.49)	35.5 (36.28)	29.5 (33.25)	30.4 (37.99)
Tot mean duration (min)	53.4 (10.45)			

Note: The standard deviation is in brackets.

Table 4. Results of linear mixed model on ACI and ACI frequency evenness ($J'f$) among Dawn Chorus (DC), Post Chorus 1 (PC1), and Post Chorus 2 (PC2) periods, including the location term as random effect.

		Estimate StD.	Error	df	T value	Pr $(> |t|)$
ACI	(Intercept)	32.747	8.612	4	3.80	<0.05
	Period PC1	−8.84	1.25	199,974	−7.08	<0.01
	Period PC2	−14.39	1.27	199,974	−11.31	<0.01
$J'f$	(Intercept)	0.365	0.04	4	8.91	<0.01
	Period PC1	−0.069	0.0038	20,290	−18.28	<0.01
	Period PC2	−0.053	0.0037	20,290	−14.21	<0.01

Species richness and dominance

Thirty-three species were identified inside the temporal interval posed between the two max-peaks of the ACI before and after sunrise (Table 2 suppl). The acoustically dominant species (>5%) included the Blackcap (*Sylvia atricapilla*), Blackbird (*Turdus merula*), European Robin (*Erithacus rubecula*), and Great Tit (*Parus major*). The Chaffinch (*Fringilla coelebs*), Nightingale (*Luscinia megarhynchos*), Song Thrush (*Turdus philomelos*), and the Subalpine Warbler (*Sylvia cantillans*) were considered to be sub-dominant (>1% and <5%) (Table 6).

There were significant differences in the number of songs before and after sunrise ($t_{(240)} = 8.82$, $p < 0.01$) at every locality, even when the number of singing species did not show significant changes ($Z = 1.36$, $p = 0.17$). The analysis applied on species resulted in differences in acoustic behaviours related to sunrise in *T. merula*
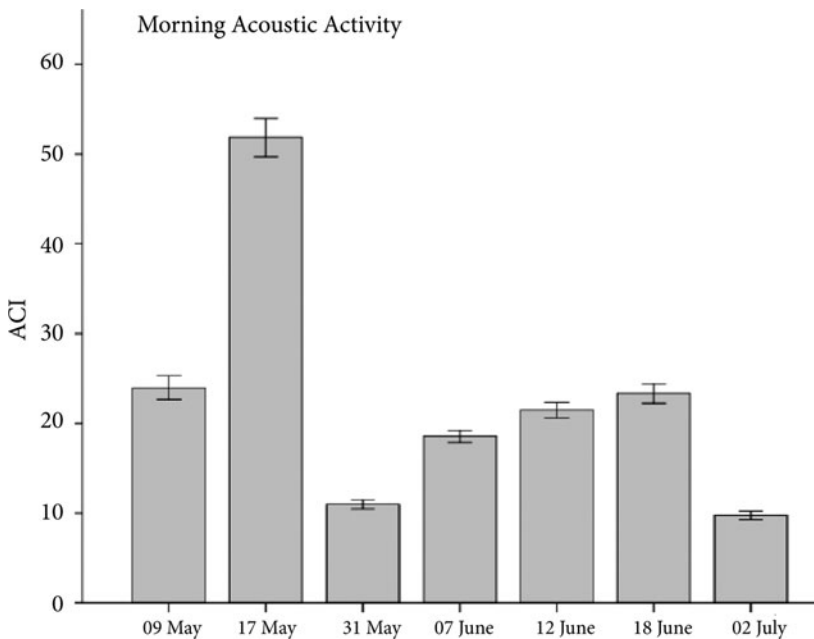

Figure 5. Morning acoustic activity along the season (ACI ± SE) when the data of all the localities are plotted together.
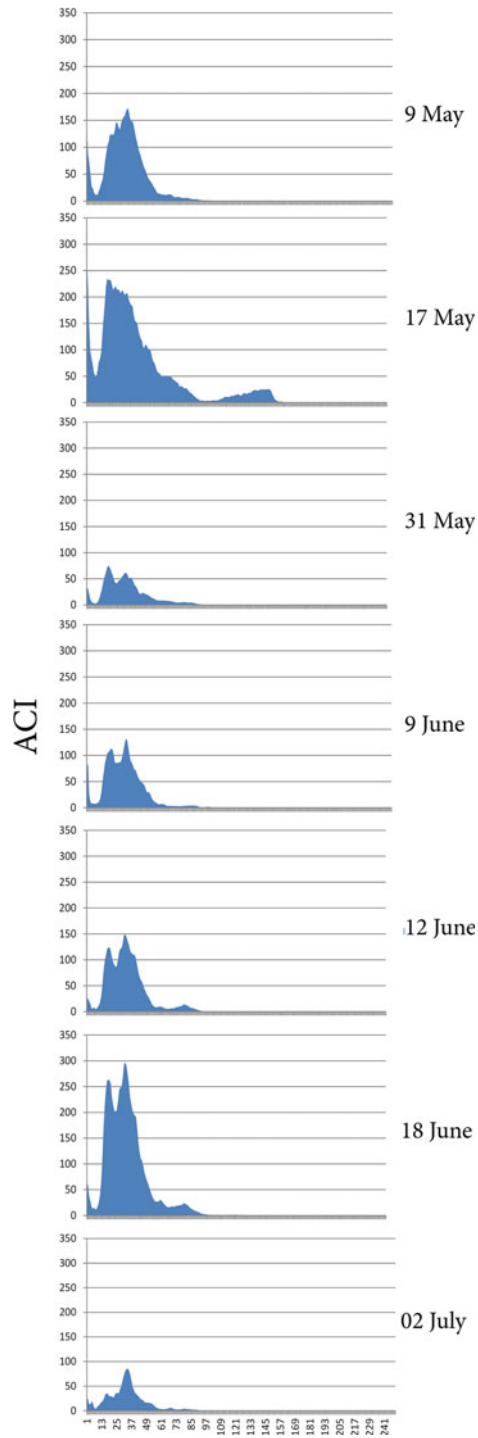
Figure 6.   Acoustic signature of the morning acoustic activity when all the localities are plotted together along the season. The higher level and the more complex pattern of the acoustic signature occurred on 17 May and 18 June.

Table 5. Results of Linear Model on ACI and chorus ratio and environmental variables.

ACI	Estimate StD	Error	*T* value	Pr $(>|t|)$
(Intercept)	363.84	48.5	7.50	<0.01
Evenness of vegetation	−356.11	57.07	−6.24	<0.01
Temperature	−2.56	0.71	−3.61	<0.01
				$R^2 = 0.338$

Chorus ratio	Estimate StD.	Error	*T* value	Pr $(>|t|)$
(Intercept)	−23.92	8.63	−2.77	<0.01
H'	8.3	3.24	2.56	<0.05
Temperature	0.3	0.15	2.03	0.05
				$R^2 = 0.25$

Notes: ACI, Residual standard error: 25.98 on 102 df; Chorus ratio, Residual standard error: 3.105 on 32 df.

(Estimate $= -5.006$, $t_{(240)} = -9.26$, $p < 0.01$), *E. rubecula* (Estimate $= -0.9$, $t_{(240)} = -2.92$, $p < 0.01$), and *P. major* (Estimate $= -0.83$, $t_{(240)} = -3.53$, $p < 0.01$) controlled by location.

Discussion

This research demonstrated the efficacy of using ecoacoustic metrics (ACI and CR) with a multi-sensor sampling design to investigate patterns and dynamics of dawn choruses and successive morning singing routines. Our results confirm that different acoustic communities exist within the selected locations and reflect specific habitat typologies. This is primarily based on the fact that there was no direct effect of recorder factor on ACI variability. The absence of significant differences between the recorders, positioned every 100 m in every location, confirms the intralocality replication of the sampling design. This result, however, was not in accordance with a prior study carried out in an evergreen Mediterranean maqui by Farina and Pieretti (2014). In that environment, a change in acoustic communities was already observed at a distance of 25–30 m; albeit this was explained by an increase in vegetation density that enhanced the heterogeneity of habitat, which ultimately favoured a more diversified acoustic community at a finer spatial scale.

The temporal model comprised three periods of identical length (Dawn Chorus, Post Chorus 1, and Post Chorus 2), with which the early morning song activity had been analysed, that accurately described the dynamics of acoustic communities within the region. According to this model, the behaviour of birds after the Dawn Chorus was expected to be quite different based on the assumption that the energy spent to continuously sing during Dawn Chorus time would be reintegrated in the same time lag by a more intense search for food; consequentially reducing acoustic activity during the Post Chorus 1. The acoustic activity of Post Chorus 2 was then expected to be generally lower than Post Chorus 1 because of a reduction in social activity (territory defence, etc.) as described in previous literature (e.g. Keast 1994; Hutchinson 2002). This reduction was followed by a resurgence in singing activity when the resources were replenished. Thereafter, foraging and singing were alternated and our results support this hypothesis.
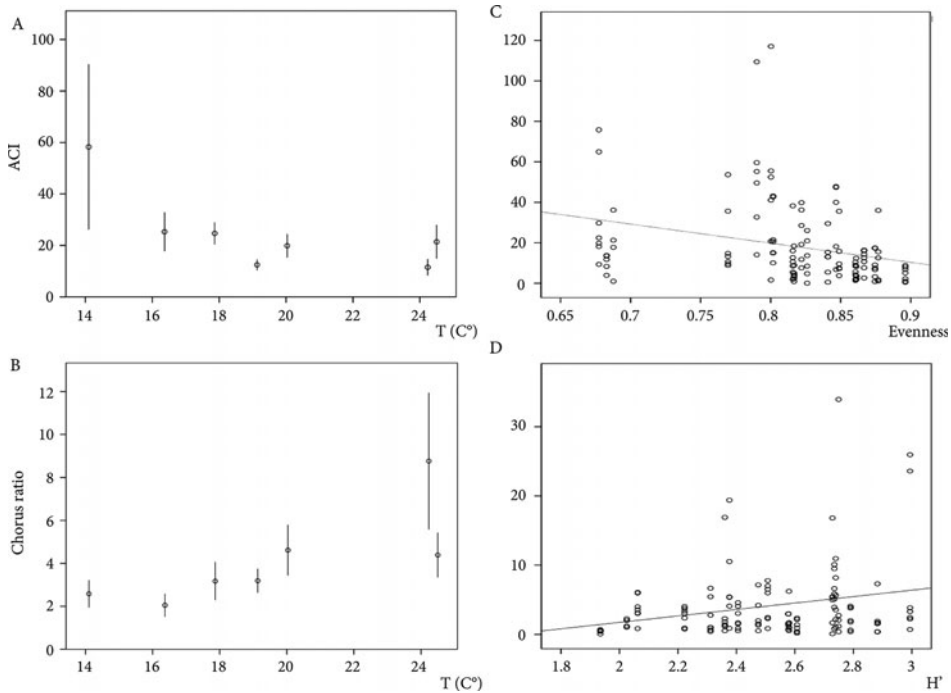
Figure 7.   (a,b) Distribution of the average of ACI values and chorus ratio related to temperature. (c,d) Scatterplot of ACI and CR, respectively, with evenness and H' of vegetation for all the localities.

Furthermore, a sudden fall of the singing activity was observed around sunrise, which was a common pattern in all the locations. This interruption in singing activity has been well described by Keast (1994) in eucalyptus forests of Australia, later discussed by Burt and Vehrencamp (2005), and was confirmed by our aural analysis. The greater frequency evenness ($J'f$) observed during the Dawn Chorus period signified a major saturation in the acoustic space (or acoustic niche *sensu* Krause 1993), which indicated that more signals were emitted at different frequencies during the Dawn Chorus. This could be due to more species singing at dawn and/or a more varied repertoire from species, such as the Blackbird, European Robin, and Great Tit, which have been known to sing significantly more before sunrise.

The acoustic signature depicted by the ACI indicated a range in variability related to seasonal weather trends. During the first half of May, the acoustic signature exhibited complex patterns, which could have been a function of the presence of early breeders (e.g. Blackcap, Blackbird, Great Tit). Whereas in June, more complex patterns in acoustic signatures may have been due to the addition of late migrant species, such as the Golden Oriole (*Oriolus oriolus*), Turtle Dove (*Streptopelia turtur*), and Subalpine Warbler (*S. cantillans*), to the acoustic community. The seasonal variation observed in ACI values seemed to be driven by temperature. The morning acoustic activity was mostly expressed before sunrise (higher values of chorus ratio) when temperatures were higher. In May, where temperatures were lower than expected, there was high acoustic activity along all morning periods. Moreover, an alternation of low and high temperatures and several rainy and windy days (especially in the second half of May) and a decrease of temperature during the second half of June, could have negatively

Table 6. Number of songs before and after sunrise in the different localities of the dominant (>5%) and sub-dominant species (1–5%).

	Croce di Tergagliana		Virolo		Monte Curto		Madonna dei Colli		Valenza	
	Before sunrise	After sunrise	Before sunrise	After sunrise	Before sunrise	After sunrise	Before sunrise	After sunrise	Before sunrise	After sunrise
S. atricapilla	4.79 (4.71)	3.09 (2.63)	6.07 (4.25)	4.08 (3.26)	2.00 (3.23)	2.19 (2.94)	5.83 (4.44)	6.46 (2.98)	5.33 (4.53)	5.62 (4.89)
T. merula	6.12 (3.87)	1.66 (2.13)	8.05 (7.60)	2.11 (3.07)	4.81 (3.94)	0.72 (2.28)	9.63 (6.20)	2.33 (3.18)	3.24 (3.52)	0.65 (1.36)
P. major	0.81 (2.12)	0.49 (1.65)	–	–	4.86 (4.10)	1.19 (2.09)	–	–	–	–
S. cantillans	1.59 (1.62)	0.15 (0.78)	–	–	0.94 (2.47)	0.68 (1.88)	–	–	–	–
S. turtur	0.0 (0.0.)	0.36 (1.05)	–	–	–	–	0.15 (0.36)	0.96 (1.41)	–	–
F. coelebs	0.03 (0.13)	0.26 (1.02)	0.45 (1.47)	0.97 (2.41)	0.26 (1.29)	0.40 (1.53)	1.10 (2.15)	1.42 (2.56)	–	–
E. rubecula	–	–	1.65 (2.45)	0.63 (2.23)	0.31 (0.85)	0.21 (0.66)	2.07 (2.70)	0.86 (2.08)	4.52 (4.41)	2.38 (4.21)
O. oriolus	–	–	0.32 (1.33)	0.45 (1.70)	–	–	–	–	–	–
L. megarhynchos	–	–	–	–	1.36 (2.39)	0.78 (1.57)	1.23 (2.64)	1.41 (3.27)	–	–
Turdus sp.	–	–	–	–	–	–	0.43 (0.80)	1.69 (2.63)	1.19 (2.69)	0.81 (2.07)

Note: In brackets is the standard deviation.

influenced the breeding dynamics as argued for other bird communities by Robbins (1981) and Bruni et al. (2014).

The morning acoustic activity phenomenon was unexpectedly more intense where vegetation was less complex (e.g. low vegetation evenness within Madonna dei Colli), as explained by the analysis of the vegetation at medium (a radius of 500 m for each locality) and small scales (ground vegetation, canopy density, and dispersion). This intensity of morning acoustic activities could be explained by the fact that the species that sing more contribute greatly to the acoustic community. This includes species such as Blackbird, Blackcap and European Robin, which prefer habitats with dense vegetation cover and are characterized by few dominant species that produce a low evenness in plant communities, especially within wet Mediterranean areas. This may also be in accordance with the presence of resources (food, shelter, and nesting places) that are more readily available within dense vegetation cover (Tucker et al. 2014). Furthermore, local variations in singing activities are also related to the number of species or interacting individuals (Timeester et al. 2010), environmental conditions (Lindenmayer et al. 2004), and food resources (Davies and Lundberg 1984).

The dynamics of morning acoustic activities, as expressed by CR, may be directly dependent on the distribution and abundance of resources, which decreases from Valenza – where vegetation evenness is low – to Croce di Tergagliana – where vegetation evenness is higher. These two locations, posed at 72–625 m, respectively, have environmental conditions sufficiently distinct in terms of either fruit or animal prey (Farina 1995, 1997).

The landscape parameters derived from satellite images were not able to explain any significant relationships with the acoustic communities. The aural analysis also did not reveal any significant differences in the composition of the acoustic community between localities during peaks in acoustic activity. Only differences in acoustic activity were noted. The consistent presence of core species (the Blackcap, Blackbird, Great Tit, European Robin, and Song Thrush were common to all the localities) at the regional scale suggests that habitat differences do not have a major effect on species richness; rather, only species abundance and behaviour are affected. In fact, woodland cover was a consistent land-cover type in all localities and was an important habitat resource for species. Woodlands are especially important in regions that are plagued with intense land abandonment (e.g. Northern Apennines) (Farina 1991; Vos and Stortelder 1992). Land abandonment has a strong effect on bird communities because of the "homogenization" of the land-use mosaic, thus producing less differentiated communities when compared to the recent past (Farina 1989). Moreover, the region is too small to account for climatic differences (9 km between the two most distant localities: Valenza and Croce di Tergagliana) to justify a high Beta diversity (*sensu* Whittaker 1960).

A relationship between the morning acoustic activity and vegetation parameters exists; however, further analysis is required. For instance, collecting information on the productivity of each locality, which was not made in this study, would provide further information to support the link between resource availability, morning acoustic activities, and ACI dynamics. Further, we observed that some species were singing more intensely at dawn (e.g. Blackbird, European Robin, Great Tit) than after sunrise. Other species, such as the Blackcap, sing without significant differences before and after sunrise along all localities. This difference was a relevant outcome to this research but still remains largely unexplained in the literature and confirms how the chorus phenomenon has many unsolved aspects that deserve further investigation.

Conclusions

The morning singing routine of birds was investigated using ecoacoustic approaches that included multi-sensor acoustic sampling, temporal characterization of morning acoustic activities (Dawn Chorus, Post Chorus 1, and Post Chorus 2), and the use of acoustic metrics (ACI and CR). Specifically, CR (derived from ACI measurements) was established as an important metric to discriminate the behaviour of different acoustic communities in the Mediterranean. Vegetation structure was an important factor in describing chorusing activities, although social interactions and weather conditions also played a major role. Vegetation parameters (canopy cover, land cover, and plant diversity) did not fully capture the complexity of morning acoustic activity and, in particular, the Dawn Chorus phenomenon. A more detailed measure of local productivity could help differentiate complex relationships between acoustic activity, species abundance, and distribution.

A distinct pattern in the morning acoustic activity emerged based on variations in ACI calculations as a function of temporal seasonality. The decreasing trend of ACI along the season was expected during the second half of the breeding season and was inversely related with the temperature. The aural identification of the acoustic communities was an important ancillary method to better interpret results obtained by the automatic acoustic processing. In conclusion, we hope that this investigation represents an example of how to apply automatic sound monitoring methods to ecoacoustic investigations and provide evidence that supports the advancement of our understanding of the dawn chorus phenomenon that has perplexed scientists for decades.

Disclosure statement

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