Temporal structure of avian dawn chorus along a landscape anthropization gradient

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Abstract

Context

If an animal community can be similar from a city to its outskirts, its rhythm of activity can be modified by anthropogenic pressures. Passive acoustic monitoring techniques offer the opportunity to assess such changes in birdsong along anthropization gradients.

Objectives

Disentangling the relative influence of anthropogenic pressures, landscape composition and the composition of the bird community on the temporal structure of dawn chorus.

Methods

Birdsongs were recorded in France in 36 stations located along an anthropization gradient through passive acoustic devices. The temporal structure of birdsongs was confronted to anthropogenic pressures (artificial lights and traffic noise), landscape composition indices (landscape diversity, areas covered by woodland and buildings) and characteristics of the bird community (abundance, species richness and diversity) around each station.

Results

For a given species, birds tend to sing earlier and during shorter periods in areas densely built, submitted to high levels of artificial lights, traffic noise, and in areas hosting the lowest conspecific abundances. Highly built and lit areas lead to a community reassembly promoting late singing species and species singing for short periods. Artificial lights and traffic noise promote a higher species temporal turnover and a lower temporal nestedness of the dawn chorus at the community level.

Conclusions

In cities, birds tend to sing earlier, during shorter periods, and the different species sing in a succession rather than in a polyphony. The full bird chorus, gathering almost all the species of a community singing together in the same time seems to have disappeared from the most anthropized areas.

Introduction

The influence of human activities on birdsong has been widely studied and benefit from detailed reviews (Marín-Gómez and MacGregor-Fors, 2021; Patricelli and Blickley 2006; Slabbekoorn 2013; Slabbekoorn and Ripmeester 2008). However, there are still research avenues to be explored to better understand the influence of humans on the timing of bird vocal activity.

Regarding the anthropogenic pressures, many studies have sought to understand how birdsongs may differ between highly contrasted environments, mainly by comparing discrete habitats, such as cities

versus countryside (Cyr et al. 2020; Fuller et al. 2007; Lowry et al. 2019; Redondo et al. 2013; Sánchez-Gonzáles et al. 2020); cities *versus* forests (e.g., Ripmeester et al. 2010); or intra-urban *versus* peri-urban forests (Marín-Gómez and MacGregor-Fors 2019). These studies revealed important differences in birdsong between habitats such as difference of amplitude, frequency, song structure, nocturnal singing rate, or singing onset in different species. However, they did not identify the respective roles of different human pressures, while differences in a birdsong between two different habitats may be due to several different anthropogenic factors. The few attempts to investigate birdsong response along anthropization gradients (rather than comparing discrete habitats) mostly focused on a single or two factors (e.g., Nordt and Klenke 2013). In addition to experimental *ex situ* studies that led to major advances (e.g., Brumm and Todt (2002) showed in a pioneer way that common nightingales (*Luscinia megarhynchos*) sang louder in the presence of anthropogenic noise), most of the *in situ* studies focusing on a single human pressure deal with the impacts of noise (73 references listed in the Web of Knowledge on 09/01/2023 with the following search terms: “bird”, “chorus”, “noise”), followed by ALAN (23 references listed in the Web of Knowledge at the same date with the following search terms: “bird”, “chorus”, “ALAN” or “Artificial light*”) on birdsong. Few studies investigated two factors such as noise and ALAN simultaneously (but see for example Da Silva et al. 2014; Fuller et al. 2007; Hennigar et al. 2019; Marín-Gómez and MacGregor-Fors 2019; Stuart et al. 2019), and the relative importance of each factor is subject to debate (e.g., noise better explains song timing in the European Robin (*Erithacus rubecula*) than ALAN according to Fuller et al. 2007, but Da Silva et al. 2014 found the opposite for five of the six species they studied). Therefore, to our knowledge, hierarchizing the respective influence of a set of different anthropogenic pressures on birdsong under natural conditions with *in situ* empirical studies remains challenging.

Looking at the model species, the majority of the studies focused on a single species or a small number of species, although an increasing number of studies worked on more than 10 species (Alquezar et al. 2020; Gil et al. 2015; Hu and Cardoso 2010a; Luther 2009; Marín-Gómez and MacGregor-Fors 2019; Polak et al. 2013; Rios-Chelen et al. 2012; Vincelette et al. 2020) and exceptionally more than 100 species in macroecology studies (e.g., Cardoso et al. 2018; Cardoso et al. 2020; Francis 2015; Hu and Cardoso 2010b). Therefore, investigating the impacts of human pressures on different species remain little explored.

From the perspective of the song variables studied, researchers proposed two families of approaches. A batch of studies developed (e.g., Sueur et al. 2008) or used (e.g., Farina et al. 2015) acoustic indices at the level of the bird community such as acoustic richness, diversity or complexity, promoting the concept of “soundscape” (Grinfeder et al. 2022). As it was not their primary purpose, such studies did not individualize the song response of the different species to human pressures. Another and much larger batch of studies focused on particular song variables at the species level, among which song frequency is by far the most studied. The pioneer study of Slabbekoorn and Peet (2003), demonstrating a change in song frequency in the Great Tit (*Parus major*) related to anthropogenic noise, opened avenues on many studies on the same species (e.g, Huffeldt et al. 2013), other tit species (Grace and Anderson 2015; LaZerte et al. 2016; Lee and Park 2019; Oden et al. 2015; Proppe et al. 2012) and several others on the White-Crowned Sparrow (*Zonotrichia leucophrys*) (Derryberry et al. 2016; Gentry et al. 2017; Luther and

Derryberry 2012; Phillips et al. 2020). In addition to song frequency, other song parameters studied such as song structure (e.g., Hanna et al. 2011) or time spent singing (Díaz et al. 2011) are far less studied than song amplitude (e.g, Nemeth et al. 2013; Shiba et al. 2016; Templeton et al. 2016) and song timing (e.g., Arroyo-Solís et al. 2013; Da Silva et al. 2014, 2015, 2016, 2017; Da Silva and Kempenaers 2017; Dorado-Correa et al. 2016; Lee et al. 2017; Sánchez-Gonzáles et al. 2020). By and large, under noise pollution, birds tend to sing louder (Brumm 2004; Brumm and Todt 2002; Derryberry et al. 2017; Lowry et al. 2012; Nemeth et al. 2013; Sementili-Cardoso et al. 2021); at higher frequencies (Job et al. 2016; Proppe et al. 2012; Slabbekkorn and Peet, 2003); they may change their song structure (Hamao et al. 2011; Hanna et al. 2011); and tend to change their time of singing (Alquezar et al. 2020; Arroyo-Solís et al. 2013; Lee et al. 2017; Sierro et al. 2017). In the presence of ALAN, birds mainly tend to sing earlier (Da Silva et al. 2014, 2015, 2016, 2017; Miller 2006; although Lee et al. 2017 found the opposite). Few studies tested the influence of human pressures on different song parameters together, what is a current challenge (see for example Sierro et al. (2017) testing the impact of aircraft noise on chorus timing, song frequency, song structure and time spent singing in European Blackbird (*Turdus merula*)).

If we focus on the timing of birdsong, almost all the studies related to the impacts of ALAN on birdsong investigated the hour of the first, or of the first and last songs of a species (Da Silva et al. 2014, 2015, 2016, 2017; Da Silva and Kempenaers 2017; Dorado-Correa et al. 2016; Kempenaers et al. 2010; Marín-Gómez et al. 2020; Miller 2006; Nordt and Klenke 2013) or the part of nocturnal versus diurnal song activity (Fuller et al. 2007). If we consider that the chorus is a time wave that increases rapidly before sunrise and then gradually decreases, then such indices of chorus start and end time or day/night rhythm of singing can be considered quite partial to study it accurately. For example, two species may start or stop singing at the same time but not have the same singing rhythm during the whole chorus.

Regarding these gaps, through an empirical approach, the objective of our study is to hierarchize the respective influences of different landscape, biotic and anthropogenic factors on the timing of bird chorus of different bird species along an urban to rural anthropization gradient. The timing of the chorus will be studied for several species individually and at the scale of the whole community as well as according to different timing parameters.

Methods

Study site and sampling design

We recorded birdsongs in 36 stations following a regular sampling of three lines of 12 stations ranging from the city of Saint-Nazaire (SE of the study site) to the countryside (NW of the study area - Fig. 1). The exact location of each station was determined by several criteria: (i) a minimum spacing of 400 meters between two stations (as 300 m is a distance avoiding dependence between sampling site in ornithological field surveys – Ralph et al. 1993); (ii) the presence of a wooded area (to sample a homogeneous bird community); (iii) the access possibility to the sites.

Song sampling and treatment

In each station, we placed and programmed an AudioMoth (Open Acoustic Devices) to record sounds continuously from midnight to noon every day from May 5 to May 13, 2022. The selected sample rate was 24 kHz. Each AudioMoth was powered by three AA batteries and their maximum memory is 32 GB. We recorded all tracks in WAV format. To protect them from the weather, we placed them in Ziploc bags, a cost-effective solution with an acceptable impact on sound measurement regarding our study objectives (see for example Law et al. 2021). The sound levels measured by the Audiomoth fleet were evaluated in a controlled laboratory environment. The tests were conducted at a distance of 5 meters from a white noise source (loudspeaker) emitting a sound level measured at 68 dB(A) with a class 1 sound level meter very close to the Audiomoth microphones. The standard deviation between the sound levels recorded by the sensors was found to be 1.53 dB(A), a low value compared to the variances observed across a range of measurement locations encompassing diverse environments, ranging from rural to urban areas.

We selected only one day to have recordings made at the same time and under identical weather conditions. May 9, 2022 was chosen because: (i) it was a weekday (a Monday) with normal human activity; (ii) and weather conditions were mild enough to make bird recordings possible (no wind, no rain). In addition, by this date, all migratory birds, including the latest, had already arrived in the study area.

For each station, we listened to the recordings in the laboratory with an EPOS Sennheiser Adapt 360 headset. The number of individuals of each species heard singing was noted on time steps of one minute every 10 minutes from midnight to noon (i.e. 73 one-minute segments for each station, for a total listening time of 2,628 minutes). Only passeriformes, cuculiformes and columbiformes were retained, thus excluding the rare other species (e.g., waders, ducks, gulls, owls). We excluded bird calls and considered only bird songs. We only included calls for 4 species: 3 species for which songs are absent or rare (Eurasian magpie (*Pica pica*), carrion crow (*Corvus corone*), western jackdaw (*Coloeus monedula*) and 1 species for which songs are difficult to distinguish from calls when a group is vocalizing (house sparrow (*Passer domesticus*)). All species names were actualized following Gill et al. (2023).

Song variables

We calculated six song variables (Table 1).

These six indices were calculated at three different scales. (1) At the station-species scale (e.g., the first song hour of the European Robin at station #28). (2) At the species scale, to be able to rank the species in relation to each other. In this case, each of the 6 indices was averaged by species for all stations combined (e.g., the average of the first song hour of the European Robin on all the stations where the species was recorded). (3) At the community level (we consider a community as the pool of species on a given station), we calculated community weighted mean (CWM) indices (Table 1, second column). A CWM index corresponds to one of the 6 species indices (Table 1, first column) within the community weighted by the respective species abundance. For example, in a community composed of one individual of the species “x” with a song index of 10, and two individuals of the species “y” with a song index of 20, the CWM will be (1 x 10 + 2 x 20) / (1 + 2) = 16.67. CWMs have been largely used in the literature to characterize temporal or spatial change in bird communities (see for example Devictor et al. 2008; Godet

et al. 2011). Here, it provides a simple metric to characterize each bird community based on one of six song indices. For example, a community with a high CMI (see Table 1) is dominated by species that sing late, and a community with a high CNI (see Table 1) is dominated by species that sing at night.

Table 1
Song variable used as dependent variables.

Full name (abbreviate name)	Related community weighted mean index (abbreviate)	Definition	Units	Meaning
First song hour index (FIRST)	Community first song hour index (CFI)	Hour of the first song.	Minutes after midnight	The value increases as the singing time gets later.
Peak song hour index (PEAK)	Community peak song hour index (CPI)	Hour when the maximum number of individuals sing. If this maximum is reached several times, the earliest time is kept.	Minutes after midnight	The value increases as the singing time gets later.
Mean song hour index (MEAN)	Community mean song hour index (CMI)	Average singing hour.	Minutes after midnight	The value increases as the singing time gets later
Median song hour index (MED)	Community median song index (CmI)	Median singing hour.	Minutes after midnight	The value increases as the singing time gets later.
Rate of nocturnal singing index (NOC)	Community rate of nocturnal singing index (CNI)	% of 1-minute time steps where the species sings before sunrise (6:41 am on May 2022 in the study area)	Percentage	The value increases as the proportion of nighttime singing increases
Duration of the song index (DUR)	Community duration of the song index (CDI)	Number of 1-minute time steps when the species sings.	0 to 73	The value increases as the duration of the song increases

Finally, we calculated two beta diversity indices, namely a temporal song turnover and a temporal song nestedness of birdsongs in each station. The temporal turnover of a given station indicates a replacement of the song of each species over time whereas temporal nestedness indicates a loss/gain of the song of each species over time. Following Baselga (2010), we used the Simpson dissimilarity index

(βsim) to estimate the temporal turnover (Lennon et al. 2001; Simpson, 1943) and the index developed by Baselga (2010) (βnes), to estimate the temporal nestedness.

Eye size of the species

For reasons detailed in discussion, bird species with larger eyes are known tend to sing earlier (Thomas et al. 2002). To test if we also found this relation in our study, we tested the correlation between the eye size and the 6 song variables listed before with simple linear models. Eye sizes were taken from Thomas et al. (2002) and we corrected this variable by the respective body masses of the species (also from Thomas et al. 2002), taking the residuals of a linear model between eye size and body mass.

Environmental factors

Three families of environmental factors were calculated.

Landscape factors. Within a radius of 300 meters around each AudioMoth, we calculated the landscape diversity (based on a Shannon index – Shannon (1948)); the area of wooded areas (in ha); and the area occupied by buildings (in square meters). The two first indices were computed from a vector data based on the land-use available for all the administrative department in 2016 (BD-MOS 44 - https://observatoire.loire-atlantique.fr/44/les-cartes/l-occupation-des-sols-en-loire-atlantique/r_8326) and the third one was extracted from a vector database produced by the IGN (BD-TOPO®) in 2018.

Traffic noise. In this study, we are employing the L50 indicator to translate the sound levels. This indicator is linked to the noise level surpassed for 50% of the measurement time, expressed in dB. This indicator holds the advantage of being resilient to sound events and providing a relatively accurate representation of the overall sound level (Can et al. 2016). Given the spatial gradient sampling in this study, and with traffic noise being the primary sound source in urban and suburban environments, we can state that in our dataset this indicator exhibits a high correlation with traffic noise levels.

Artificial lights. Two different indices were used to assess the level of artificial lights at night. The first index in the number of street lights in a 300 meters radius around each AudioMoth (extracted from a vector database of the energy syndicate “Territoire d’énergie Loire-Atlantique”). The second is the level of ALAN in a 300 meters radius around each AudioMoth extracted from the VIIRS Stray Light Corrected Nighttime Day/Night Band Composites for the month of April 2022.

Biological factors

For each station, we calculated the bird abundance (total number of individuals of all the species detected), bird species richness (total number of species of all the species detected), bird species diversity (Shannon Index of all the individuals of all the species detected – Shannon, 1948), the TFSD (which captures the amplitude and tonal temporal changes, at a frequency around 4kHz, and is associated with the density of bird song phrases (Aumond et al. 2017)). For the analyses at the species level, we also calculated the number of individuals of conspecifics (i.e. the number of individuals of the same species).

Statistical analysis

We performed a Principal Component Analysis (PCA) on the values of the six song indices of all the recorded species (37 species) to sort the species according to their song characteristics.

At the species level, we selected the 20 species that have been recorded in at least 10 of the 36 stations to hierarchize the influence of the 11 factors on their 6 song indices. For each of these 20 species, and for each song index, we considered the song index as a dependent variable and the 11 factors as independent variables. Hierarchical partitioning of variance (based on R^2) was used to determine the proportion of variance of each song index explained by each factor (Chevan and Sutherland 1991; Mac Nally 2000). This method enables the identification of variables whose independent correlation with the dependent variable is large, in contrast to variables that have little independent effect but a high correlation with the dependent variable resulting from joint correlation with other independent variables. Factors were then identified that independently explained a larger proportion of variance than could be explained by chance, by comparing the observed value of the independent contribution to the explained variance *I* to a population of *Is* from 1000 randomizations of the data matrix. Significance was accepted at the upper 95% confidence limit (Z-score of 1.65; Mac Nally, 2000; Walsh et al. 2004). Note that because the partitioning of variance does not require non-correlated factors, we include all the factors (See Appendix S1.1 for a correlation plot of all the factors).

Hierarchical partitionings of variances were also used to test the influence of the factors on (1) the total species abundance, species richness and species diversity; (2) the different community weighted mean indices (CFI, CPI, CMI, CmI, CNI, CDI); (3) β temporal song turnover and β temporal song nestedness. To avoid any circularity, because the values of abundance, species richness, species diversity but also β turnover and β nestedness are directly linked to the abundances and numbers of the species present, we exclude the 4 biological factors for these dependent variables.

Results

Species-specific approach

Among the 37 species recorded (Appendix S1.2). Each species was recorded on average in 13 stations (Appendix S1.3) with mean abundances per species and per station ranging from 0 to 5 individuals (Appendix S1.4.).

From midnight to noon, the number of singing individuals sharply increases from 5 a.m., reaches a peak at 6:31 a.m. (i.e. 10 minutes before sunrise), then slowly decreases until noon (Fig. 2-A).

Species can be sorted from early singers (e.g., common nightingale (*L. megarhynchos*), song thrush (*Turdus philomelos*) and common blackbird (*T. merula*)) to late singers (e.g., Eurasian nuthatch (*Sitta europaea*), garden warbler (*Sylvia borin*) or common cuckoo (*Cuculus canorus*)) according to the first hour of their song (FIRST), the peak hour of their song (PEAK), the mean hour of their song (MEAN), the

median hour of their song (MED), as well as their night song rate (NIGHT) (Fig. 2-B). Species can also be sorted from short-time to long-time singers according to their song duration (DUR) (Fig. 2-B). For detailed values of every indices for every species, see Appendix S1.5 to S1.9.

Note that the five song timing indices (FIRST, PEAK, MEAN, MED, NIGHT) of the different species are correlated (R^2>0.7 for all pairs, Appendix S1.11). Song duration (DUR) is the index the less correlated with the 5 other song timing indices.

Species with larger eye sizes are species with the earliest song (linear models between PEAK and eye size: $F_{1,22}$=5.36, p = 0.03, R^2=0.20; between MEAN and eye size: $F_{1,22}$=5.56, p = 0.03, R^2=0.20; and between MED and eye size: $F_{1,22}$=6.78, p = 0.02, R^2=0.24) and species that sing more at night (linear model between NIGHT and eye size: $F_{1,22}$=10.51, p = 0.004, R^2=0.32 – see Appendix S2 for detailed results).

Intra-specific approach

In this section, we only used the 20 species that have been recorded in at least 10 stations (see Appendix S1.3.).

The song indices of 17 species are linked to at least one of the landscape metrics (Fig. 3). As built area increases, six species tend to sing earlier, four sing more at night, five sing during shorter period (only two sing during longer periods). As landscape diversity increases, species react in contrasting ways: three sing earlier, two later, one sing less during night, four song during longer period and two during shorter periods. As wooded area increases, two species sing later, one earlier, one less at night, one more at night and three sing during longer period.

Birds tend to sing earlier, more at night, and during shorter period in areas submitted to high artificial lights (ALAN or number of street lights) and traffic noise (Fig. 3). With increasing levels of anthropogenic lights, nine species sing earlier, five species sing for shorter periods (only 1 species sings during longer period). With increasing levels of traffic noise, six species sing earlier, four species sing for shorter periods (only one species sings during longer period).

With increasing abundances, species richness, species diversity, and TFSD in the community, more species tend to sing later, less at night, and during longer periods, but few species have opposite relationships (Fig. 3). Almost all the species (16) sing during longer periods when the abundance of conspecifics are high. With increasing abundances of all the species pooled together, six species sing later and three sing earlier, one single species sings more at night, and five species sing during longer periods. Eurasian wren (*Troglodytes troglodytes*) is the only species with contrasting relations (Fig. 3). With increasing levels of species richness, four species sing earlier and four sing later, one species sings more at night, two sing less an night, one sing during shorter periods and only one during longer periods. With increasing levels of species diversity, six species sing later, two sing earlier, three sing less at night, two sing during shorter periods and one during longer periods. With increasing levels of TFSD, three

species sing later, one earlier, two sing less at night, five during longer periods, only one species sings during shorter periods.

Community approach

The total abundance and species richness are not significantly linked with any landscape nor anthropogenic indices but species diversity is significantly lower, first with increasing artificial lights, then with increasing built areas, and finally with the number of street lights (Table 2).

First (CFI), peak (CPI), mean (CMI) and median song community (CmI) indices are significantly higher first with increasing number of street lights, then with increasing levels of ALAN and built areas, whereas nocturnal song community index (CNI) and duration song community index (CDI) are significantly lower (Table 2). In other words, in areas dominated by high levels of built areas and high number of artificial lights, bird communities tend to be more dominated by late singing species, by species singing less at night and species singing during shorter periods. The other factors have lower parts of explained variance (Table 2).

Temporal turnover significantly increases whereas temporal nestedness significantly decreases with increasing landscape diversity, street light numbers and traffic noise (Table 2).

For an illustrative purpose, a graphical representation of the temporal structure of all the stations are displayed in Appendix S3.

Discussion

An old story: each species has his own song timing and large-eyed species sing earlier

In this study, we used several metrics to measure the song timing of different species, going beyond measurements of the time of first song of each species per station. Using this diversity of metrics, we were able to classify species by song time and duration. Our approach is above all a refinement to reveal that each species has its own song timing, as already shown several years ago (e.g., Allard 1930; Allen 1913). However, the robustness of our classification is confirmed by comparing our results with other studies. From unpublished data from Lluisia, Aubin and Sueur, Gil and Llusia (2020), found a similar sorting of the 11 species shared in their study and our study (Linear model based on the time ranks of the first song of the species of the two datasets: $F_{1,9}$=22.56, R^2=0.71, p = 0.001 – Appendix S4).

In agreement with Thomas et al. (2002), the second point is that large-eyed species tend to sing earlier than others. Eye-size is a good proxy of the visual capacity at low intensity (Thomas et al. 2002). Large-eyed species can start singing early as soon as they can see enough to detect potential rivals or predators (Thomas et al. 2002). Another explanation would be that birds sing until they can see enough to forage.

Birds that have high visual capacity can start to forage early, and thus sing before this time, what has been demonstrated by an experimental approach on great tits (*P. major*) by Kalcenick (1979).

A broadening of knowledge: individuals of the same species adjust their song timing to their environment

Beyond the species-specific approach, we found that for most bird species studied, individuals of the same species adjust their song timing to their environment. Most of the previous studies focuses on one or a small set of species. Our study demonstrate that different species may have similar responses to environmental conditions. In general, individuals sing earlier and for shorter periods of time in the most anthropized areas, especially in areas subject to artificial lights and, to a lesser extent, traffic noise, and which are the most densely built-up. Conversely, birds sing longer where the abundances of their conspecifics are high. These results reveal on a larger number of species what has been partly suggested or demonstrated in the literature.

Beyond the song timing onset, one of the novelties of our approach is to investigate several song timing indices, including song duration. For comparison purposes with other studies, if the "song duration" factor is set aside, we found that 9 species among 20 sang earlier in the more artificially lit areas. Although the importance of artificial lights seems not important in birdsong timing on tropical areas (e.g., Dorado-Correa et al. 2016; Marín-Gómez et al. 2019, but see Marín-Gómez 2022), many studies documented results similar to ours in temperate areas. Miller (2006) already found that american robin (*Turdus migratorius*) sing earlier in lit areas. More precisely, like in our study, other authors found that the same species, namely European robin (*E. rubecula*), common blackbird (*T. merula*) (Da Silva et al. 2014; Kempenaers et al. 2010,) as well as song thrush (*T. philomelos*) (Kempenaers et al. 2010) sing earlier with increasing artificial light levels. We also found no response of 11 species among 20, among which common chaffinch (*Fringilla coelebs*) as showed by Kempenaers et al. (2010) and Da Silva et al. (2014). Contrary to Kempenaers et al. (2010) and Da Silva et al. (2014) we did not find that Eurasian blue tit (*Cyanistes caeruleus*) and great tit (*P. major*) sing earlier with increasing light level. If we add song duration in the song indices, 5 species sing during shorter period, and only one sing during longer period in lit areas. Species that are the most responsive to lights are early singers (e.g., European robin (*E. rubecula*), common blackbird (*T. merula*), song thrush (*T. philomelos*), as already demonstrated by Kempenaers et al. (2010) but also Da Silva et al. (2014). The greater response of early singers has been explained by the fact that these species are more sensitive to light than late singers (McNeil et al. 2005; Thomas et al. 2002).

We also found that 6 species sing earlier and 4 during shorter periods in noisy areas. Birds are thought to avoid rush hour of high traffic noise and thus sing earlier (Arroyo-Solís et al. 2013; Dorado-Correa et al. 2016; Nordt and Klenke 2013). The relative effects of lights compared to noise is still debated in the literature. Fuller et al. (2007) found that daytime noise better explains nocturnal singing of European robin (*E. rubecula*) than light pollution, and Nordt and Klenke (2013) had difficult to fully separate the effects of both factors. According to Dorado-Correa et al. (2016), in tropical area, noise but no light has effect on song timing. On the other hand, several studies demonstrated that artificial light better explain

song timing than noise (Da Silva et al. 2014; Lee et al. 2017; Marín-Gómez 2022). Our results suggest that light has greater impacts than noise on birdsong timing: for almost each song timing variable and each species, we found that light better explains song timing than noise, and 3 species react to light but not to noise.

Among the landscape indices, built area is the factor that best explains song indices. With increasing level of built area 7 species sing earlier and 5 song during shorter periods. Only two species known to be highly synanthropic (Eurasian collared dove (*Streptopelia decaocto*) and house sparrow (*P. domesticus*) – see Guetté et al. 2017) sing during longer period in increasing level of built area. Similar results were obtained by Marini et al. (2017) who found that mountain chickadees (*Poecile gambeli*) sing earlier in cities than in rural areas and Sanchez-Gonzáles et al. (2020) who found that urbanization level (estimated by percentages of built structures and green area), but neither light nor noise, explain earlier start of song in the vermilion flycatcher (*Pyrocephalus obscurus*). The difference between urban and rural areas in the song timing may be explained in different ways. The most probable explanation is the effect of the urban heat island (temperatures are higher in built areas). Birds are known to sing earlier in warmer than in colder environments, the later requiring high energy costs (Ward and Slater 2005). Therefore, in colder areas (like in rural areas) birds will start to sing later than in urban areas. The lower song duration in highly built areas can also be explain by a lower quality of urban ecosystems due to a lower food resource: the longer birds spend foraging, the less time they have to sing. van Oort and Otter (2005) and van Oort et al. (2006) found for example that black-capped chickadees (*Poecile atricapillus*) tend to have lower song outputs in young forest than in old forest, due to food limitation in the former.

The abundance of conspecific is, by far, the factor that best explain the song duration: 16 species among 20 sing during longer period with increasing abundance of conspecifics. Although it is impossible to distinguish the different individuals along the recordings, we can only hypothesize that either each individual tends to sing during a longer period or that individuals take turns to song. In dusky flycatchers (*Empidonax oberholseri*), Stehelin and Lein (2014) found that singing rates were higher on the day of playback than on the day before playback, suggesting that bird sing more when stimulated by conspecific songs. In eastern kingbirds (*Tyrannus tyrannus*), Sexton et al. (2007) also demonstrated that songs are longer with increasing number of neighbors.

If we focus on the influence of abundance of conspecific on the 5 other song timing indices (i.e. song duration set apart), we found that 7 species tend to sing later, only one sing earlier, and two sing earlier or later according to the song index used. However, we hypothesize that the increase in mean song hour, median song hour, and decrease in nocturnal song rate are driven by the important increase in song duration. When focusing on the song onset itself, as revealed by the first song hour (FIRST), two species sing earlier when abundance of the conspecific increases (Eurasian blackcap (*Sylvia atricapilla*) and common chaffinch (*F. coelebs*)). The increase in the number of neighbors is known to promote earlier songs in many species (e.g., Stehelin and Lein 2014; Stuart et al. 2019), and is even identified as more important than lights and noise by Stuart et al. (2019).

In other words, with the increase of conspecific abundances, most of the species sing during longer period, two species start to sing earlier, and the others have later mean and median song hours as well as lower night song rate, what is probably driven by the fact that their songs are spread over the whole morning (i.e. increase in song duration).

A new step in knowledge: anthropization changes song timing of bird communities

At the community level, we found that built areas and artificial lights tend to decrease species diversity. Understanding which species and according to what life history traits is filtered by anthropogenic factors was not our purpose, and has been already well studied (see for example Croci et al. 2008). However, to our knowledge, the inclusion of song timing parameters among these traits remains understudied. We found that anthropized areas, and mostly lit and built area promote communities dominated by late singing species and species singing during short periods.

To our knowledge, the only study that has attempted to understand how the temporal structure of birdsong varies at the scale of a community, by taking into account the temporal place occupied by each species, is that proposed by Marín-Gómez et al. (2020). In their pioneer study, they proposed, first theoretically, that the temporal patterns of the dawn chorus of a community can follow a random structure (i.e., the different bird species sing randomly in time), modular (i.e., each species sing one after the one – what we called “beta temporal turnover” in our study) or nested structure (i.e., the song of each species is added to the previous one over time – what we called “beta nestedness turnover” in our study). Through an empirical study, they demonstrated that peri-urban and intra-urban bird communities followed a modular pattern but that only the peri-urban had a clear sequential temporal structure. By studying a very different bird community (there are almost no species in common between their study and ours) in a very different area (temperate versus tropical), different sampling methods, and different metrics used to quantify the temporal structure of the dawn chorus, we surprisingly come with comparable conclusions. The temporal structure of the dawn chorus in peri and intra-urban, that corresponds to high to moderate level of anthropization, follows a beta temporal turnover, whereas in rural areas (not studied in Marín-Gómez et al. (2020)) the structure follows a nestedness turnover. We may interpret our result as an alteration of the temporal structure of the dawn chorus by the anthropization. Beyond this evidence, the consequences of this change for the ecology and the communication of birds at the interspecific level remain to be explored.

Conclusions

To conclude, to our knowledge, this study is one of the first to document the impact of anthropization on the temporal structure of birdsong at the intraspecific, the inter-specific and the community levels in a temperate area. The different facets of anthropization influence bird chorus in a similar way: artificial lights and built areas decrease bird species diversity and promote late-singing and short-singing species. For a given species the individuals living in lit, noisy, and built areas tend to sing earlier and during shorter

periods. We also found that the abundance of conspecific, that could also be driven by the level of anthropization, has a strong effect on the song timing and particularly song duration of almost all the species: bird sing during shorter period where conspecific abundances are low. Finally, lit and noisier areas have a more important temporal song turnover with species singing one after the other rather than adding up over time (Fig. 4).

Declarations

Ethical approval

Not applicable. No animals were handled and no human data were used in this study.

Competing interests

The authors declare that they have no competing interests.

Authors's contributions

All authors contributed to the study conception and design. Data collection was performed by LG and AP. Bird data analysis was performed by LG, AP, VL. Remote-sensing data analysis was performed by JN. Traffic noise analysis was performed by PA. The first draft of the manuscript was written by LG and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Availability of data and materials

Although the data are not yet stored on a repository, they are all available on request to the authors. It should also be noted that most of the raw and complete data concerning the analyses are provided in the appendices attached to the manuscript.

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Table

Table 2 is available in the Supplementary Files section.

Figures

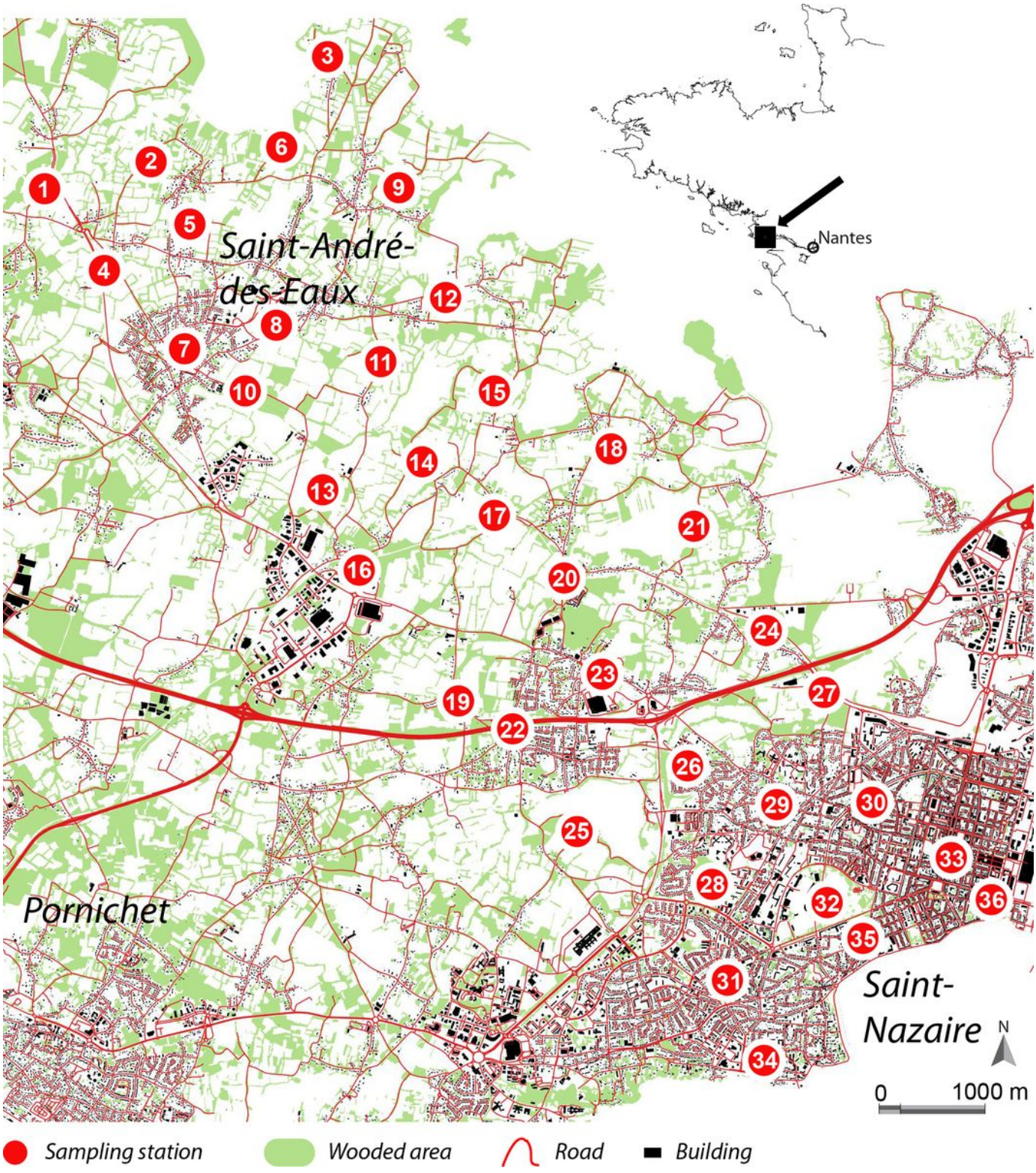

Figure 1

Study area and sampling design.

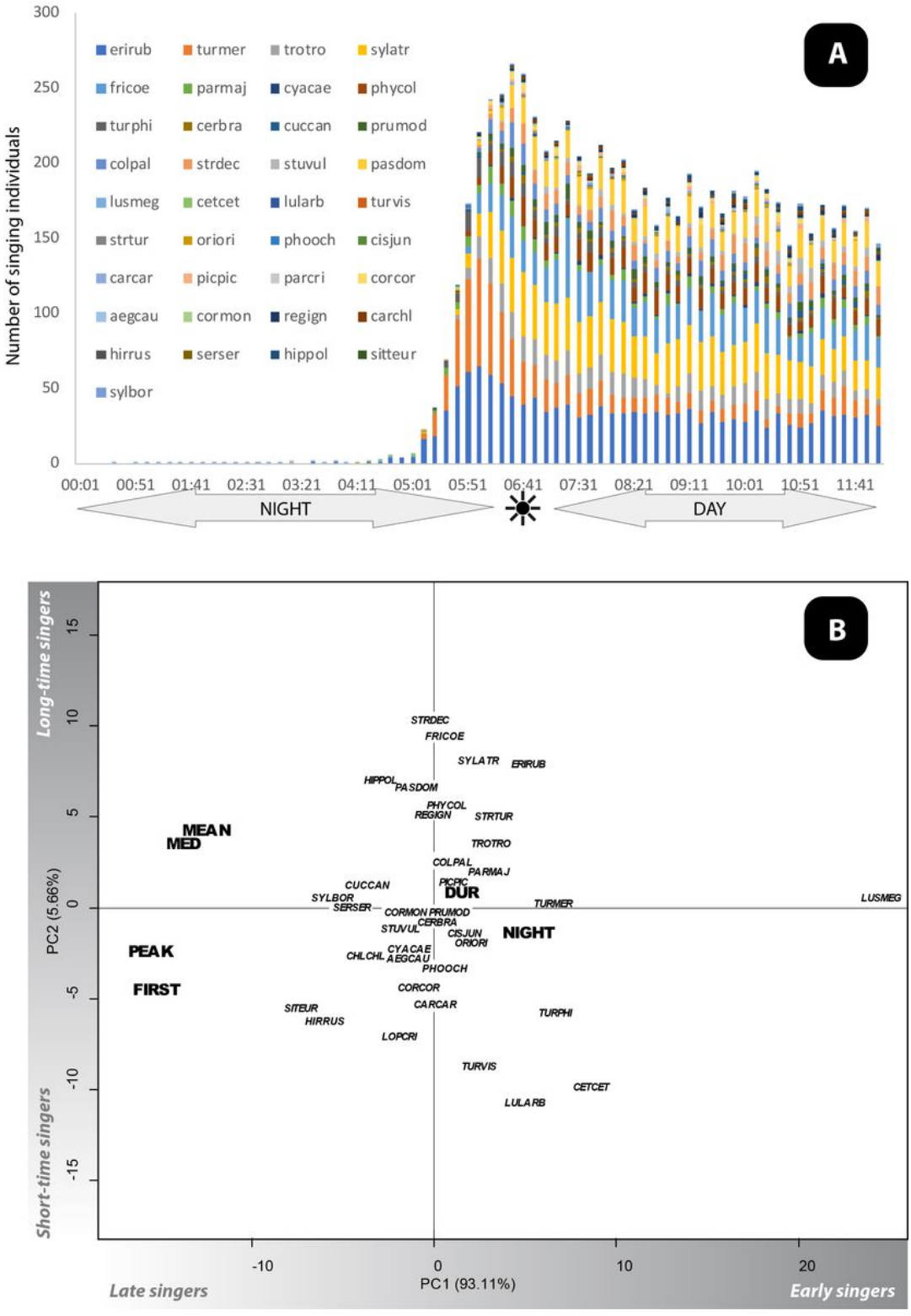

Figure 2

(A) Song chronology of all the species in every station. Bars represent the abundance of singing individuals with different colors for each species. The time of sunrise was 6:41 am. (B) First factorial plan of the Principal Component Analysis (PCA) on the 6 song indices (in bold - FIRST: first song hour; PEAK: peak song hour; MEAN: mean song hour; MED: median song hour; NIGHT: night song rate; DUR: song duration) for the 37 species (in italics). See Appendix S1.1 for species names abbreviations.

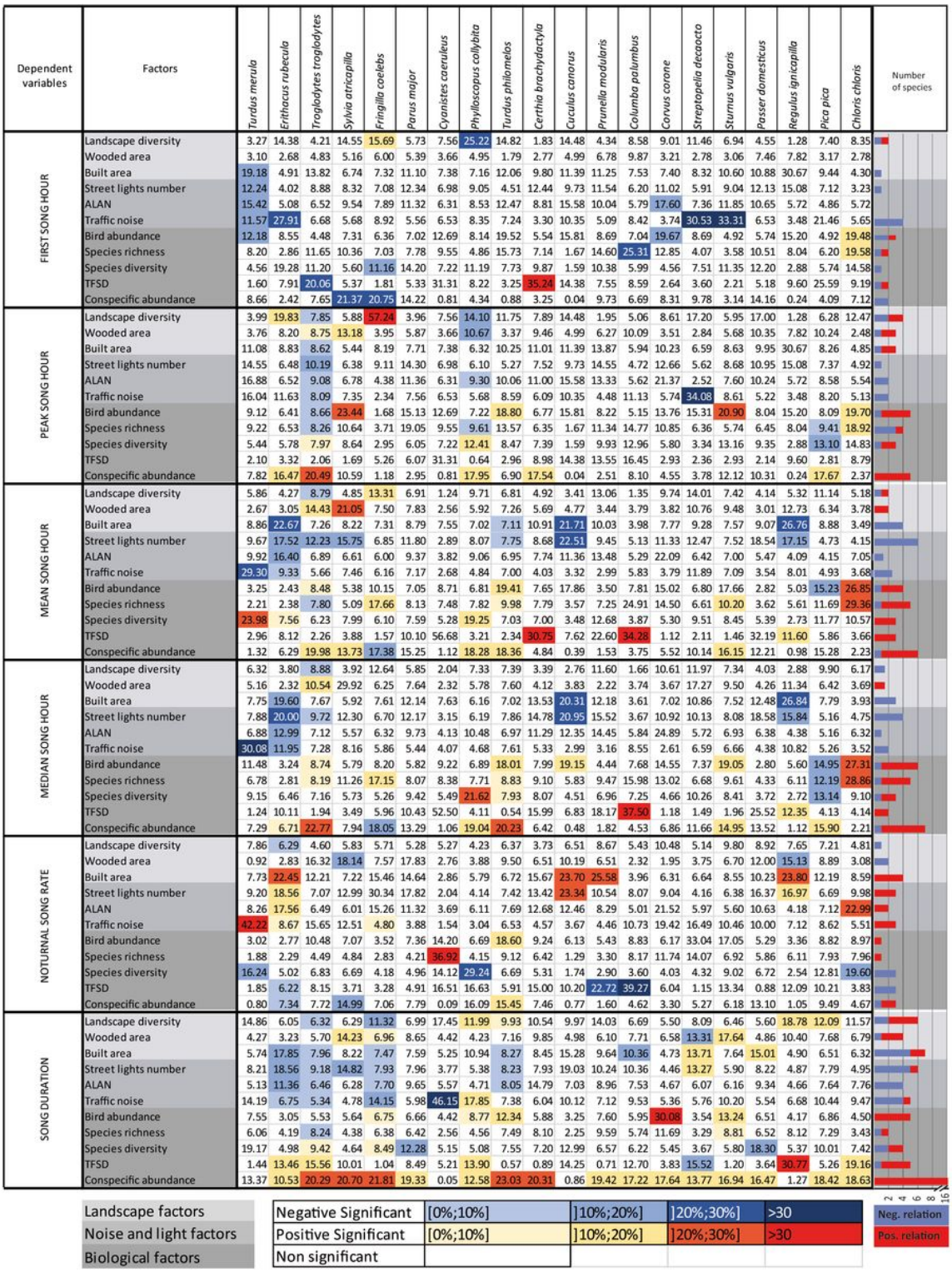

Figure 3

Relationships between the 6 song indices (first, peak, mean and median song hour; nocturnal song rate; song duration) and the 11 factors (in light grey: landscape indices; in medium-grey: anthropogenic noise and light; in dark-grey: biological factors) for the 20 species sampled in at least 10 stations. Values indicate the percentage of explained variance in a song index for each of the 11 factors independently (i.e. the total is equal to 100% for a given species and a given song index) obtained through hierarchical

partitioning of variance. White cells indicate non-significant relationships; light to dark-blue negative and significant relationships; yellow to red positive and significant relationships. For first, peak, mean and median hours a negative relation (in blue) means that the increase in the values of a factor is linked with earlier hours; a positive relation (from yellow to red) with later hours. For song duration, a negative relation (in blue) means that the increase in the values of a factor is linked with a shorter song period; a positive relation (from yellow to red) with a longer song period. On the right part of the figure: number of species for each dependent variable and each factor (in blue: number of species with a negative and significant relation; in red: number of species with a positive and significant relation).

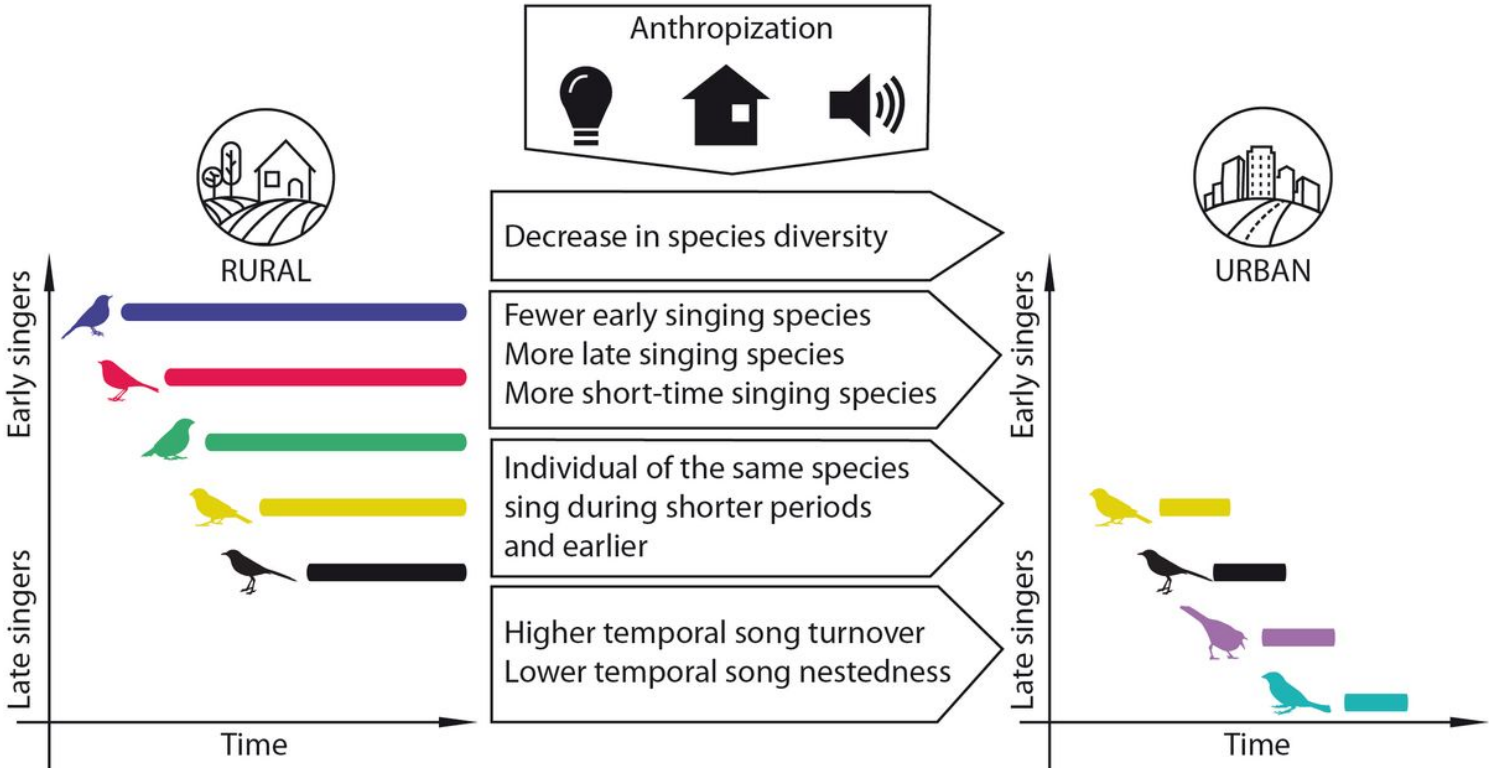

Figure 4

Graphical synthesis of the main results.

Supplementary Files

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- Appendix1.docx
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- Appendix4.docx
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