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Original research article

Large-scale semi-automated acoustic monitoring allows to detect temporal decline of bush-crickets[☆]

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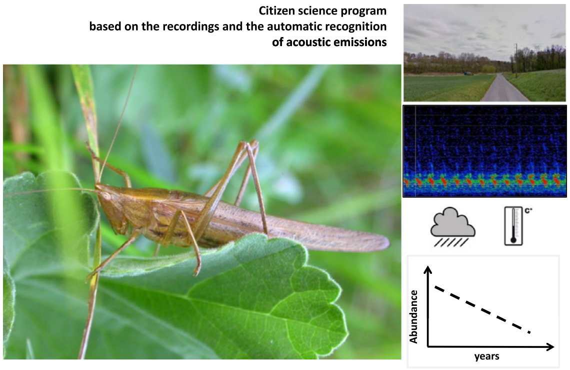
HIGHLIGHTS

- We assessed the relevance of a method to detect Orthoptera trends at large scale.
- We used acoustic monitoring coupled with automatic recognition of species sounds.
- The spatial variations were explained by the geoclimatic conditions and land use.
- The temporal variations were correlated to the climatic conditions of the year.
- Such method offers several advantages for assessing Orthoptera biodiversity trends.

GRAPHICAL ABSTRACT



A relevant way to monitor Orthoptera species at large scale

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ABSTRACT

Monitoring biodiversity over large spatial and temporal scales is crucial to assess the impact of global changes and environmental mitigation measures. However, large-scale monitoring of invertebrates remains poorly developed despite the importance of these organisms in ecosystem functioning. The development of new recording techniques and new methods of automatic species recognition based on sound detection and easily applicable within a citizen-science framework, offers interesting possibilities. However, the value of such protocols has not been tested for the study of temporal trends on a large spatial scale.

We used an acoustic region-wide citizen-monitoring program of Orthoptera, conducted along roads, to assess the relevance of automatic species recognition methods to detect temporal trends while taking into account spatial and seasonal patterns of two Orthoptera species activity (*Tettigonia viridissima* Linnaeus, 1758, and *Ruspolia nitidula* Scopoli, 1786)

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at a large scale. Additionally, we tested the effect of climate and land-use variables on spatio-temporal abundance patterns using generalized linear mixed models. We found negative temporal trends for the two species across the survey period (2006–2012). The spatial variations were largely explained by the geoclimatic conditions and, to a lesser extent, by land use (negative effects of urbanization). The temporal variations were highly correlated to the climatic conditions of the year, and of the previous year (nonlinear effect of temperature, precipitation).

To our knowledge, this paper describes the first successful attempt to calculate large-scale temporal trends of insect populations on the basis of an automatic identification process of acoustic data. We argue that acoustic monitoring along roads, coupled with the automatic recognition of species sounds, offers several advantages for assessing Orthoptera biodiversity response to global changes and environmental measures.

1. Introduction

Large-scale standardized monitoring schemes are crucial to assess changes in species distributions and abundances and to predict long-term biological responses to global changes, especially anthropogenic pressures (Balmford et al., 2003; Pereira and Cooper, 2006; Balmford et al., 2005; Green et al., 2005; Jones et al., 2011). These programs have been increasingly developed in recent decades (Devictor et al., 2010; Theobald et al., 2015) and have been helpful to highlight ongoing community changes facing land use and climate changes (Devictor et al., 2012).

Large-scale monitoring schemes are, however, largely focused on plants and vertebrates (especially birds). Few programs monitor terrestrial arthropods and, almost solely focus on butterflies (Thomas, 2005; Theobald et al., 2015) and, to a lesser extent, on pollinators (Deguines et al., 2012). However, insects constitute over 50% of species diversity and significant biomass, playing a crucial role in ecosystem functioning (Weisser and Siemann, 2004). Even though their conservation status is still a low priority, insect conservation is of increasing concern (Dunn, 2005; Régnier et al., 2015). More importantly, the study of insect spatio-temporal trends may be informative and complementary to those of more long-lived species, such as vertebrates, in understanding the mechanisms underlying biodiversity responses to global changes. Insect abundances and community composition are known to vary in response to both intrinsic and extrinsic factors (notably temperature and precipitation), but understanding the relative roles of each factor in population and community processes is a long-standing problem in ecology (Turchin, 2003). The improved assessment of insect dynamics will finally help to predict their future trends in regard with environmental changes, which is of great concern for decision-makers and practitioners due to the role of insects in ecosystem functioning and their importance in ecosystem services (pollination, biological control) and damages (in crops).

To date, most of the existing insect surveys generally focus on particular habitats and single species, or small groups of species providing services or causing damages, for example, the oak processionary moth (Wagenhoff and Veit, 2011; Williams et al., 2013) in forests, or butterflies in grasslands (van Swaay et al., 2008). Agricultural landscapes gather the largest number of long term surveys—for example, on pollinators, such as bees (Genersch et al., 2010), and agriculture pests, such as aphids (Wang et al., 2014) or Orthoptera (Acrididae) (Fielding and Brusven, 1990; Jonas and Joern, 2007). While these monitoring programs allowed the survey of population changes within these habitats, relatively few programs allow the assessment of nation- or region-wide trends, especially across diverse habitats (but see Deguines et al., 2012). Finally, most programs focused on low trophic levels (phytophage), while global changes that affect communities and ecosystem functions are expected to affect species interactions within and among trophic groups (Wisz et al., 2013; Blois et al., 2013). Developing complementary nation- and region-wide monitoring programs on insects of intermediate trophic level (feeding on smaller insects), whose population and community dynamics are expected to rapidly reflect the dynamics of the lowest level, is crucial to better assess the mechanisms underlying biodiversity dynamics.

Monitoring based on standardized collected data of insect population abundance is likely the best approach to estimate population trends (Yoccoz et al., 2001). However, it implies being able to develop a large temporal and spatial effort to improve detection, and the precision of trends estimation (Yoccoz et al., 2001; Nielsen et al., 2009; Lindenmayer et al., 2011). Citizen-monitoring schemes with standardized and designed protocols are thus considered to be a powerful solution to collect large amounts of data (Dickinson et al., 2010, 2012; Bonney et al., 2014; Theobald et al., 2015). Digital technologies, such as photographs, videos and sound recordings, could substantially increase the amount of data collected and reduce the bias due to variation in the observers (Sueur et al., 2008; Dickinson et al., 2010; Penone et al., 2013b). Digital technologies are noninvasive techniques, they also reduce the need for human interpretation compared to traditional methods, and allow subsequent data validation by experts. Furthermore, some of these technologies can be coupled with automated signal recognition (Blumstein et al., 2011) to further reduce both observer bias and the time spent on data analysis. Acoustic techniques may be particularly useful for monitoring (Mankin et al., 2011; Marques et al., 2013) the insects which produce loud and species specific sounds. This is the case of Orthoptera, which produce mating calls (Ragge and Reynolds, 1998) involved in reproduction (Paterson, 1985). Hence, Orthoptera stridulations are reliable signals for species classification (Riede, 1998) and can even yield precise information about species abundances (Fischer et al., 1997). Moreover, automatic identification systems have already been implemented for Orthoptera, notably at the species level (Riede et al., 2006; Ganchev et al., 2007; Lehmann et al., 2014). Consequently, sound detection, which is a non-destructive and well-accepted sampling method, appears to be a powerful monitoring technique for Orthoptera monitoring (Lehmann et al., 2014) and might be well suited to a citizen-science framework.

Previous studies showed that citizen-based acoustic monitoring programs, in which volunteers sampled Orthoptera based on acoustics along roads, allowed the detection of spatial variation in Orthoptera abundances in response to anthropogenic changes at a regional scale (Penone et al., 2013b). In the current study, we extend these analyses to a larger spatio-temporal scale and aim at linking annual trends with spatio-temporal changes in the environment. We used the dataset of the national Orthoptera citizen-based monitoring program developed by the French National Museum of Natural History. To assess the potential of automatic acoustic detection in providing reliable data on species trends, we tested whether we could detect temporal abundance trends (2006–2012) for two large Orthoptera species with relatively high trophic levels: the Great Green Bush-Cricket (*Tettigonia viridissima* Linnaeus., 1758) and the Large Conehead (*Ruspolia nitidula* Scopoli, 1786), accounting for factors that influence the recorded activity. For that purpose, we also examined whether the large-scale patterns of these species were linked to climate and land use. The abundances of the two species were expected to be negatively related to urban cover (Penone et al., 2013a), and positively related to temperature and precipitation (Fielding and Brusven, 1990; Skinner and Child, 2000) (quadratic response) due to the dependence of population dynamics on environmental conditions (notably for food availability) in respect with energetics rules (Brown et al., 2004).

2. Methods

2.1. Orthoptera data

2.1.1. Species

To examine whether it is possible to detect temporal trends in Orthoptera using automatic sound recognition, we used the dataset of the national acoustic biodiversity-monitoring scheme developed and coordinated since 2006 by the French National Museum of Natural History (see dataset attached to the publication, and the link of the monitoring scheme: http://vigienature.mnhn.fr/page/suivi-des-orthopteres-nocturnes-son). To explore the feasibility of the approach, and the possibilities offered by automatic recognition, we specifically chose to study the Orthoptera species which satisfy the following four criteria: (i) common and widespread across our study area, (ii) easily detectable (>100 m radius and continuous sound emissions), (iii) produce sound emissions that could be efficiently automatically detected through existing software (see below), and (iv) no frequency overlap with other common Orthoptera species that could lead to misclassification. This led us to focus on two species, the Great Green Bush-Cricket and the Large Conehead. The Great Green Bush-Cricket is one of the largest European species (28–42 mm; 1450 mg) and is considered as mainly carnivorous, feeding on other Orthoptera species, caterpillars, flies, or butterflies (see Knechtel and Popovivi-Baznoanu, 1959 and Baur et al., 2006). The Large Conehead is a medium size species (556 mg; 20–29 mm) with a more generalist diet, including both small insects and plants (Guillet et al., 2000).

2.1.2. Protocol

The data were collected along road circuits that allow an easy access to various landscapes, and gathering of a large amount of data (Dickinson et al., 2010). A set of 30-km circuits (1 circuit per volunteer) located throughout France was surveyed at a constant speed of approximately 25 km/h, twice a year (in June–July and August–September), during dry nights when the temperature was greater than 12 °C, from 30 to 120 min after sunset, i.e. during the peak activity of most bush-cricket species. Circuits had to meet two requirements: first, to ensure the volunteers' safety, the circuit had to be performed at night at low speed (recording at a constant speed of 30 ± 5 km/h), second, the circuit was designed such that it crossed different habitats according to proportions which were representative of the area, as well as possible. Once the circuit was validated by the Museum, the starting plot was randomly chosen. Each circuit was divided into ten 2-km road portions, separated by 1-km road portions in which no recording was performed (Fig. 1). Given that volunteers are sometimes locally coordinated by structures such as Regional Natural Park, and NGOs, circuits are currently clustered in space. Due to the protocol constraints, all roads were maximum 10 m wide, paved, and with low traffic. This sampling design resulted in a strong representativity of the proportion of habitats sampled in regard with the proportion of habitats at the regional and national scale (correlation coefficient: $r = 0.95$, Appendix S1).

Along each circuit, observers continuously recorded sounds on a Zoom H2 digital recorder (Samson) plugged into an ultrasonic detector (*Tranquility Transect, Courtpan Design Ltd*). This protocol allowed the monitors to record unbiased insect acoustic activity occurring over 8 kHz (i.e. all local bush-crickets; *Orthoptera Tettigoniidae*), thus preventing the activity from being masked by car noise. The detector was fixed to the passenger-side window at a 45° angle so that the distance to road edges was similar all along the circuits (Appendix S1). *Tranquility transect* detectors were set to record sound during 320 ms at each trigger event and then to transmit the sound to the recorder on a 10*x* time-expansion basis, thus during 3.2 s.

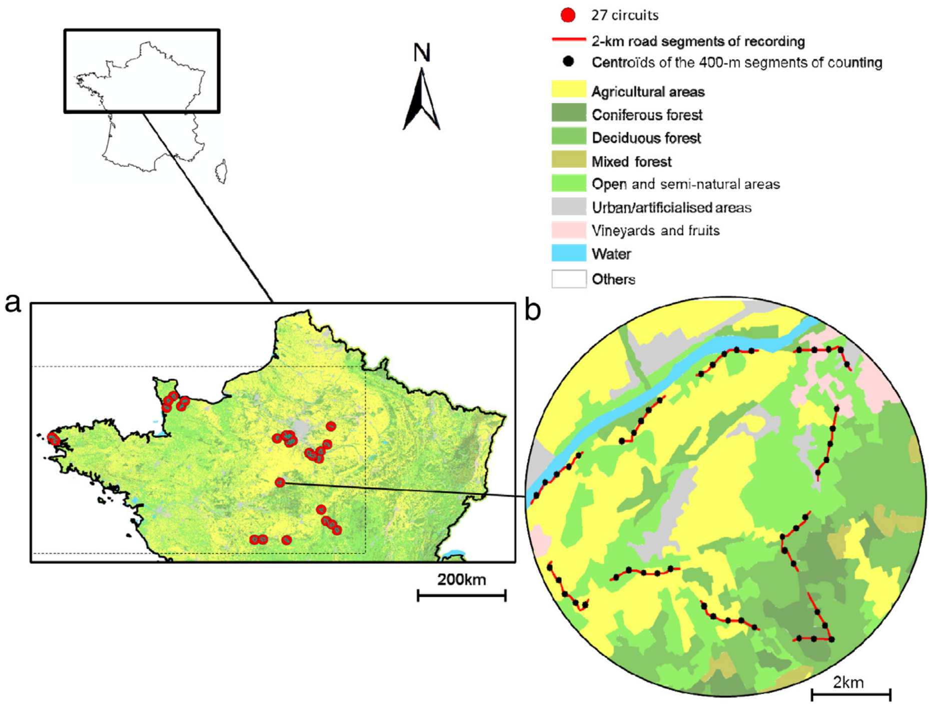

Fig. 1. Circuit locations (a) and configuration (b), the dashed frame in (a) delimits the region of study.

2.1.3. Orthoptera sound analyses

Sound recordings were analyzed with SCAN'R software (Binary Acoustic Technology) to automatically detect sound emissions from the two studied species. From SCAN'R outputs (all detected calls, with 19 parameters measured for each), we first filtered signals by peak frequency to select the sounds of the two species, in a 9–13 kHz interval for potential Great Green Bush-Cricket emissions, and 14–18 kHz for potential Large Conehead emissions; these criteria eliminated most other common bush-cricket species.

Even though the Great Green Bush-Cricket could exhibit a strong energy peak at approximately 20 kHz at close range, the lower peak at approximately 10 kHz suffers less sound attenuation and thus ensures a larger detection radius.

The additional criteria used to classify Large Conehead were: the slope at the start of the signal (Su) being strictly higher than the general slope of the signal (Slope), the general slope of the signal being negative (Slope), the time interval between two calls (Prev) comprised between 5 and 40 ms, and the duration of the signal higher than, or equal to 1.8 ms.

Lastly, we applied an ultimate filtering step to these two subsets in order to obtain a negligible false positive rate (detection while the species is absent) possibly coming from noise (Fig. 2, and Appendix S2). For this purpose, we aggregated detections at the scale of trigger events because all syllables recorded within this 320 ms window were likely to be from a single individual. Thus, all trigger events containing strictly less than four, and two syllables (energy peaks) per 320 ms-window for Great Green Bush-Cricket, and Large Conehead, respectively, were assumed to be false positives, and thus absences. This supplementary filtering step (before syllables aggregation into calls) reduced the false positive rate from 20% to 8%, and from 8% to 0%, respectively.

The calls (as groups of true positive syllables) were used as a proxy of individual detection to calculate species abundance, because male activity is highly correlated to population abundance (Fischer et al., 1997).

We divided the continuous recording made on each 2-km road segment into 5 equal parts corresponding to 400-m segments. We allocated all the individuals detected to the coordinates of the central point of the corresponding 400-m segment. For each segment, we collated the local temperature at the beginning of the recording. To optimize the spatio-temporal coverage and continuity of the sampling, we focused on the circuits that have been followed for at least three years. Because surveys in the south of France were almost absent during the first half of the survey period, thus potentially biasing the representativeness of the temporal trend, we chose to focus our analyses on the circuits that are located in the northern half of France (over 46°26′20, 799″N). Thus, the analyses were based on 1350 400-m segments (nested in 27 circuits).

2.2. Environmental data

2.2.1. Habitats

We delineated a circular area (hereafter buffer) with a 200-m radius around the midpoint of each road segment and calculated for each buffer the proportion of the main habitats (urban, agricultural, semi-natural and woodlands, Appendix

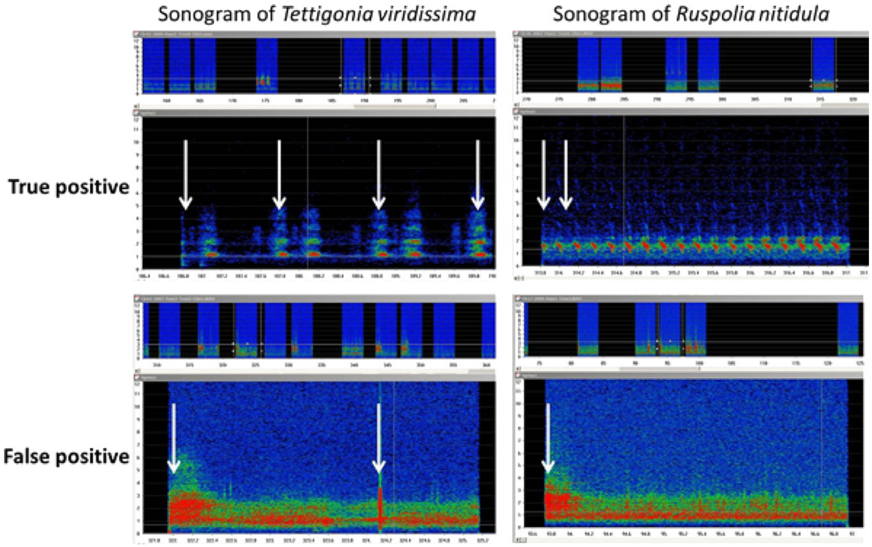

Fig. 2. Example cases of sonograms of *T. viridissima* (left) and *R. nitidula* (right) showing true (up) and false (bottom) positive detection. Signals are indicated by white arrows and consist in true (up) or false (bottom) syllables, depending on the case.

S1) using the georeferenced Corine Land Cover database (CLC, 2006). Penone et al. (2013a) reported that a 200-m radius is sufficiently large for detecting landscape effects on the species. Furthermore, at this distance, buffers did not overlap, thus limiting data dependence. The urban cover was defined by built and impervious surfaces and was expected to be negatively related to the abundance of the two species (Penone et al., 2013a), principally due to habitat loss, because the habitats of the Great Green Bush-Cricket and Large Conehead are rather natural or semi-natural areas. In particular, the Large Conehead would be most often associated with open semi-natural habitats, avoiding short grassland areas and closed habitat (e.g. wet meadows, shrubs along grasslands, or rural areas) (Kristin et al., 2007), whereas the Great Green Busch-Cricket overall depends on deciduous forest edges and hedgerows (avoiding sempervirent forests) (Bellmann and Luquet, 2009). Thus, we included the proportion of urban (*Urban*, mean = 10.2 [SD23.6]%), semi-natural (*SemiNat*, mean = 40.8 [SD41.6]%), deciduous forest (*Decid*, mean = 15.3 [SD29]%), and sempervirent forest (*Conif*, mean = 2.7 [SD14.6]%) covers as co-variables in the models. Crop cover (mean = 28.7 [SD 38]%) was excluded because it was collinear with the other co-variables (see also Appendix S3). All landscape analyses were performed using ArcGIS9.3® (ESRI, 2008).

2.2.2. *Climatic data*

For each segment and each date, we calculated the climatic variables expected to influence the variations in the abundance of the two Orthoptera species (Fielding and Brusven, 1990; Skinner and Child, 2000; Jonas and Joern, 2007): (i) The monthly summer (July–August–September) mean temperature (*LastSummerTemp*) and the mean precipitation (*LastSummerRain*) of the previous year were assumed to play a role in the species dynamics through their impact on the insect spawning. (ii) The monthly spring (April–May–June) mean temperature (*SpringTemp*) and precipitation (*SpringRain*) of the year of observation were assumed to influence the vegetation cover and thus the resource availability for the contemporary populations. Because these climatic variables are partly correlated, we focused our analysis only on the effect of *LastSummerTemp* and *Spring Rain* on the abundance of the two Orthoptera species abundance based on ecological knowledge, and the relevance of the ecological hypothesis (Skinner and Child, 2000). (iii) Finally, the summer mean temperature of the last twenty years (1993–2013) was used to reflect the characteristics of the recording sites within the main geographic and climatic regions at the national scale (*BiogeoclimPos* for large biogeoclimatic positions). The calculation of these variables was based on temperature and precipitation which were available for each month for all the years between 2006 and 2012, at a spatial grain of $8 * 8$ km (data provided by Météo–France, calculated by the model SAFRAN, Quintana-Seguí et al., 2008).

2.2.3. *Environmental conditions affecting species detectability*

In addition to the large scale climatic variables, we took into account in our analysis local meteorological information such as the temperature (*TempSurvey*) measured by the observer at the beginning of each recording session as lower temperatures are known to negatively influence sound emission activity (Penone et al., 2013b). We also considered both the yearly and daily phenology of each species by including as co-variables (i) the date of the observation (calendar day, *Date*) and (ii) the road segment number (used as a proxy of time after sunset, *NumSeg*, Shaw and Galliart, 1992).

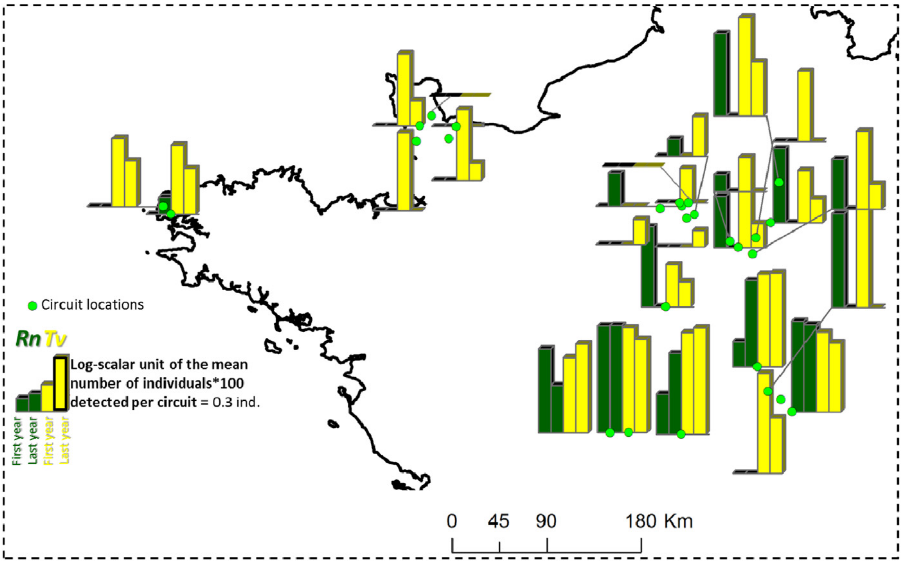

Fig. 3. Log-transformed mean abundances of the two species, Large Conehead (*Ruspolia nitidula*, *Rn*, in green) and Great Green Bush-Cricket (*Tettigonia viridissima*, *Tv*, in yellow), at the first (left bars), and the last year (right bars) of survey for each circuit (light green points) in the region of study. (Previously to log-transformation, the mean abundances were multiplied by a factor 100 in order to facilitate the data visualization at this mapping scale.) (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

2.3. Statistical analyses

To model the annual variations (year effect) in the two species abundances and to determine which environmental variables (climatic, habitat variables and biogeoclimatic position) were the most useful predictors of insect abundances, we used generalized linear mixed modeling (GLMM). According to the nested structure of the study design (segments within circuits), we included a random effect of the circuit identity on the intercept. Because of the overdispersed nature of the abundance data, we used a zero-inflated GLMM method that allows modeling a negative binomial distribution (log link) with zero-inflated data (function 'glmmadmb', package R {glmmADMB}, Fournier et al., 2012; Skaug et al., 2014).

The spatial autocorrelation was handled by including an autocovariate term in the model (i.e. a distance-weighted function of neighboring response values, Dormann et al., 2007, function 'autocov_dist', package R {spdep}, Bivand, 2014). According to the results from exploratory spatial correlograms, the autocovariate term was calibrated on a maximum distance of 100 km (*Ac_100km*), a distance above which the spatial auto-correlation of the abundance data was not significant (Moran's test, package R {ncf}, Bjornstad, 2013). Prior to modeling, we checked multicollinearity in the explanatory variables by calculating variance-inflation factors (VIF) on the full models (Fox and Monette, 1992) and all variables had a satisfactory VIF<2 (Graham, 2003, Appendix S3). We scaled all continuous predictor variables to allow the comparison of their relative effect sizes. As some relationships were expected to be non-linear but unimodal, we introduced the quadratic effect of the following terms: *Date*, *TempSurvey*, *LastSummerTemp*, *SpringRain*, and *BiogeoclimPos*.

Thus, our statistical models were structured in the following way for the two bush-cricket species:

$$\begin{aligned}[\mathit{species\ activity}] \sim\ & \mathit{Year} + \mathit{Date} + \mathit{Date}^2 + \mathit{TempSurvey} + \mathit{TempSurvey}^2 + \mathit{NumSeg} + \mathit{LastSummerTemp} \\ & + \mathit{LastSummerTemp}^2 + \mathit{SpringRain} + \mathit{SpringRain}^2 + \mathit{Urban} + \mathit{SemiNatural} + \mathit{Conif} + \mathit{Decid} \\ & + \mathit{BiogeoclimPos} + \mathit{BiogeoclimPos}^2 + \mathit{Ac\_100km} + 1|\mathit{circuit\ identity}.\end{aligned}$$

Our hypotheses were tested based on the significance and the estimates of the terms according to model outputs. To minimize the number of false discovery (overfitting) due to the large size of the dataset (e.g. Lin et al., 2013), we adopted the conservative significance threshold of 0.01 for the *p*-value evaluation in the models' outputs. All data processing and statistical analyses were performed with the statistical computing software R (R Core Team, 2014).

3. Results

We detected 4976, and 3933 singing individuals belonging to the Great Green Bush-Cricket, and Large Conehead species, respectively (see more details: http://vigienature.mnhn.fr/page/suivi-des-orthopteres-nocturnes-son). The Great Green Bush-Cricket was detected in most circuits (24 out of 27 circuits), whereas the Large Conehead was almost absent in all the West part of the study region and elsewhere showed abundances which collapsed to zero in half of the cases (Fig. 3).

Table 1
Results from the GLMM analyses of the species abundance depending on scaled spatial variables, factors influencing detectability, habitat at the landscape scale, climate variables, and time in terms of years. *BiogeoclimPos* = the biogeoclimatic characteristics of the location of recordings based on the summer mean temperature of the last twenty years, *Ac_100km* = autocovariate, *TempSurvey* = the local temperature at the beginning of the recordings, *Date* = calendar day of the survey (i.e. *n*th day of the year), *NumSeg* = the road segment number used as a proxy of time after sunset, *Urban* = urban area, *SemiNatural* = semi-natural area, *Decid* = deciduous forest, *Conif* = sempervirent forest proportions in a buffer of 200 m radius around the midpoint of each segment, *LastSummerTemp* = the summer (July–August–September) monthly mean temperature. *SpringRain* = the spring (April–May–June) monthly mean precipitation (mm/month).

		T. viridissima				*R. nitidula*			
		Estimate	Std error	*Z* value	*P*-value	Estimate	Std Error	*Z*value	*P*-value
Spatial variations	*BiogeoclimPos*	−0.074	0.107	−0.69	$p = 0.49$	1.597	0.361	4.4	**$p < 0.0001$**
	BioclimPosˆ2	0.106	0.066	1.6	$p = 0.11$	−0.824	0.196	−4.2	**$p < 0.0001$**
	Ac_100km	0.568	0.042	13.6	**$p < 0.0001$**	0.397	0.044	9.0	**$p < 0.0001$**
Factors-detectability	*TempSurvey*	0.410	0.038	10.8	**$p < 0.0001$**	0.131	0.058	2.3	**$p = 0.023$**
	TempSurveyˆ2	−0.028	0.021	−1.3	$p = 0.18$	0.243	0.045	4.6	**$p < 0.0001$**
	Date	0.162	0.030	5.4	**$p < 0.0001$**	2.283	0.106	21.6	**$p < 0.0001$**
	Dateˆ2	−0.565	0.054	−10.5	**$p < 0.0001$**	−1.381	0.095	−14.6	**$p < 0.0001$**
	NumSeg	−0.060	0.025	−2.4	**$p = 0.017$**	−0.032	0.32	−1.0	$p = 0.32$
Habitat	*Urban*	−0.127	0.035	−3.6	**$p = 0.0003$**	−0.164	0.044	−3.7	**$p = 0.0002$**
	SemiNat	0.006	0.033	−0.2	$p = 0.85$	−0.004	0.047	−0.1	$p = 0.94$
	Decid	−0.107	0.032	−3.3	**$p = 0.0008$**	−0.142	0.040	−3.5	**$p = 0.0004$**
	Conif	−0.150	0.051	−3.0	**$p = 0.0030$**	−0.058	0.040	−1.5	$p = 0.14$
Climate	*LastSummerTemp*	−0.032	0.044	0.7	$p = 0.46$	0.093	0.084	1.1	$p = 0.27$
	LastSummerTempˆ2	−0.067	0.024	−2.8	**$p = 0.0051$**	−0.264	0.039	−6.8	**$p < 0.0001$**
	SpringRain	0.062	0.050	1.2	$p = 0.21$	0.003	0.102	0.0	$p = 0.97$
	SpringRain̂2	−0.364	0.034	−10.8	**$p < 0.0001$**	−0.545	0.060	−9.1	**$p < 0.0001$**
Annual variations	*Year*	−0.471	0.045	−10.5	**$p < 0.0001$**	−0.332	0.071	−4.7	**$p < 0.0001$**

As a result of the modeling, we found a significant decrease of abundance for both species across time (Table 1). The Great Green Bush-Cricket was found to decrease by 26.3% per year (22.0%–30.4%; 95% CI) and the Large Conehead by 19.3% per year (11.8%–26.3%; 95% CI).

The abundance detected for the two species significantly varied according to the recording date (Table 1), with an abundance peak on the 8th, and 28th of August for the Great Green Bush-Cricket, and Large Conehead, respectively (Table 2). The detected abundance also increased with the local temperature during recording (Table 1), with an optimum at approximately 16 °C. Note that the Great Green Bush-Cricket activity decreased linearly with time after sunset (segment number: *NumSeg*), while this effect was not detected for the Large Conehead. Inversely, detected abundance of Large Conehead expressed significant variations according to biogeoclimatic conditions whereas Great Green Bush-Cricket did not.

Habitat also strongly affected the abundances, with a significant negative effect of the proportion of urbanized and deciduous covers on the detected abundance of the two species, and of coniferous cover on the Great Green Bush-Cricket detected abundance (Table 1).

In addition, we detected a significant effect of spring and previous summer climatic variables on the species abundances. The relationships with climate variables both showed a bell-shaped quadratic pattern (Table 1), indicating optimal temperatures and precipitation levels for both species within the studied gradients (Table 2). The optimum value of the previous summer temperature was slightly higher for the Large Conehead, while the optimum value of the spring precipitation was slightly higher for the Great Green Bush-Cricket (Table 2).

4. Discussion

4.1. The detection of spatio-temporal trends

Our results showed that the citizen-monitoring program coupled with automatic recognition of orthopteran songs, recorded as digital acoustic data, provided relevant data to assess temporal changes in the abundances of Orthoptera species at a large scale. Our protocol, less time-consuming than classical methods, provided a measure of the relative abundance of the Great Green Bush-Cricket and the Large Conehead and enabled the detection of abundance trends at a larger spatial and temporal scale than previous studies (Jonas and Joern, 2007; Penone et al., 2013a,b). These new acoustic methods proved to be useful to address conservation questions about these two species. We must remain cautious about the relevance of this short-term trend in terms of conservation, yet to our knowledge, these declines of common species went unnoticed by other sources of data, most of which were based on opportunistic presence data.

Our results were also relevant in other contexts: (i) in ecology, as we highlighted species' affinity for different habitats, (ii) in conservation biology, as we showed the negative effects of anthropogenic land uses (Marini et al., 2008; Nufio et al., 2009), (iii) in phenology, as we detected abundance peaks in summer (Logan et al., 2006), and, finally, (iv) in population

Table 2
Optimum values (change of slope) calculated from the quadratic relationships revealed by the GLMM analyses (according to the basic formula: -*estimate of the simple effect*/(2 ∗ *estimate of the quadratic effect*)) linking the abundances of *T. viridissima*, and *R. nitidula* to biogeoclimatic characteristics of the location of recordings based on the summer mean temperature of the last twenty years (*BiogeoclimPos*), to factors that influence detectability: the local temperature at the beginning of the recordings (*TempSurvey*), the date of the recording in calendar format (i.e. *n*th day of the year, *Date*), and to climate variables: the summer (July–August–September) monthly mean temperature (*LastSummerTemp*), and the spring (April–May–June) monthly mean precipitation (*SpringRain*).

		T. viridissima	*R. nitidula*
Spatial variations	*BiogeoclimPos* (°C)	NA[**]	17.9
Factors-detectability	*TempSurvey* (°C)	NA[**]	16.6[*]
	Date (*day number*)	220	240
Climate	*LastSummerTemp* (°C)	16.7	17.3
	SpringRain (mm/month)	63.2	61.2

[*] All quadratic functions, except one, are downward parabolas, thus optimum values show the conditions at which the abundance is maximal.

[**] Quadratic coefficients not significantly different from zero (i.e. fitted response close to a linear one).

dynamics. The protocol detected, for example, an important variability in abundance across the years and the effect of local climatic conditions (especially those of early spring and of the previous summer) on abundance fluctuations. Both variability and fluctuations are well known in Orthoptera dynamics (Jonas and Joern, 2007). More interestingly, our results showed a significant decline of the two species over the 2006–2012 period in northern France. This trend was significant despite strong climatic variations among the years that also drove both species' abundances. This result also appears consistent with the long-term monitoring surveys in grasslands; for instance, Jonas and Joern (2007) found that yearly shifts in Orthoptera species composition (1983–2005) were best explained by local weather events occurring early in the grasshopper life cycles and that the annual mean frequencies of grasshoppers were significantly correlated to the North Atlantic Oscillation (NAO). Our monitoring scheme thus detected large temporal and spatial changes in Orthoptera abundances that could be linked to land use changes (for example in agricultural practices – pesticides –, roadside management), which should deserve attention in future studies on these taxa.

These findings highlight the importance of such schemes because most baseline data for Orthoptera consist of inventories that give poor information on trends, especially for widespread species such as the Great Green Bush-Cricket and the Large Conehead (Joseph et al., 2006). The decrease of Orthoptera abundance over time could be related to recent declines of other common and widespread insects (van Swaay et al., 2006). This decline is, however, surprising for the Large Conehead, which has been reported to expand its range all over Europe (Hathway et al., 2003; HoluSa et al., 2007; Kristin et al., 2007); all reports of range expansion, however, date back to the early 2000s, before our study period. A seven-year period is indeed too short to draw conclusions on species conservation status and possible long-term declines (Mace et al., 2008). Nonetheless, given that we detected significant short-term trends and that we are able to gather a similar amount of data in future years, this study provided good confidence about our ability to detect longer trends that will be more relevant in surveying biodiversity changes and addressing conservation concerns.

This study highlights the particular interest of car transects for Orthoptera monitoring, with thousands of different individuals detected for relatively short duration sampling. Although it was designed for bats (Roche et al., 2011; Penone et al., 2013b), this type of sampling seems even more competitive for Orthoptera monitoring in comparison to more classical pedestrian transects or point counts. It increases both coverage and the number of contacted individuals, particularly for poorly mobile taxa, such as bush-crickets. Moreover, these species emit high frequency sounds over 8 kHz, frequencies at which the masking noise produced by a car engine is negligible. However, sampling from roads can also be biased (Betts et al., 2010); for example housing landscapes can be oversampled (Dickinson et al., 2010), highlighting the need to account for land cover information in data analyses. A good solution would be to couple road surveys, that allow estimating abundance, and static detectors that allow more representative surveys. In addition, another constraint related with citizen-monitoring program is the strong spatial link between the location of sampling sites and the volunteers' place of living for proximity reasons. This may lead to bias in the representativeness of the data or spatial structure, thus coordinators of such schemes must pay attention to the representativeness of habitat sampled and ensure a proper spatial coverage of the sampling.

4.2. *Methodological developments and recommendations*

To our knowledge, this paper describes the first successful attempt to calculate the large-scale temporal trends of insect populations based on automatic identification process. We showed that a simple automatic process followed by a manual check of only a few hundreds of sound files could lead to at best less than 1% error rates on a very large dataset. We chose a conservative approach minimizing the false-positives (detection while the species is absent) which could more likely bias our results than false-negatives (no detection while the species is present) (see Oertli et al., 2005). Indeed, false-positives are mostly due to the detection of the songs of other species, whose activity and abundance may vary differently in time and space, so if these biases in detection had not been minimized, they could have affected the relevance of our results.

Nonetheless, the link we assumed between our counts of singing individuals and the species abundance could have been hindered by variations in detectability that we therefore had to take into account. As expected, the detectability of both species varied significantly according to temperature during the survey, and date (seasonal phenology). Moreover, the detectability of the Great Green Bush-Cricket decreased with time after dusk (*NumSeg*). Hence considering these variations was imperative for analyses of this type of acoustic data.

4.3. Toward more complete monitoring of insects

In the present study, we chose two species for which manual identification is unambiguous, but we anticipate that, once improved, automatic detection of the whole Orthoptera community could be a cost-effective solution that might improve the persistence of the program (Marques et al., 2013). The creation of online worldwide sound databases in general should also be helpful in stimulating acoustic monitoring programs (Riede et al., 2006) in other regions. Coupling Orthoptera programs with other nocturnal species monitorings having similar protocols, such as bats (Roche et al., 2011) or amphibians, could also benefit a rapid and easy set-up of nocturnal Orthoptera monitoring around the world. Automatic detection associated to standardized protocols would produce datasets that could be compared, and used to analyze trends in biodiversity on various spatial and temporal scales. This technology would also both reduce the amount of time spent by volunteers at identifying species and suppress the bias linked to observers. Existing data can even be analyzed in this new way with little effort. Monitoring multiple bush-cricket species would greatly contribute to insect conservation by building indicators in addition to the most well-known ones (butterflies, pollinators), notably because of their relatively high trophic level, and their broad ecological amplitude. Therefore, building large-scale monitoring schemes for this group coupled with automatic detection should significantly improve our understanding and the predictability of the future fate of the largest biodiversity components.

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Appendix A. Supplementary data

Supplementary material related to this article can be found online at http://dx.doi.org/10.1016/j.gecco.2016.02.008.

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