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Urbanisation effect on Orthoptera: which scale matters?

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Abstract. 1. The characteristics of communities are determined by dispersal processes that are driven by landscape structure and species characteristics (traits). Understanding these processes requires a better assessment of the spatial scales that matter to species, based on their traits. This can be particularly addressed in an urban context where habitats are highly fragmented.

2. We assessed the effects of urbanisation intensity on Orthoptera at different spatial scales and focused on two species traits: dispersal ability and habitat specialisation.

3. We recorded Tettigoniidae sounds from running trains along 209 km of five railway lines. As an urbanisation measure, the percentage of impervious surfaces around the railway edges was calculated at 11 spatial scales around the railways. We then tested the effect of urbanisation on species richness, abundance, and traits and determined at which spatial scale the relationship was strongest.

4. Urbanisation had a negative effect on total species richness, abundance and community specialisation. This pattern was stronger at larger spatial scales, and the results differed according to the species' functional traits: mobile species were more sensitive to urbanisation at larger scales than sedentary species, and no scale effect on specialisation was detected.

5. We conclude that insects may respond to landscapes over a broad set of spatial scales and that considering their specific traits is essential in spatial scales studies. Finally, we argue that railway edges can play a role in insect conservation in urban landscapes.

Key words. acoustic, biotic homogenisation, dispersal ability, functional trait, metacommunity, mobility, railways, sound, specialisation, transportation.

Introduction

Spatial processes have a strong influence on the structure and dynamics of populations and communities (Hanski, 1999; Cottenie, 2005). Indeed, composition and richness of communities and abundance of species are partly affected by immigration and dispersal processes (Dunning et al., 1992) that are driven by the landscape structure

at different spatial scales (or area-sensitivity Desrochers et al., 2010) also depend on species characteristics such as habitat preference, dispersal abilities and degree of specialisation (Tscharntke et al., 2002; Marini et al., 2012). It has been suggested that mobile species are more influenced by landscape composition on a larger scale than are sedentary species (With & Crist, 1995); similarly generalist species are more influenced by the amount of habitat on a larger scale than are specialist species. However, very few studies

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2012 The Royal Entomological Society and, in particular, by the amount (quality and area) of available habitat in the surroundings (Desrochers et al., 2010). However, the processes that result in different relationships with landscape

319 have tested these relationships (Morris, 1996). Furthermore, the scale effect on species abundance and richness is seldom considered despite its importance for assessing the sensitivity of organisms to landscapes (Chust et al., 2004; Desrochers et al., 2010). Comparison of scale effects on species according to their traits may thus be informative for the assessment of mechanisms underlying biodiversity trends. In addition, comparisons can

also inform decisions to either favour high-quality localised green areas (local scale) or to globally increase the amount of green area at a larger scale (Thomas et al., 2001).

Assessing scale effects on species richness and abundances is particularly useful in the context of habitat fragmentation and degradation (Donovan & Lamberson, 2001). Those processes are largely linked to the intensification of urbanisation. Nevertheless, until now only few studies have assessed the influence of urbanisation on populations or communities at different spatial scales (Hostetler & Holling, 2000). In an urban context, landscapes are predominantly impervious (built and paved) and habitat patches are often small, fragmented and located in a heterogeneous matrix (Irwin & Bockstael, 2007). As a consequence, urbanisation leads to a decrease of overall species abundance and richness and to a biotic homogenisation of communities (Clergeau et al., 2006; Devictor et al., 2007). This results from the fact that many species (losers) are more impacted than others (winners) due to their specific characteristics (McKinney, 2006). Losers include habitat specialists and sedentary species, which have both been shown to be more affected by urbanisation than either generalists or mobile species (e.g. for birds Devictor et al., 2007; Møller, 2009).

Urbanisation effects on arthropod communities in particular have rarely been assessed (McIntyre, 2000; Niemelä & Kotze, 2009), however, different authors (McIntyre, 2000; Hunter & Hunter, 2008) have expressed great interest in studying these taxa to understand how they are affected and to improve conservation efforts in urban contexts. The main limitation to insect studies is identification since there is a lack of taxonomy experts and identification by non-specialists is often uncertain, especially for certain groups (Diniz-Filho et al., 2010). Therefore, the detection of acoustic signals (Blumstein et al., 2011) such as singing Tettigoniidae (Orthoptera) ultrasounds, appears to be a promising way to study arthropods better because it allows automatic records collection (and even identification) and is a non-destructive method. Orthoptera have been included in analyses of local and landscape factors (Stoner & Joern, 2004; Bata´ry et al., 2007; Marini et al., 2008), but they have received very little attention in both spatial scale and urbanisation studies (but see Marini et al., 2008; Nufio et al., 2009; Didham et al., 2010).

In this study, we examined the effect of scale on the relationships between singing Tettigoniidae and urbanisation, considering richness, abundance, dispersal abilities and specialisation. We focused on railway edges, which are ideal settings to study the effects of urbanisation because of they are part of linear vegetation patches that penetrate into dense urban areas. In addition, railway edges have potential as areas for biodiversity conservation, yet they have been seldom been considered as such (Eversham et al., 1996; Tikka et al., 2001). These edges could provide a habitat for Orthoptera because the majority of Orthopteras are open land species and some occur at roadsides (Theuerkauf & Rouys, 2006).

We thus expected that (i) Tettigoniidae's richness and abundance decrease with an increasing percentage of urbanisation, (ii) the strength of this relationship varies

according to the spatial scale considered, and (iii) the strength of this relationship differs among species according to their dispersal abilities and their habitat specialisation: generalists and mobile species should be more sensitive to urbanisation at larger scales than specialists and sedentary species.

Methods

Data collection

Because Orthoptera produce mating calls (Ragge & Reynolds, 1998), it is possible to collect large standardised data sets using recording devices. Orthopteras' calling song has a role in pre-mating isolation, and its structure is an important component to their mate recognition system (Paterson, 1985). Therefore, the analysis of calling songs may allow identification to the species level (Ragge & Reynolds, 1998) and even give reliable information on species abundances (Fischer et al., 1997). Nevertheless, it does not give an exact estimation of species abundances mainly because only adult males stridulate. However, this method can provide relative measures of abundance (rather than absolute abundance), which is adequate to detect spatial changes in species abundances. Acoustic recording has also an interest because it is a remote, non-destructive way to collect a large amount of data (Riede, 1998).

To examine the impact of urbanisation, we recorded Orthoptera sounds in 2010 (August 3rd to 13th) along 209 km of five railway lines (41 ± 3 SD km) in the Parisian region, France (see figure F1 in Supporting Information Data S1). Sounds were continuously recorded on a Zoom H2 digital recorder (Samson) at a sampling rate of 96 ks s⁻¹ from the high frequency output of a bat detector (Tranquility Transect; Courtpan Design Ltd, Cheltenham, UK). To obtain large data sets, and sample a large number of landscapes, surveys were conducted from running trains (see Supporting Information DataS1 for more details). In addition, railways are well adapted to study urbanisation effects because they often go through urban gradients. We focused on insects that produced powerful stridulations with frequencies above 10 kHz, which were not masked by the noise produced by trains. However, species with such characteristics, for example Tettigoniidae's species, are most active around dusk. Therefore, recordings started in the early evening (between 31 and 74 min after dusk, mean 53 min \pm 10 SD). All recordings took place during dry nights with wind speeds lower than 10 km h⁻¹ and temperatures around 18°C (\pm 0.89 SD). The average train speed was 76.5 (\pm 31 SD) km h⁻¹.

The sonograms were analysed using Syrinx, a program designed for research in animal acoustic communication (Burt, 2006). Each insect was identified at the species level and geo-located along a railway line using time and speed parameters. In many cases, it was not possible to discriminate between *Phaneroptera nana* and *P. falcata* stridulations, so we pooled the songs from both species. These two species are known to share quite similar ecological niches (Koc´arek et al., 2008).

Landscape analysis

For data analysis, railway lines were subdivided in 400-m segments using GIS (ARCGIS 9.3; ESRI, Redlands, CA, USA), similarly to other studies done on linear features (Grilo et al., 2009). All Tettigoniidae detected along a segment were allocated to the coordinates of its central point. We obtained a total of 501 segments. For each segment, we collected the following data: train speed, time elapsed after dusk (in minutes), type of railway verge (i.e. vegetated or paved railway verge at most 10 m in width) and the amount of urbanisation at different landscape scales. We considered that the type of verge was vegetated when more than half of the segment was vegetated. To measure the extent of urbanisation at different landscape scales, we built 11 circular buffers around the centre of each segment, and the radii varied between 200 and 3200 m (200, 300, 400, 600, 800, 1200, 1600, 2000, 2400, 2800 and 3200 m) to account for potential large-scale effects (Reinhardt et al., 2005). For each of these 11 nested spatial scales, the percentage of the area covered with impervious surfaces (i.e. without vegetation) was quantified using the Normalised Difference Vegetation Index calculated on Landsat 7 – Thematic Mapper at a 15-m resolution (IAURIF, 2000). Similarly to Zhou et al. (2004), we considered this a measure of urbanisation intensity.

Species traits

Each species was characterised for dispersal ability according to Reinhardt et al. (2005) and Marini et al. (2010) and for habitat specialisation through the calculation of a Species Specialisation Index (SSI) following the Julliard approach (Julliard et al., 2006). To define habitat specialisation, we used an independent data set provided by the national biodiversity monitoring scheme coordinated by the French National Museum of Natural History (<http://vigienature.mnhn.fr/>; for more details on the data set used see Supporting Information DataS2). The SSI was calculated for each species using the coefficient of variation of the species' abundance across habitats. Because SSI is expected to be biased by low sample sizes, we calculated corrected SSI values (see Supporting Information DataS2). The SSI varied between 0.27 and 1.42 for the more specialised species (Table 1). The SSI value for *Phaneroptera* spp. was the mean SSI of the two *Phaneroptera* species.

The Community Specialisation Index (CSI) for each segment was calculated as the average SSI of the species detected, weighted by local species abundance, as follows:

$$CSI_j = \frac{1}{n} \sum_{i=1}^n a_{ij} SSI_i$$

where n is the total number of species recorded and a_{ij} is the abundance of individuals of species i (with a SSI_i specialisation index) in segment j (Devictor et al., 2008a). The CSI reflects the relative abundance of more or less specialised species in local

assemblages and is therefore expected to decrease following the relative declines of specialists (species with a high SSI). For the analyses, we kept only the segments with a non-null abundance ($n = 331$, i.e. 66% of the data set) because a null CSI does not describe a generalist community.

Statistical analyses

The response variables were (i) total species richness, (ii) total abundance and (iii) CSI per segment. We also made separate abundance analyses for the most frequent species, that is species detected in more than 50 segments. We conducted analyses for species dispersal abilities by summing, on the one hand, the abundances of mobile species, and on the other hand, the abundances of sedentary species. Only one species had an intermediate dispersal ability (*P. albopunctata*); this species was removed from the analyses on this trait.

We first used generalised additive model plots (Hastie and Tibshirani (1990), R package *mgcv*) to detect potential non-linear relationships. Then, using a type II analysis of variance for general linear models (GLMs) with a negative binomial distribution (to account for overdispersion following the approaches by Faraway (2006) and Crawley Table 1. Species abundance and traits.

Species name	Dispersal ability*	SSI	n
<i>Tettigonia viridissima</i>	Mobile	0.42	894
<i>Leptophyes punctatissima</i>	Sedentary	0.55	378
<i>Phaneroptera nana</i>	Mobile	0.27	239
<i>Phaneroptera falcata</i>	Mobile	0.27	239
<i>Ruspolia nitidula</i>	Mobile	0.52	252
<i>Pholidoptera griseoptera</i>	Sedentary	0.91	198
<i>Platycleis albopunctata</i>	Intermediate	0.49	21
<i>Conocephalus fuscus</i>	Mobile	0.84	10
<i>Conocephalus dorsalis</i>	Sedentary	NA	8
<i>Platycleis tessellata</i>	Sedentary	1.42	3

SSI, Species Specialisation Index.

*According to (Reinhardt et al., 2005) and (Marini et al., 2010).

(2009)), we tested the effects of the following predictor variables: train speed, time elapsed after dusk, type of railway verge (hereafter referred to as 'first analysis'), taking also into account a potential effect of the recording date. In addition, we included the quadratic effect of train speed to model the non-linear relationships between train speed and species richness and abundance (see figure F2, Supporting Information DataS3). Given the spatial structure of our sampling design, we took into account spatial autocorrelation by adding an autocovariate to our models (Dormann et al., 2007) using the `autocov_dist` function in R (package *spdep*). We then visually checked the absence of unexplained spatial autocorrelation in examining the variograms of model residuals. Note that for CSI, we used analysis of variance for GLMs assuming a normal distribution. We evaluated the multi-collinearity in the explanatory variables by calculating variance inflation factors (function `VIF` in R package *car*) on the full models. According to (Heiberger &

Holland, 2004) as all variables showed a VIF value <5 there was no striking evidence of collinearity.

In a second step, taking into account the effects of the previous covariables, we tested the effects of urbanisation intensity (hereafter referred to as ‘urbanisation analysis’). We performed this analysis on the 200-m buffer areas including all the subsets (because the 200-m buffers did not overlap; see figure F3, Supporting Information DataS1). Because the segments were close to each other, buffers larger than 200 m overlapped. To ensure data independence, we partitioned the data set into 16 subsets containing distinct segments for which the largest buffers (3200-m) did not overlap (i.e. 31 or 32 segments per subset). Then for each of these 16 independent subsets, we ran the analyses separately for each buffer size and examined the effect of the proportion of urban surfaces within a buffer on species abundances, richness and CSI (hereafter referred to as ‘subset urbanisation analysis’) (for more details, see figure F3 Supporting Information DataS1). In total, we thus ran 176 models (11 buffers 9 16 subsets). Whatever the buffer radius used, the buffers centres were the same because our aim was to examine the scale effect. We also examined how the proportion of urban surfaces was distributed within the buffers at each spatial scale.

Finally, we tested whether the slope of the relationship between the dependant variable (abundance, richness, CSI) and the proportion of urban surfaces changed with scale; we tested the effect of buffer size on estimates from previous models using a GLM with a normal error structure because the response variable was normally distributed (hereafter referred to as ‘scale analysis’). We gave to the response variable (i.e. estimate of slope) different weights according to their associated standard error (1 per SE²) obtained from the previous analysis (subset urbanisation analysis). Following Schmidt et al. (2008) and Desrochers et al. (2010), we considered that a stronger estimate (either positive or negative) corresponded to the most relevant spatial scale to explain species distribution. All analyses were conducted using R version 2.10.1 (R Development Core Team, 2009).

Results

We detected 2003 individuals belonging to 10 species of bush-crickets from the Tettigoniidae family along 209 km of railway edges. This represented 59% of Tettigoniidae species known to exist in the region (n = 17) (Voisin, 2003). Five species (or species groups) were found in more than 100 segments and each of them represented more than 10% of all individuals detected: *Tettigonia viridissima*, *Leptophyes punctatissima*, *Phaneroptera* spp. (*Phaneroptera nana* and *Phaneroptera falcata*), *Ruspolia nitidula* and *Pholidoptera griseoaptera* (see Table 1). Species richness per segment varied between 0 and 6 (mean 1.47 ± 1.41), and total abundance varied between 0 and 28 (mean 3.44 ± 4.60). The percent of urban surfaces varied among buffers across all scales from 0 to 95.38 (mean 17.85 ± 19.69).

In the first analysis, we found that the type of railway verge had a significant effect on total species richness, abundance and

species traits (see Table 2). However, the distribution patterns were not identical for all species: with the exception of *R. nitidula*, species were more abundant at vegetated railway edges than at paved ones. The CSI was also higher (i.e. specialists were relatively more abundant) in segments with vegetated verges. The time elapsed after dusk had a significant negative effect on species richness, abundances and species traits, except for *R. nitidula*. The data were best explained by models that included a quadratic effect of train speed. This effect (described by a humpbacked curve) was significant for all response variables except for *R. nitidula*, *Phaneroptera* sp. and for mobile species abundance (see Supporting Information DataS3: table T1, figures F1–F3).

Table 2. The effect of railway verge type (here vegetated) on total species abundance, richness and species abundances.

	Vegetated railway verges			
	Estimate	SE	v^2_8	P (ANOVA)
Total abundance	0.62	0.01	18.8	<0.001
Species richness	0.41	0.01	12.0	<0.001
Species abundances <i>Tettigonia</i>				
<i>viridissima</i>	0.64	0.01	12.8	<0.001
<i>Leptophyes punctatissima</i>	0.60	0.03	6.2	0.017
<i>Phaneroptera</i> spp.	0.59	0.03	5.6	0.019
<i>Ruspolia nitidula</i>	0.35	0.03	1.5	0.228
<i>Pholidoptera griseoaptera</i>	1.21	0.04	8.1	0.005
Trait abundances				
Mobile species	0.57	0.01	14.6	<0.001
Sedentary species	0.80	0.02	13.5	<0.001
Specialisation				
CSI	0.07	0.02	25.5	0.008

CSI, Community Specialisation Index.

Urbanisation

We found a negative correlation between species richness and abundance and urbanisation intensity. The analyses for the 200-m buffer area (including all the subsets) revealed negative estimates for all response variables, including dispersal abilities and CSI (see Table 3). These results were confirmed by the analysis of subsets; for each response variable, we obtained 176 estimates, most of which were negative (see table T2 in Supporting Information DataS3), and the majority of significant relationships were negative.

Spatial scales

The strength of relationships with urbanisation increased significantly with scale for total abundance ($F_{1,174} = 15.1$, $P < 0.001$), richness ($F_{1,174} = 15.9$, $P < 0.001$), for two individual species [*T. viridissima* ($F_{1,174} = 11.3$, $P < 0.001$) and *R. nitidula* ($F_{1,174} = 13.5$, $P < 0.001$)], and for mobile species as a group ($F_{1,174} = 10.9$, $P = 0.001$). Indeed, this relationship became more negative with increasing scale.

For the three other species [*L. punctatissima* ($F_{1,174} = 1.1$, $P = 0.39$), *Phaneroptera* spp. ($F_{1,174} = 1.5$, $P = 0.21$) and *P. griseoptera* ($F_{1,174} = 0.9$, $P = 0.33$)], for the CSI ($F_{1,174} = 1.8$, $P = 0.18$) and for sedentary species ($F_{1,174} = 0.1$, $P = 0.12$) the relationships with urbanisation were similar at all spatial scales (see Fig. 1). The proportion of urban surfaces was not similarly distributed within buffer areas across all spatial scales (see figures F5 and F6 in Supporting Information DataS3). Indeed, at small scales there were more buffers that had a high proportion of urban surfaces than at larger scales. Due to this artefact, the relationships between species richness, abundance and proportion of urban surfaces were expected to be stronger at smaller scales. These relationships reinforce our results because they are likely to be attenuated by this artefact (because we found the opposite pattern). Moreover, scale dependency was not an artefact of statistical power because we had the same number of buffers in each subset and the same number of subsets for each scale.

Discussion

Table 3. The effect of urban surfaces on total species abundance, richness and species abundances, adjusted for the vegetated railway verges (200 m buffer – all subsets).

	Urbanisation			
	Estimate	SE	v^2_9	$P_{(ANOVA)}$
Total abundance		0.002	49.4	<0.001
Species richness	0.019	0.002	35.3	<0.001
Species abundances	0.014			
<i>Tettigonia viridissima</i>	0.021	0.004	34.1	<0.001
<i>Leptophyes punctatissima</i>	0.024	0.005	22.2	<0.001
<i>Phaneroptera</i> spp.		0.004	6.5	0.012
<i>Ruspolia nitidula</i>	0.011	0.007	26.7	<0.001
<i>Pholidoptera griseoptera</i>	0.032	0.009	11.6	0.002
Trait abundances	0.028			
Mobile species	0.020	0.003	45.6	<0.001
Sedentary species	0.021	0.004	24.5	<0.001
Specialisation				
CSI	0.032	0.005	24.8	<0.001

CSI, Community Specialisation Index.

Urbanisation

Overall species abundance, richness and the average specialisation of community were negatively influenced by urbanisation at every spatial scale. Because the first analysis highlighted a strong positive effect of vegetated railway verges on Orthoptera, urban surfaces (thus loss of habitat) could be a major component in the negative urban effect found in the urbanisation analysis. Hence, the presence and abundance of these insects has been shown to be linked to local factors and in particular to vegetation parameters, even for species that are not strictly herbivorous (Strauss & Biedermann, 2006). In fact, this urbanisation measure is likely coupled to other urban effects that affect biotic communities such as fragmentation, human presence, and abiotic conditions including temperature, moisture, edaphic factors and pollution (McDonnell et al., 1997). However, different species showed contrasting responses to urbanisation with respect to both the direction and the significance of the relationships. Three species (*T. viridissima*, *L. punctatissima* and *R. nitidula*) were negatively related to urbanisation in most of our data subsets, whereas two others (*Phaneroptera* spp. and

P. griseoptera) had more contrasting responses. For the second group of species, this may reflect a particular tolerance to urban contexts that include the presence of impervious or paved surfaces. However, to our knowledge this topic has not been considered in previous studies.

Consistent with our predictions, we found a negative relationship between urbanisation and Tettigoniidae community specialisation. Interestingly, this was not expected to be due to the decrease of both species richness and abundance per se. This pattern is likely linked to the more pronounced decrease of specialist species (losers) than of generalist species (winners). Our analysis was done with only eight species and would deserve to be performed with more species. However, our findings are consistent with recent studies on other taxonomic group (bird, butterfly) that showed that specialists (species with restricted niche breadth) are more negatively affected than generalists (Julliard et al., 2004) by anthropogenic disturbances such as fragmentation (Devictor et al., 2008b), intensifying land use in agricultural landscape (Ekroos et al., 2010), and also urbanisation (Devictor et al., 2007). Our results confirmed that this process affects taxa at different trophic levels.

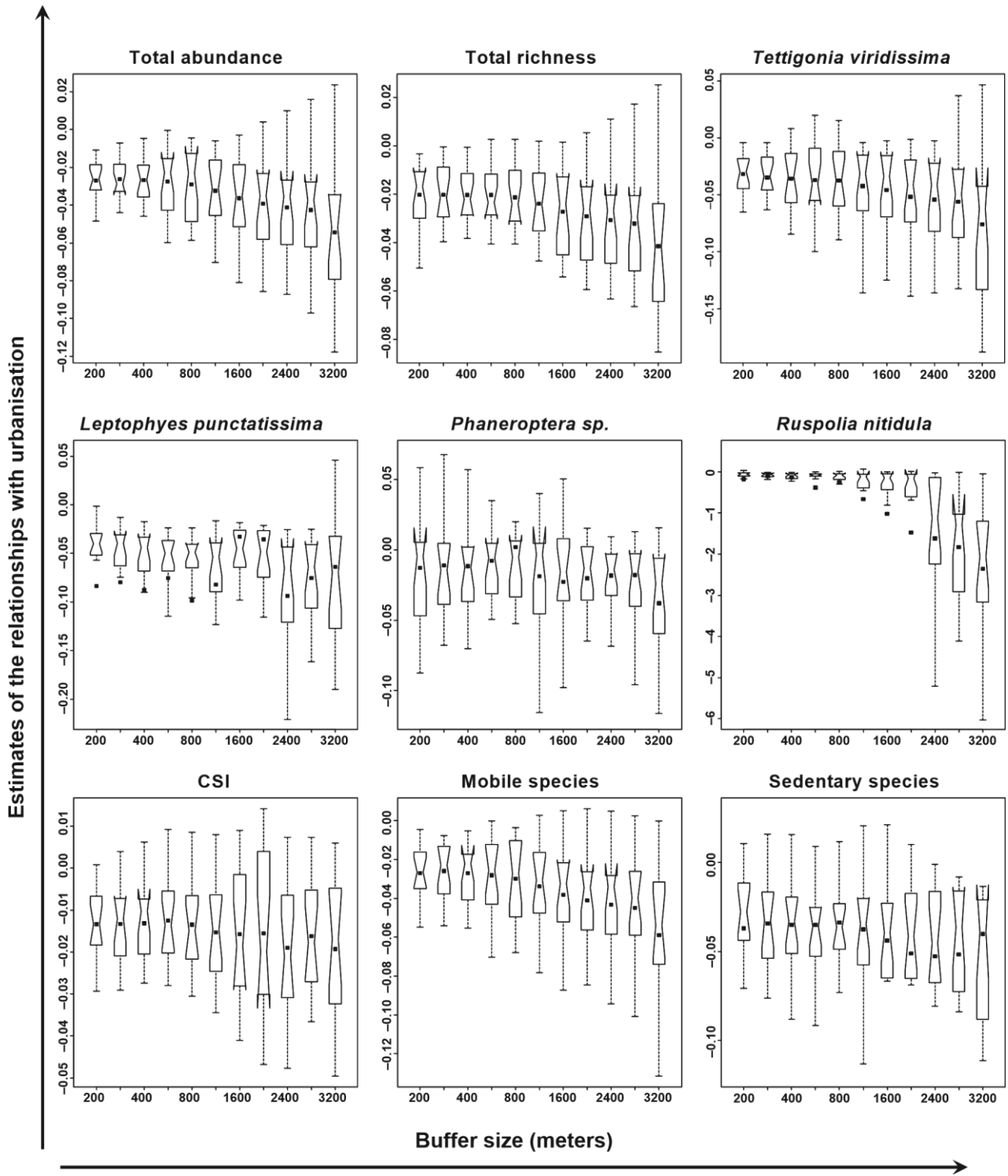


Fig. 1. Orthoptera relationships with urbanisation at different spatial scales. X-axis: size of the buffer in which the percentage of the area covered with urban surfaces was calculated; Y-axis: estimates of the relationships between urbanisation and total abundance, total richness, abundance of the four main species, community specialisation and abundance of mobile and sedentary species (taken from the ‘subset urbanisation’ analysis). Each point for each buffer size indicates the mean of the 16 estimates (one estimate per subset) of the models. Notches extend to $\pm 1.58 \text{ IQR} / \sqrt{n}$ such as defined by Chambers et al. (1983). Note that because most of the relationships between the response variables and urbanisation were negative, the more negative relationships are the strongest ones. See also figure F4 in Supporting Information DataS3.

Spatial scales

Although urbanisation had a negative effect on singing Tettigoniidae at all spatial scales, surprisingly the largescale landscape had a tendency to more strongly influence taxa distribution than the immediate surrounding one. This was not particularly expected for invertebrates and is often difficult to highlight due to buffer overlapping in many studies (Strauss & Biedermann, 2006). Species richness and abundance in urban patches have been shown to be partly determined by local conditions and small-scale habitat selection, which depend on habitat quality (e.g. food availability, microclimate and competition) (Desrochers et al., 2010; Chisholm et al., 2011) and affect species' reproduction and survival. Species richness and abundance in habitat patches are also determined by immigration, emigration and habitat selection at large scales, which are linked to metapopulation and metacommunity dynamics and to species dispersal abilities (Clobert et al., 2009; Logue et al., 2011). Thus, the fact that landscape measured at large scale was a better predictor of species distribution may be explained by two assumptions. (i) Orthoptera may be more sensitive to large-scale urbanisation effects (urban heat island, pollution, noise, human presence) than to the local presence of urban features. (ii) These species may disperse over large distances. The species we studied revealed different degrees of dependence to landscape scale effects. Our results suggested that all mobile species were sensitive to large-scale effects, in contrast to sedentary species, for which we did not detect any scale effect. Even if these results should be considered cautiously because they are only based on eight species (four mobile and four sedentary), they are not surprising because the dynamics of mobile species are known to be driven not only by local dynamics but also by recolonisation processes (Hanski, 1998). Therefore, we are confident with our findings, that are, in addition, consistent with previous studies on birds as well as individual insect species (With & Crist, 1995; Desrochers et al., 2010). Interestingly, this is, to our knowledge, the first time that such pattern has been highlighted for several Orthoptera species.

We did not find any difference between the spatial-scale effects on specialists and generalists (i.e. no scale effect on CSI). In fact, few studies have examined the link between specialisation and spatial scales; in rodents, generalist species have been shown to be less affected at fine scales, likely because they are able to exploit many different habitats, unlike specialists (Morris, 1996). In this study, we did not take into consideration the amount of species focal habitat, but rather, we considered non-target habitats (urbanisation, i.e. impervious surfaces) that represent a negative value of all the potential favourable habitats for Orthoptera. Using a measure for urbanisation intensity, we were able to detect a decrease in community specialisation, but because we did not account for target habitats, we were unable to detect the use of many different habitats by generalists. Multiple habitat use by generalists has been proposed as an explanation for the

difference in scale responses between generalists and specialists (Morris, 1996).

Conclusions and implications for management and conservation

We highlighted the negative relationship between urbanisation and insect species abundance, richness and species traits not only at the landscape scale but also at smaller spatial scales. Interestingly, vegetated verges had a strong positive effect on most species. Hence, small-scale revegetation processes, either artificial or natural, coupled with extensive management, may help counteract the negative large-scale effects of urbanisation.

We also underscored the potential interest of using acoustic surveys to generate large data sets on insects for comparative approaches with relatively little effort. These large data sets address previous claims about the lack of standardised methods to produce comparable data across studies (Gardiner et al., 2005). Expected biological effects were detectable using our study design. For example, species' response to time elapsed after dusk is likely linked to temperature decline, and this has already been described by other authors (Franklin et al., 2009). Although our approach did not exhaustively sample Orthoptera species due to the fact that our criteria excluded species with calls under 10 kHz (e.g. grasshoppers and crickets), one of our objectives was to examine relative species abundances and highlight biological patterns (e.g. the negative effect of urbanisation on habitat specialisation). We believe that this rather simple and cost-efficient sampling method could be of interest for standardising long-term and large-scale surveys, in particular, for the monitoring of singing Tettigoniidae.

We also highlighted the importance of considering, when data are available, species traits, (especially dispersal abilities) in spatial scale studies, to understand the mechanisms underlying species responses. In our study trait calculation was based on few species, this approach would be certainly more efficient if founded on more species. Assessing these traits could be useful for conservation planning at the landscape scale by identifying the most critical habitat patches and the distances between patches while maintaining connectivity (Pascual-Hortal & Saura, 2007; Marini et al., 2012).

Finally, our results suggested that railway edges could provide habitats for singing Tettigoniidae and, interestingly, even for specialist species that are more heavily affected by anthropogenic changes. Thus, if extensively managed (Marini et al., 2008), these structures could play a role in the conservation of ordinary biodiversity in urban areas. Moreover, in the context of climate changes, where insect species tend to expand northwards (Hickling et al., 2006), it would be interesting to understand if railways could play a corridor role for Orthoptera, allowing them to cross highly urbanised landscapes. This would be of interest in densely urbanised regions such as the one we studied here.

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Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: doi: 10.1111/j.1752-4598.2012.00217.x:

Data S1. Railway lines map and details on raw data.

Data S2. Dataset used for SSI calculation.

Data S3. Supplementary results.

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