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Management is more important than urban landscape parameters in shaping orthopteran assemblages across green infrastructure in a metropole

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Abstract

Urbanisation significantly shapes species abundance, diversity, and community structure of invertebrate taxa but the impact on orthoptera remains widely understudied. We investigated the combined effects of spatial, urban landscape and management-related parameters. Additionally, we discussed different sampling strategies. We sampled orthopteran assemblages on green infrastructure associated with the public transport system of Vienna, Austria. Sampled areas include railroad embankments, recreational areas or fallows. Using LMs, (G)LMMs and nMDS, we compared quantitative sampling using transect counts and semi-quantitative sampling which also included observations made off-transects. We found that vegetation type was the most important parameter, whereby structure-rich fallows featured highest species diversities and, together with extensive meadows, highest abundances, while intensive lawns were less suitable habitats. The semi-quantitative data set revealed an underlying species-area-relationship (SAR). Other important but highly entangled parameters were the mowing intensity, vegetational heterogeneity and cover of built-up area in a 250 m radius. Most found species have high dispersal abilities. Urban assemblages are most significantly shaped by management-related parameters on the site itself, which highlights the potential of conservation efforts in urban areas through suitable management. Sites of different vegetation types differ greatly and need adjusted management measures. Urban landscape parameters, such as the degree of soil sealing, appeared less important, likely due to the high dispersal abilities of most observed orthoptera species. The indicated species-area-relationship could be used to prioritize sites for conservation measures.

Keywords Diversity · Invertebrates · Conservation · Urbanisation · Green infrastructure · Species-area-relationship · Public transport

Introduction

Urbanisation is a major concern in biodiversity research (Miller and Hobbs 2002; McKinney 2002) and comes along with climate change, habitat destruction, invasive species, nutrient loading and pollution, as well as overexploitation (Puppim de Oliveira et al. 2011) as the main drivers of worldwide biodiversity loss (Millennium Ecosystem Assessment 2005; Secretariat of the Convention on Biological Diversity 2006). While 55% of the global human population is living in urban surroundings today, by 2050 approximately 70% are projected to be urban dwelling (Grimm et al. 2008; Roberts 2011; United Nations 2019). Thus, it is very likely that global biodiversity will be even more threatened by urbanisation in the future (Seto et al. 2012). Urbanisation is causing regional extinctions of native species (Czech et al. 2000) and severely affects species richness, species composition and presence of specialists of various invertebrate species such as ants (Egerer et al. 2017; Melliger et al. 2018), wild bees (Matteson et al. 2008; Hernandez et al. 2009; Fortel et al. 2014; Egerer et al. 2017; Cardoso and Gonçalves 2018), butterflies (Blair and Launer 1997; Clark et al. 2007; Lizée et al. 2011; Ramírez-Restrepo and MacGregor-Fors 2017), carabid beetles (Niemelä et al. 2002; Venn et al. 2003) or spiders (Magura et al. 2010; Egerer et al. 2017; Melliger et al. 2018). Gathering detailed knowledge on how urbanisation affects biodiversity is therefore

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a pre-requisite for effective species conservation in urban environments (McKinney 2002).

Research on the impact of urbanisation on orthopteran species, such as katydids, crickets and grasshoppers, parallel the general trends found in birds and other insect species (Blair and Launer 1997; Clark et al. 2007; Hernandez et al. 2009; Fortel et al. 2014; Van Nuland and Whitlow 2014; Concepción et al. 2016; Ramírez-Restrepo and MacGregor-Fors 2017; Piano et al. 2019). Urbanisation can lead to decreasing species richness (Heß 2001; Marini et al. 2008; Penone et al. 2013; Cherrill 2015; Melliger et al. 2017; Glaw and Hawlitschek 2018; Piano et al. 2019) and abundance (Heß 2001; Penone et al. 2013; Glaw and Hawlitschek 2018; Piano et al. 2019). Additionally, it affects species composition and guild structure in a way that strongly urbanised areas are more homogenised (Piano et al. 2019), feature less large carnivorous species (Hironaka and Koike 2013) and more xerothermophilous species (Heß 2001), as well as more generalists than specialists (Heß 2001; Penone et al. 2013).

Nevertheless, the overall amount of published research on this topic is, at least compared to popular insect groups like wild bees or butterflies, remarkably limited. One reason for these limitations might be that orthoptera react sensitively not only to a single, but to a long series of environmental parameters. Orthoptera in general are known to respond significantly to intensified management, which is associated with decreases in species richness and abundance (Batáry et al. 2007; Braschler et al. 2009; Marini et al. 2009; Humbert et al. 2012), although not all studies confirmed a decline in abundance (Chisté et al. 2016). At the same time, completely refraining from management measures can cause declines in species richness and abundance as well (Kolshorn and Greven 1995; Kenyeres and Szentirmai 2017). Moreover, detrimental effects of habitat fragmentation and isolation on orthopteran abundances were reported (Herrmann 1995; Sachteleben et al. 2007; Cherrill 2010; Zulka et al. 2014). Several studies postulated the underlying presence of species-area-relationships (SARs) for orthoptera (Collinge 2000; Sachteleben et al. 2007; Nufio et al. 2009; Marini et al. 2010; Melliger et al. 2017), but others could not confirm a SAR within man-made habitats (Heß 2001). An increase in orthopteran species might result from an increase in available habitat types (Herrmann 1995), which is indeed known to influence orthopteran diversity (Marini et al. 2010; Schirmel et al. 2010; Essl and Dirnböck 2012). Other postulated factors are plant species diversity (Essl et al. 2013), structural diversity (Herrmann 1995), aridity and/or precipitation (Steck et al. 2007; Lengyel et al. 2016), elevation (Fournier et al. 2017), soil composition (Fournier et al. 2017), continuity in land use (Steck et al. 2007) as well as the land cover types in surrounding areas (Herrmann 1995; Marini et al. 2008).

In consequence, it might be possible that changes in the factors mentioned above, which can be associated with urbanisation, overlay pure urbanisation effects. For example, Cherrill (2010) did not find a significant relationship between species richness and urbanisation, but a strong impact of agricultural intensification. In a later study of the same author, it was advised to characterise urbanisation by the remaining potential habitat matrix rather than by the uninhabitable environment (Cherrill 2015). Furthermore, sampling effort increases around human settlements due to the higher number of resident experts on orthopteran diversity, which leads to more frequent records of orthopteran species in areas with a dense human population (Cantarello et al. 2010).

In short, the relatively small number of studies on urban orthoptera diversity, compared to the high amount of other potential parameters, might cause severe gaps in the understanding of the underlying ecological patterns. To study orthopteran assemblages of urban green infrastructure, we sampled along several traffic lines within the European metropole Vienna (Austria). This provided a unique sampling design, as it included sampling on areas which are not open to the public and were not investigated before. As management-related parameters, we recorded the local vegetation type, mowing intensity and vegetation heterogeneity. To account for species-area-relationships, the patch area was included. To measure the local degree of urbanisation, we measured the amount of built area and green area in a 250 m radius, located around the centre of the sampling site.

By incorporating management-related, spatial and urban landscape parameters, we intended to disentangle and quantify their effects on orthopteran diversity and provide a framework for future conservation measures in urban surroundings. Additionally, we used two separate data sets. One data set was sampled in a strictly quantitative way, based on standardised transects. For the other one, quantitative data was complemented with spontaneous observations of less abundant orthopteran species that could not be observed along transects and during the standardized sampling period. Thus, our additional aim was to shed light on how different sampling approaches (quantitative vs. semi-quantitative) affect the significance of parameters tested and to determine which approach is more sensible to apply for future studies.

Material and methods

Sampling size and urban landscape parameters

All sampling sites were situated in Vienna (48°12’N, 16°22’E, 151–542 m.a.s.l., 415 km^2, 1.88 million inhabitants), the capital of Austria. We sampled 23 sites, located

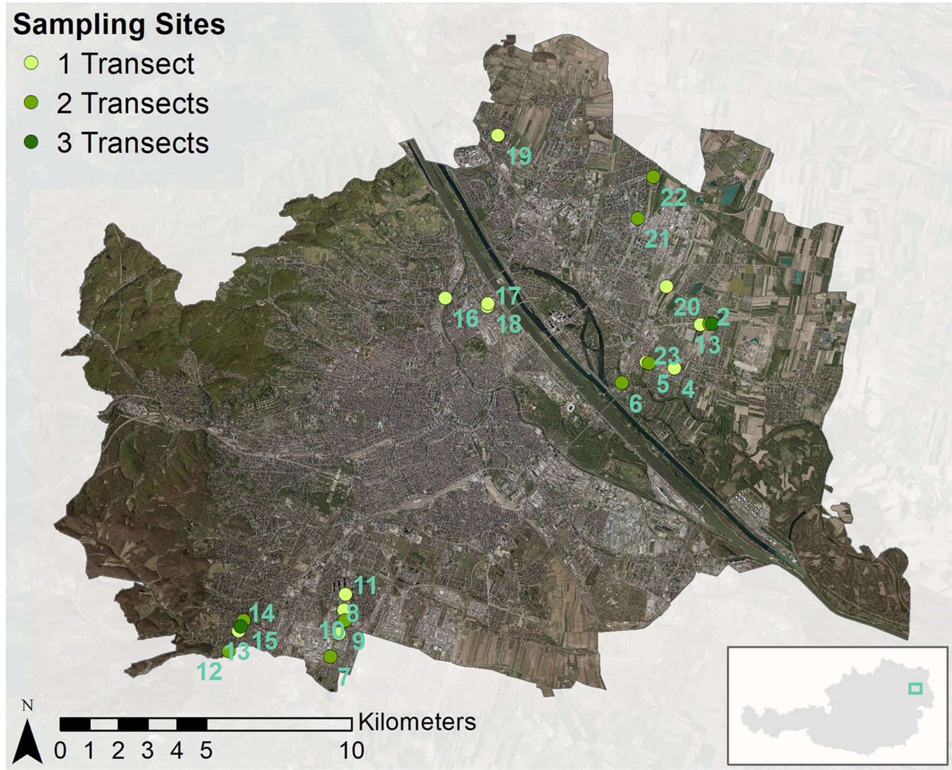

Fig. 1 Locations of 23 sampling sites with 36 transects in Vienna, Austria. The number of transects is indicated by colours; light green = 1 transect, medium green = 2 transects, dark green = three transects. Map credits: Processed in ArcMap 10.6 (ESRI Inc. 2017), administrational borders obtained from the Federal Office of Metrology and Surveying Austria retrieved from the Federal Ministry for Digital and Economic Affairs Austria (n.d.) in November 2020; orthophoto from Basemap Austria (n.d.)

in various parts of the city (see Fig. 1) and covering a total area of 36,983 m^2 (min. 260 m^2, max. 5,217 m^2, on average 1,479 m^2 per site; see Table 1). All sampling sites were in close vicinity to areas of the public transport system (i.e., the 'Wiener Linien'), including railroad embankments (n = 8), decorative and recreational areas in close vicinity to respective stations (n = 7), fallows remaining from previous construction activities (n = 5) and other areas in close vicinity to stations, or other public transport buildings (n = 3). In consequence, about half of our sampling sites (n = 12) were not open to the public.

For each sampled site and transect, we recorded data on management parameters, spatial parameters, urban landscape parameters and site-specific parameters (see Table 1). Management intensity and vegetational features varied greatly between sampling sites but formed three general vegetational categories (VEG): fallows (n = 7), which were in general structure-rich and featured ruderal and spontaneous vegetation; extensively managed meadows (n = 3), which were dominated by grasses and other flowering herbaceous plants; and intensive lawns (n = 13) with short, grass-dominated vegetation and little to no flowering aspects. Additionally, mowing frequency was documented from March to August 2019 and classified into three categories (MOW): category 1 (n = 8) with no to one mowing event during the observation period, category 2 (n = 5) with

Table 1 Structure and abbreviations of independent variables

Parameter Group	Variable	Abbreviation	Type	Levels / Range
Management	Vegetational heterogeneity	HET	ordinal	1 – 5
Management	Mowing frequency	MOW	ordinal	1 – 3
Management	Vegetation category	VEG	categorical	"intensive lawn" "extensive meadow" "structure-rich fallow"
Spatial	Patch Area	AREA	continuous	260 – 5,217 m^2
Urban Landscape	Relative cover of buildings in 250 m radius	COVERBUILT	continuous	0.06 – 0.39
Urban Landscape	Relative cover of green area in 250 m radius	COVERGREEN	continuous	0.17 – 0.62
Site-specific	ID of sampling site	site ID	categorical	1 – 23
Site-specific	Number of transects per sampling site	TRANSECTS	ordinal	1 – 3

more than one but less than three mowing events (including several areas that were not mown entirely at a certain point in time, e.g. mown twice entirely and a third time only close to the railroad) and category 3 (n = 10) with three or more complete mowing events. Furthermore, to quantify structure-related vegetational features, the presence or absence was noted on each sampling site for 1) bare ground, such as pebbles, earth or sand, 2) short vegetation, i.e., grasses and herbaceous plants with less than 35 cm height, 3) high vegetation for grasses and herbaceous plants which exceeded 35 cm, 4) shrubs, and 5) trees. From that, we calculated each sampling sites vegetational heterogeneity (HET) by summing up the occurrences of the different above-mentioned vegetational characteristics, thus resulting in an ordinal score (from 1 to 5) for each site.

For all sampling sites, urban landscape parameters were analysed based on a land allocation map of the Municipal Department for Surveying and Mapping of the City of Vienna retrieved from the Federal Ministry for Digital and Economic Affairs Austria (n.d.) in April 2019. The map is digitized in 51 different land cover categories, from which we extracted the relative cover of buildings ($COVER_{BUILT}$) and green areas ($COVER_{GREEN}$) in a 250 m radius (approx. 196,350 m^2) around the centre of the sampling site using ArcMap 10.6 (ESRI Inc. 2017). The 250 m radius included the sampling site itself which made up between 0.1 and 2.7% of the total area, thus the effect of patch area (AREA) on $COVER_{BUILT}$ and $COVER_{GREEN}$ was considered negligible. $COVER_{BUILT}$ and AREA were log-transformed. $COVER_{GREEN}$ and log($COVER_{BUILT}$) were not correlated between sampling sites ($r(21) = -.65$, $p = .526$).

Sampling methods and data sets

Sampling sites were visited three to four times in total, twice in 2019 (from mid of July to early September) and once or twice in August 2020. Quantitative sampling took place exclusively at the sampling sessions in 2019, along transects of 50 m length and 2 m width. For each sampling site, the number of transects was chosen according to the total patch area and occurrence of vegetational features; therefore, larger sites as well as sites with more vegetational features were represented by more transects. Each of the 36 transects was sampled for 10 min during the warmest hours of the day (between 9 a.m. and 5 p.m.) while avoiding rainy or cloudy days. Species composition and abundance were determined non-invasively via bioacoustic and visual classification. Sweep-netting was conducted at least four times along each transect as well as to capture individual specimen located visually.

In addition to quantitative sampling, occurrences of species observed beside the standard transects as well as species observed during the visits in 2020, when the standard transect approach was not applied, were noted to compile an exhaustive, semi-quantitative species list for each sampling site. In consequence, we gained two different data sets: one transect-based, strictly quantitative data set sampled within one year, and one less standardized but more in-depth data set per sampling site. Lastly, we gathered information on each species dispersal ability from literature (Reinhardt et al. 2005; Marini et al. 2012), categorized in three categories (high dispersal ability, intermediate dispersal ability, low dispersal ability) and deduced information for two missing species from ecologically similar species of the same genus (see Appendix, Table 5).

Statistical analysis

Data analysis was conducted using R 4.0.2 (R Core Team 2020) and confidence intervals were set at 95%, corresponding to a significance level of $p \leq 0.05$. The effects of management and urban landscape parameters were investigated using two different approaches: linear methods (Linear Models (LM), Linear Mixed Models (LMM) and Generalized Linear Mixed Models (GLMM)) and non-metric multidimensional scaling (nMDS). Both methods were applied on the quantitative and the semi-quantitative data set. To determine if there was a relationship between raw abundance and prevalence in the quantitative data set, we performed Pearson's correlations. To check if the semi-quantitative sampling provided higher species occurrences than the quantitative sampling, we performed a one-sided Student's t-test on the square root transformed species numbers per sampled unit (sampling sites for semi-quantitative sampling, transects for quantitative sampling).

For linear regressions, we calculated the exponential Shannon Index per site for the semi-quantitative data set ($\exp(H'_{SQ})$) or per transect for the quantitative data set ($\exp(H'_{Q})$) as dependent variable, therefore assuming a Gaussian error distribution. As independent variables, we considered management parameters (VEG, MOW and HET) as well as urban landscape parameters (log($COVER_{BUILT}$), $COVER_{GREEN}$ and log(AREA)). For model selection, covariates were added one by one and models were compared by calculating the Akaike Information Criterion, corrected for small sample sizes (AICc), whereby a $\Delta AICc \geq 2$ was set as threshold for finally adding a covariate. Additionally, we applied the same procedure and fixed and random factors on a generalized linear mixed model (GLMM) on the total abundance of orthopteran individuals along transects, assuming a Poisson error distribution. For the semi-quantitative data set, we opted for LMs and added the number of transects per sampling site to the management and urban landscape parameters. For the quantitative data set, we used LMMs and fitted the site ID as random term. (G) LMMs were built with (g)lmer() using the *lme4* package

(Bates et al. 2015). The AICc was calculated with AICc() of the *MuMIn* package (Barton 2019), which also provided r.squaredGLMM() to calculate the conditional R^2-values for the LMMs. Partial (Type III) significance values (χ^2-tests) were applied to assess the significance of explanatory terms using the package *car* (Fox and Weisberg 2019), and *LMERConvenienceFunctions* (Tremblay and Ransijn 2015) was used for model validation. Furthermore, data visualization was facilitated by packages *ggplot2* (Wickham 2016) and *viridis* (Garnier 2018). To perform the nMDS of the quantitative and semi-quantitative data set, we included a dummy species with an abundance of $n = 1$ on each site or transect to control for sparse samples (Clarke et al. 2006). The nMDS was performed with a Bray–Curtis similarity as distance measure and two axes, using metaMDS() of the package *vegan* (Oksanen et al. 2019). Management and urban landscape parameters were fit with envfit() of the vegan package, with 999 permutations. Here, we incorporated the site ID for the quantitative data set and the number of transects for the semi-quantitative data set. Additionally, we used the ordisurf() command for log($COVER_{BUILT}$) to account for its non-linear relationship with the nMDS.

Results

Species occurrence, abundance and diversity

With quantitative sampling, we detected 1,453 individuals of 21 orthopteran species, of which eleven belonged to the suborder Ensifera and ten to Caelifera. Species occurrence and abundance within each species correlated highly significantly ($r(19) = .94$, $p < .001$), in a way that species that were high in total abundance also were present on more sampling sites. The most abundant species were primarily Caeliferan species, especially Gomphocerinae, such as *Euchorthippus declivus* (Brisout de Barneville, 1848) (344 individuals on 31 transects), *Chorthippus biguttulus* (Linnaeus, 1758) (283 individuals on 32 transects), *Chorthippus brunneus* (Thunberg, 1815) (222 individuals on 27 transects) and *Pseudochorthippus parallelus* (Zetterstedt, 1821) (145 individuals on 25 transects), along with *Calliptamus italicus* (Linnaeus, 1758) (143 individuals on 19 transects). The most abundant Ensiferan species were *Platycleis grisea* (Fabricius, 1781) (48 individuals on 15 transects), followed by *Bicoloriana bicolor* (Philippi, 1830) (43 individuals on 11 transects) and *Phaneroptera nana* Fieber, 1853 (21 individuals on 7 transects). Semi-quantitative sampling enhanced the total species number to 25 species, as *Aiolopus thalassinus* (Fabricius, 1781), *Ruspolia nitidula* (Scopoli, 1786), *Stenobothrus lineatus* (Panzer, 1796) and *Tetrix tenuicornis* (Sahlberg, 1893) were observed exclusively off-transects. Due to the sampling design, quantitative sampling registered less species per sampled unit than semi-quantitative sampling ($t(39.7) = -1.99$, $p = .027$; see Fig. 2). Overall, 2,043 observations were made for the semi-quantitative sampling (590 records made aside from quantitative sampling). Of the 25 orthopteran species observed during the entire sampling process, 18 (72%) had high, 5 (20%) intermediate and 2 (8%) low dispersal abilities. All in all, they represent about 28% of all orthoptera ever observed in the metropole of Vienna (Wöss et al. 2020).

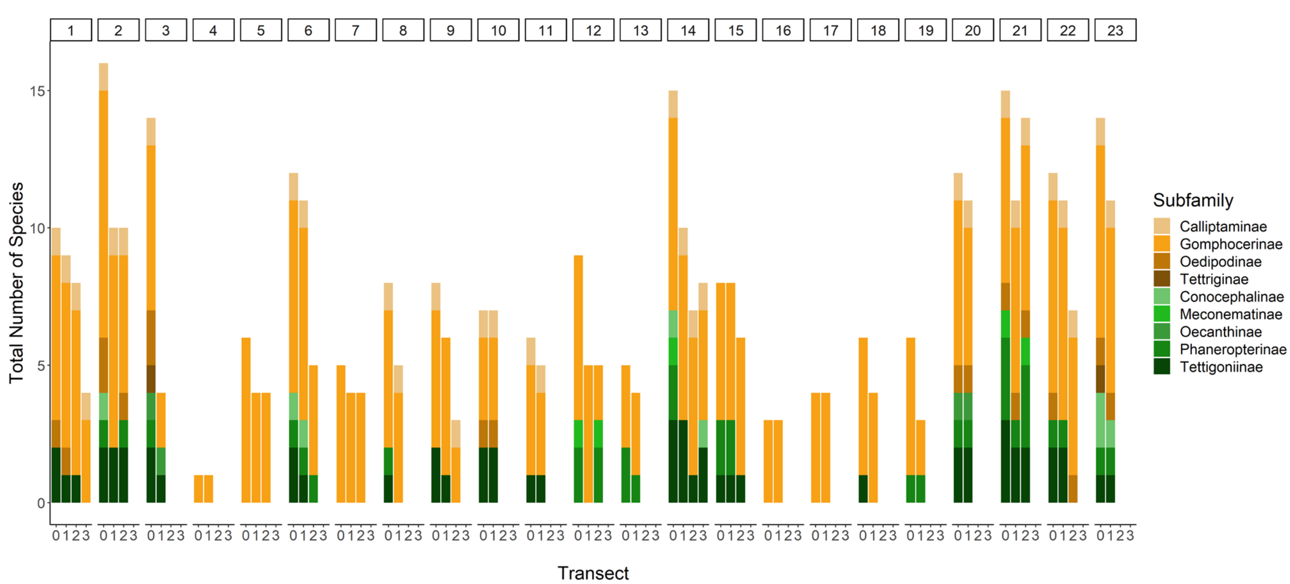

Fig. 2 Number of species taxonomically grouped as subfamilies per sampling site (No. provided above columns) and transects (No. below). Transect Number 0 encodes for the entire sampling site, i.e., representing the semi- quantitative data set. Empty slots were not sampled

Linear regressions

For modelling Shannon diversity exp(H'$_Q$) of the quantitative data set, the final model with a R^2LMMc = .42 χ^2-tests, fitted VEG and COVER$_{GREEN}$ as fixed factors and site ID as random term (see Table 2). According to the χ^2-tests, VEG was significant ($\chi^2_{(2,36)} = 20.26$, $p < .001$) and intensive lawn resulted in lowest exp(H'$_Q$), structure-rich fallows featured highest exp(H'$_Q$) and extensive meadow led to intermediate exp(H'$_Q$). COVER$_{GREEN}$ was not significant ($\chi^2_{(1,36)} = 2.57$, $p = .11$), but showed that lower COVER$_{GREEN}$ led to higher exp(H'$_Q$). The model on the total abundance of individuals along transects fitted exclusively VEG as significant factor ($\chi^2_{(2,36)} = 33.23$, $p < .001$), where extensive meadow and structure-rich fallow were associated with higher species abundances. The final model on exp(H'$_{SQ}$) of the semi-qualitative data set fitted VEG and log(AREA) with an adjusted $R^2 = .64$ (see Table 3). The factor level extensive meadow of VEG differed significantly ($t(19) = .38$, $p < .001$) from the reference category, intensive lawn, while structure-rich fallows showed no significant difference. Additionally, log(AREA) influenced exp(H'$_{SQ}$) in a way that larger areas featured a significantly higher species diversity ($t(19) = .86$, $p = .025$). Illustrations of relationships between dependent variables and significant independent variables can be found in the Appendix (see Appendix, Fig. 5).

Table 2 Models on the effects of management and urban landscape parameters as determined with quantitative sampling. The LMM on orthopteran species richness (exp(H'Q)) fitted vegetation category and relative cover of green area in the 250 m radius as fixed factors and site ID as random term (R^2LMMc = .42). The GLMM on total abundance of individuals (nTotal) fitted vegetation category as fixed factor and site ID as random term (R^2GLMMc = .96)

	Estimate	SE	Test statistic	*p* [a]	Sign. [b]
lmer(exp(H'Q) ~ VEG + COVERGREEN + (1|site ID))					
Intercept	4.85	1.19	4.08	< .001	***
VEG [c]				< .001	***
extensive meadow	1.94	.81	2.40		
structure-rich fallow	2.40	.61	3.94		
COVERGREEN	-3.46	2.73	–1.26	.206	-
glmer(nTotal ~ VEG + (1|site ID))					
Intercept	2.83	.15	18.91	< .001	***
VEG [c]				< .001	***
extensive meadow	1.24	.32	3.84		
structure-rich fallow	1.25	.24	5.22		

[a] *p*-values calculated using partial (Type III) significance values (χ^2-tests)

[b] Significance levels: *** $p < .001$; ** $p < .01$; * $p < .05$; - $p \geq .05$

[c] VEG: intensive lawn used as reference category

Table 3 Final LM for the effects of management and urban landscape parameters on orthopteran species richness as determined with semi-quantitative sampling, fitting vegetation category "extensive meadow" and patch area as significant factors (adjusted $R^2 = 0.64$)

	Estimate	SE	Test statistic	*p* [a]	Sign. [b]
lm(exp(H'sQ) ~ VEG + log(AREA))					
Intercept	-1.66	2.45	-.68	.507	-
VEG [c]					
extensive meadow	.34	.89	.38	< .001	***
structure-rich fallow	3.42	.61	5.65	.708	-
log(AREA)	.86	.35	2.43	.025	*

[a] *p*-values calculated from t-tests

[b] Significance levels: *** $p < .001$; ** $p < .01$; * $p < .05$; - $p \geq .05$

[c] VEG: intensive lawn used as reference category

Non-metric multidimensional scaling

For the quantitative data set, a two-dimensional solution with Stress = .19 was found (see Fig. 3). The envfit analysis revealed that VEG, MOW and site ID affected species abundances per transect (see Table 4). Plotting VEG into the nMDS revealed remarkable overlapping between intensive lawn, extensive meadow and structure-rich fallow. MOW showed clearer clustering of the sampled transects, and especially intensive mowing led to more similar species compositions, while the species compositions on transects with little to no mowing were least aggregated. For the nMDS of the semi-quantitative data set with Stress = .13, envfit analysis illustrated VEG, MOW, HET, log(AREA) and log(COVER$_{BUILT}$) as significant variables (see Fig. 4; Table 4). Sampling sites with different VEG were more clearly separated from each other than in the nMDS of the quantitative data set. Concerning MOW, intensive mowing regimes were again more clustered than the others but showed more data points outside the cluster than for the quantitative data set. Sampling points with lower HET were more aggregated and in general, lower to higher heterogeneity categories were ordered along a similar axis to the vector of log(AREA). The surface of log(COVER$_{BUILT}$) featured two to three elliptical centres (see Fig. 4).

Discussion

Management-related parameters

Of the three tested management-related parameters, vegetation type consistently had significant effects on orthoptera species diversity and individual abundance. Structure-rich fallows were associated with high species diversity

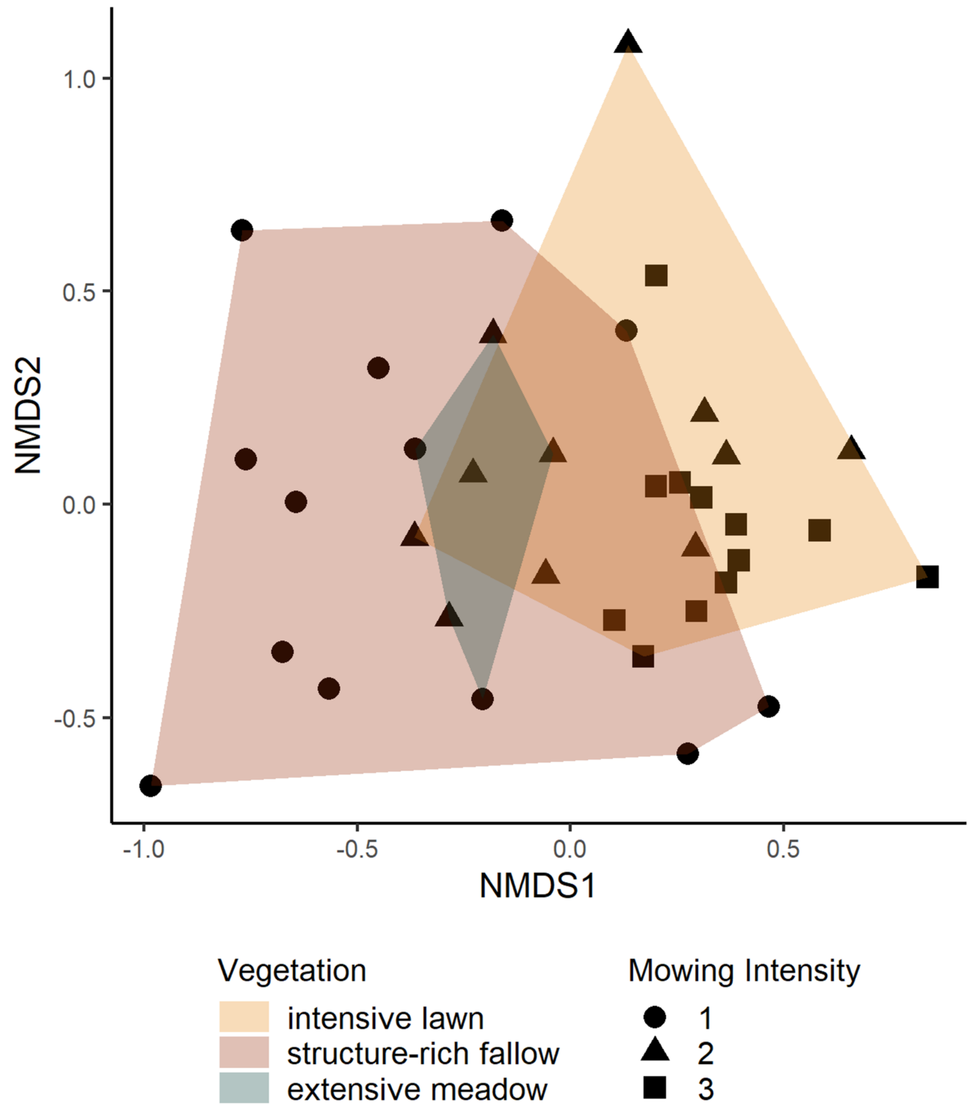

Fig. 3 Two-dimensional nMDS for the species composition of each transect of the quantitative data set, with Stress = .19. The permutation procedure of the envfit analysis featured vegetation category (VEG) and mowing intensity (MOW) as significant factors, as well as site ID (not displayed)

compared to intensive lawns, and extensive meadows featured intermediate species diversity. On structure-rich fallows and extensive meadows, significantly more individuals were found than on intensive lawns. Mowing intensity and vegetational heterogeneity were not included as relevant parameters in the final models explaining species diversity.

Table 4 Results of the envfit analysis for the quantitative data set (featuring vegetation category, mowing frequency and site ID as significant variables) and the semi-quantitative data set (featuring vegetation category, mowing frequency, vegetational heterogeneity, patch area and relative cover of buildings in the 250 m radius as significant variables)

	quantitative data set			**semi-quantitative data set**		
	R^2	***p*** [a]	**Sign.** [b]	**R^2**	***p*** [a]	**Sign.** [b]
VEG	.29	.001	**	.46	.001	**
MOW	.29	.001	**	.42	.001	**
HET	.14	.316	-	.32	.028	*
log(AREA)	.05	.431	-	.33	.010	*
log(COVERBUILT)	.07	.300	-	.32	.031	*
COVERGREEN	.07	.267	-	.17	.152	-
site ID	.83	.004	**			
transects				.08	.461	-

[a] *p*-values calculated from permutations

[b] Significance levels: *** $p < .001$; ** $p < .01$; * $p < .05$; - $p \geq .05$

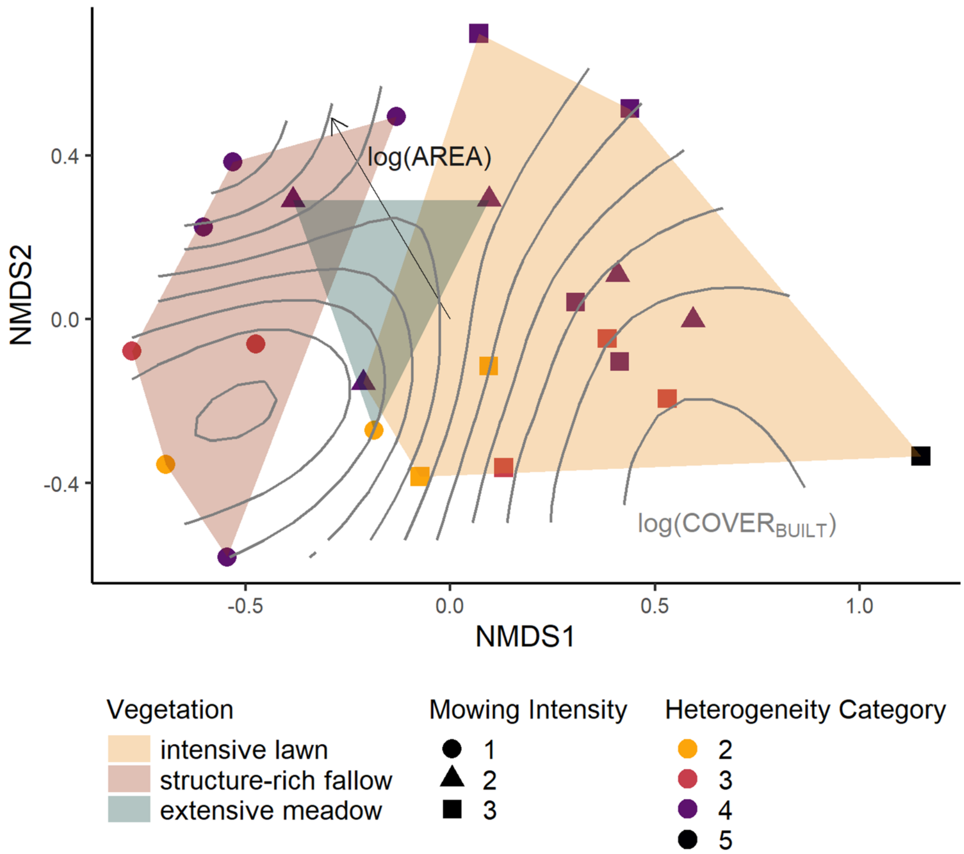

Fig. 4 Two-dimensional nMDS for the species composition of each sampling site of the semi-quantitative data set, with Stress = .13. The permutation procedure of the envfit analysis featured the management parameters vegetation category (VEG), mowing intensity (MOW) and heterogeneity category (HET). Additionally, the envfit analysis revealed the urban landscape parameters log-transformed patch area (log(AREA)) and log-transformed relative cover of buildings in a 250 m radius around the sampling site (log(COVER$_{BUILT}$) as significant. While the first showed a linear relationship with the nMDS results and is therefore displayed as vector, the latter was non-linear and needed to be fitted as surface using ordisurf

In case of mowing intensity, this contradicts several previous studies, which found a significant reduction of abundance (Humbert et al. 2010, 2012; Chisté et al. 2016) and species diversity with increased mowing and management intensity (Sachteleben et al. 2007; Marini et al. 2008, 2009), or vice versa. The importance of habitat diversity within each sampling site, which we aimed to reflect by categorizing the vegetational heterogeneity, was highlighted before as well (Marini et al. 2010; Schirmel et al. 2010; Essl and Dirnböck 2012; Cherrill 2015). Despite not explaining species diversity and abundance, both mowing intensity and vegetational heterogeneity affected species composition, where they were highly entangled with each other as well as with vegetation type. We assume, that if more sampling sites of similar vegetation types were inspected, it is very likely, that one would indeed find effects of mowing intensity and vegetational heterogeneity. Additionally, to focus on the effects of mowing and habitat diversity within sampling sites of the same vegetation type, two further temporal parameters could be used in future studies: firstly, it might be sensible to estimate the time gap between the last mowing event and the sampling date, as species diversity and abundance decrease directly after mowing events due to enhanced mortality, emigration and changes in microclimate (Gardiner and Hassall 2009; Humbert et al. 2010; Kenyeres and Szentirmai 2017), and increase again with time from the last cut (Chisté et al. 2016). Secondly, species richness and/or density could be affected by the age of the specific habitat, which is proven for non-urban environments (Kohlmann 1996; Badenhausser and Cordeau 2012; Fartmann et al. 2012).

Spatial and urban landscape parameters

Of all parameters which cannot be altered through management, patch area seemed to be the most relevant parameter. Larger areas were associated with higher species diversities, at least for the semi-quantitative data set. The indicated existence of a species-area-relationship (SAR) for orthopteran species has been postulated by several other studies before (Collinge 2000; Sachteleben et al. 2007; Nufio et al. 2009; Marini et al. 2010), although only one was conducted in an urban environment (Melliger et al. 2017). However, SARs might be less obvious in urban surroundings and only become visible when very large green areas are considered (Heß 2001). Another study conducted in isolated, xerothermic habitats inferred that the rise in species numbers is less influenced by the patch area itself but rather by the increase in different vegetational structures coming along with the increase in patch area (Herrmann 1995). To discriminate between the effect of patch area and the effect of structural heterogeneity, we implemented management-related parameters. Nevertheless, we did not find a SAR for the quantitative data set but only for the semi-quantitative data set. This indicates that the relationship is only significant when species which were not found along transects are integrated into the analysis. Such species were either species occurring in lesser densities, or species that were found on specific structures, such as hedges, that did not lie within the transects.

We investigated two urban landscape parameters: the relative cover of both green area and built-up area in a 250 m radius around the sampling site. Contradicting several previous studies, these parameters appeared rather uninformative. The relative cover of green area was included into the final linear model of the quantitative data set but was not significant. The relative cover of built-up area on the other hand appeared significant in the multivariate analysis of the semi-quantitative data set, nevertheless, the relationship was not linear and featured at least two centres, contradicting Piano et al. (2019), who documented a clear loss in species diversity with higher relative cover of built-up area. But we mostly observed highly mobile species, whose distribution in urban surroundings might be less limited by the surrounding habitat matrix. This was previously demonstrated in other environments (Collinge 2000). Less mobile species might already disappear with slight urbanisation, i.e., along a broader urbanisation gradient than the range we sampled. In addition, we measured urban landscape parameters on a rather small scale, thus focusing on local factors, yet the decline in species diversity through urbanisation is stronger for mobile orthopteran species at larger spatial scales (Penone et al. 2013). For several of the most frequent species, literature provides data on which distances can be overcome: *Chorthippus biguttulus* (Linnaeus, 1758) for example can cover distances of 300 m, while *Chorthippus albomarginatus* (De Geer, 1773) can move 500 m between inhabitable patches (Laußmann 1993). The frequent *Calliptamus italicus* (Linnaeus, 1758) can travel several hundred meters (Detzel 1998). And some species such as *Aiolopus thalassinus* (Fabricius, 1781) and *Chorthippus brunneus* (Thunberg, 1815) possibly overcome several kilometres (Laußmann 1993; Maas et al. 2002). Even species with reduced wings can overcome surprisingly large distances by passive transport, for example *Meconema meridionale* (Costa, 1860) which once was documented to passively travel 360 km on a car (Maas et al. 2002). For such a species, it might be possible to passively spread along the public transport system, too. In any case, a radius of 250 m around the sampling site probably has little effect on the distribution of highly mobile species. Additionally, we see another potential reason why the relative cover of built up or green area in a 250 m radius might matter less to species diversity and abundance: Previous studies indicated, that investigating the relative cover of built-up or green area is oversimplifying the important factors of the urban landscape. Besides focusing more on inhabitable landscape parameters than man-made elements such as the relative built-up cover (Cherrill 2015), it might be more informative to sample the relative cover of identical habitat types instead of the plain relative cover of green area (Haacks 2007).

We conclude that within a radius of 250 m around the sampling sites, we could not find clear effects of urban landscape parameters, albeit there might be underlying processes visible at larger spatial scales. Most sampled species are likely to overcome barriers imposed by the urban landscape through their high mobility, which might be a pre-selection due to the urban environment affecting all our sampling sites. The resulting species pool of highly mobile orthopteran species in urban environments are therefore primarily shaped by local vegetation and management parameters, although our data indicate an underlying non-linear species-area-relationship. This is in line with a previous study by Marini et al. (2010), which demonstrated that orthopteran species richness is more correlated to habitat diversity than to patch area.

In addition, we need to stress that, at least to our knowledge, all available studies on how urbanisation affects orthopteran diversity were performed on a spatial scale (i.e., rural to urban gradients) but not on a temporal scale (i.e., before vs. after urbanisation within a specific area), which highlights the lack of long-term studies on orthoptera in urbanising areas.

Differences between the applied sampling and statistic strategies

We applied two different sampling approaches, i.e., quantitative and semi-quantitative sampling. While the first was strictly focused on pre-defined sampling transects, the latter also included non-systematic observations of further species off-transects and in the consecutive year. We found strong differences between both data sets, caused by species that occur in low densities or that require specific vegetation-related structures that were scattered nonuniformly over the sampling site. Such structures include hedgerows, shrubs, and spots with higher vegetation or bare ground. In our opinion, this stresses the importance of targeted searches on such vegetational structures. We infer, that for investigating orthopteran species diversity in urban surroundings, transect-bound sampling might come along with the high potential to miss certain specialists if transects are not placed properly, i.e., in a way, that all microhabitats of a given sampling site are covered within one transect. However, we found no significant influence of the number of transects per sampling site on its species diversity, indicating that the likelihood of finding more species when simply increasing the standardized sampling intensity was rather low. Thus, it appears like the exact placing of transects crucially affects the sampling outcome and transects placed to fit a wide range of different insect species, such as the transects used in the present study, fail to represent the total orthopteran diversity. Either transects need to be placed very sensibly, covering the specific structures with high importance to structure-bound species that can be expected in urban environments, or additional targeted searches off-transects will remain necessary.

Conclusions

Orthoptera are highly affected by several different parameters, which influence their habitat. However, our findings demonstrated that management-related parameters appear to have a stronger impact on local urban assemblages than urban landscape parameters. This might be due to a pre-selection to (highly) mobile species with strong dispersal abilities to persist in urban surroundings with fragmented and ephemeral habitats.

Especially fallows, which can occur in highly urbanised surroundings, are usually small, temporary, and mostly isolated from similar habitats, were significantly correlated with high abundance and species diversity, further emphasizing the importance of management-related parameters. These findings have strong implications for conservation efforts in urban surroundings to enhance orthopteran species richness, as management is easily influenced and adjusted than the urban landscape itself. This is in line with previous findings on orthopteran diversity (Marini et al. 2008), and arthropod diversity in general (Buchholz et al. 2018).

Despite the importance of our findings for conservation efforts, we summarize, that assemblages of different habitats (i.e., structure-rich fallows, extensive meadows, and intensive lawns) differ greatly and need adjusted management measures. Our results point towards an underlying non-linear species-area-relationship. For conservation measures, larger (and potentially more heterogenous) areas should be prioritized as they likely feature higher species diversity. For future studies on orthopteran assemblages in urban surroundings, it might be advisable to investigate different vegetation types separately. Including more specific information on management parameters, such as the time gap between the sampling date and the last cut, or the age of the specific sampling site, might help to finally disentangle the parameters affecting urban orthopteran assemblages.

Appendix

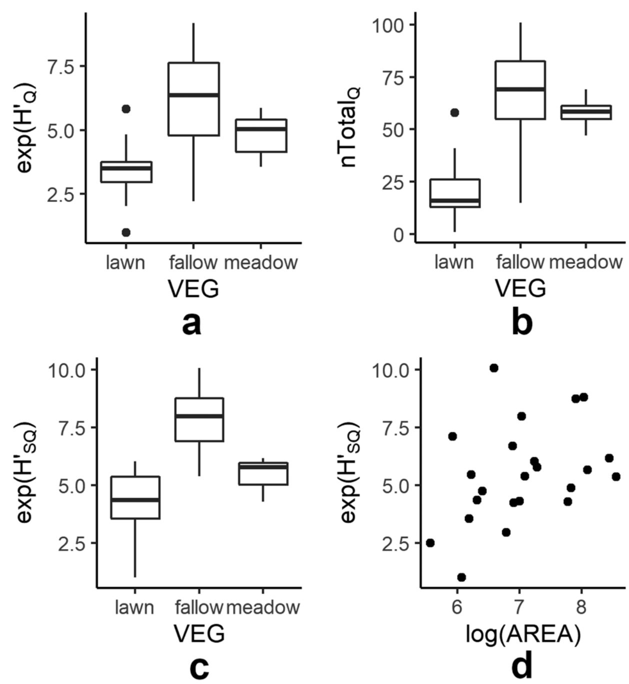

Fig. 5 Illustrations of relationships between dependent variables and significant independent variables: **a** Exponential Shannon Index of the quantitative data set on vegetation category; **b** Total abundance of the quantitative data set on vegetation category; **c** Exponential Shannon Index of the semi-quantitative data set on vegetation category; **d** Exponential Shannon Index of the semi-quantitative data set on logarithmic patch area

Table 5 Species per site as found through semi-quantitative sampling, indicated as occurrences. The dispersal ability (Disp.; classified in three categories: 1 = low, 2 = intermediate, 3 = high) was taken from the respective reference (Ref.; A = Reinhardt et al. 2005; B = Marini et al. 2012). The dispersal ability for *Phaneroptera nana* was extrapolated from *Phaneroptera falcata*, and for *Platycleis grisea* from *Platycleis albopunctata*

Species	Disp.	Ref	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Aiolopus thalassinus (FABRICIUS, 1781)	3	A		x	x																				
Bicolorana bicolor (PHILIPPI, 1830)	2	A	x	x	x			x			x	x				x						x	x	x	
Calliptamus italicus (LINNAEUS, 1758)	2	A	x	x	x			x		x	x	x	x			x						x	x	x	x
Chorthippus albomarginatus (DE GEER, 1773)	3	A	x	x			x															x		x	
Chorthippus apricarius (LINNAEUS, 1758)	2	A		x	x			x			x			x	x	x								x	x
Chorthippus biguttulus (LINNAEUS, 1758)	3	A	x	x	x		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Chorthippus brunneus (THUNBERG, 1815)	3	A	x	x	x		x	x	x	x		x		x	x	x	x	x	x	x	x	x	x	x	x
Chorthippus dorsatus (ZETTERSTEDT, 1821)	3	A		x			x	x						x		x	x			x			x		x
Chorthippus mollis (CHARPENTIER, 1825)	3	A	x	x	x			x	x	x	x	x		x		x			x		x	x	x	x	x
Conocephalus fuscus (FABRICIUS, 1793)	3	A						x								x									x
Euchorthippus declivus (BRISOUT DE BARNEVILLE, 1848)	3	A	x	x	x		x	x	x	x	x	x	x	x		x	x	x	x	x	x	x	x	x	x
Leptophyes albovittata (KOLLAR, 1833)	3	A																						x	
Leptophyes punctatissima (BOSC, 1792)	3	A												x	x	x	x					x	x		
Meconema meridionale COSTA, 1860	3	A												x		x							x		
Oecanthus pellucens (SCOPOLI, 1763)	3	A			x																	x			
Oedipoda caerulescens (LINNAEUS, 1758)	3	A	x	x	x							x										x	x	x	x
Phaneroptera falcata (PODA, 1761)	3	A		x																			x		
Phaneroptera nana FIEBER, 1853	3	A			x			x		x				x	x	x	x				x		x		x
Pholidoptera griseoaptera (DE GEER, 1773)	1	A						x								x									
Platycleis grisea (FABRICIUS, 1781),	2	A	x	x	x					x	x	x	x			x	x			x		x	x		x
Pseudochorthippus parallelus (ZETTERSTEDT, 1821)	3	B	x	x	x	x	x	x	x	x	x		x	x		x	x			x	x	x	x	x	x
Ruspolia nitidula (SCOPOLI, 1786)	3	B		x																					x
Stenobothrus lineatus (PANZER, 1796)	2	A		x																					
Tetrix tenuicornis (SAHLBERG, 1891)	1	A			x																				x
Tettigonia viridissima (LINNAEUS, 1758)	3	A																					x	x	

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Availability of data and material The authors confirm that the data supporting the findings of this study are partly available within the article and its supplementary materials. Additionally, absolute species numbers per site and R codes for analysis of this study are available from the corresponding author, KH, upon reasonable request.

Declarations

Ethics approval Not applicable.

Consent to participate Not applicable.

Consent for publication Not applicable.

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