

## ORIGINAL ARTICLE

## The Ecology and Conservation of Urban Insects

## Functional traits drive the fate of Orthoptera in urban areas

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## Abstract

1. The replacement of natural areas due to urbanisation represents a major threat to wildlife. Wild species may be classified according to their response towards urban areas. Such responses lead to persistence (exploiters and tolerant) or local extinction (avoiders) of species within cities, which in turn contributes to shaping the assemblages found therein, usually according to specific sets of ecological and morphological traits.
2. Here, we focus on Orthoptera as a model group to test hypotheses on the relationships between species' traits and persistence in urban environments, using the city of Rome, Italy, as study area. By compiling and comparing species checklists for two distinct time frames, we assessed assemblage variation across the last three decades and revealed that local extinction of Orthoptera in urban areas is trait-biased.
3. Species with low mobility and fertility, and narrower—more specialised—climatic niches showed higher probability of local extinction.
4. Our results point at both climate and land use changes as potentially major drivers of orthopterans' local extinction in urban areas, suggesting that strategies to increase natural habitat preservation and connectivity, and mitigate climate-change induced events, may both prove effective in sustaining richer insect communities within urban areas.

## KEYWORDS

checklists, ecomorphology, extinction risk, insect conservation, urban ecology

## INTRODUCTION

Urban areas are expanding at alarming rates all over the world (Yang et al., 2018), with well-recognised adverse effects on biodiversity due to habitat deterioration and direct replacement with deeply modified cover, for example, the impervious surfaces of buildings and infrastructures (Piano et al., 2020). Such replacement has profound impacts on wildlife, which may be classified according to their response by urban ecologists as either exploiters/tolerant or avoiders of urban areas (Callaghan et al., 2021; Fischer et al., 2015; Santini et al., 2019; Tryjanowski et al., 2020). Such responses in turn lead to persistence or local extinction of species within cities, a process that—together with colonisation and introduction events—determines the structure of urban wildlife assemblages (Aronson et al., 2016).

Despite that urbanisation per se mostly implies the disappearance of natural habitats, many cities around the world are characterised by a set of green spaces derived by different processes, for example, specific urban development planning or unintentional abandonment (Gandy, 2016). Cities may thus still feature relatively species-rich wildlife assemblages, particularly in the case of highly mobile taxa such as birds and butterflies (Hall et al., 2017; MacGregor-Fors et al., 2016). Yet, the high unpredictability of urban areas due to, for example, renovation and development, jointly with the implicit higher risk of stochastic events of small areas and populations living therein, poses a serious challenge to wildlife, with high rates of local extinction being recorded, in comparison to more natural areas (Aronson et al., 2017; Grimm et al., 2008). The urban environment is known to selectively filter species from the surrounding natural habitats according to

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specific traits—or sets of traits—that play major roles in allowing species to persist in such highly modified areas (Aronson et al., 2016; Grilo et al., 2022; Planchuelo et al., 2020). Specific key traits are well known and relatively conserved among vertebrates, with species characterised by high behavioural plasticity, reproductive outputs and dispersal capabilities being more likely to adapt and persist to life in the city. Conversely, very little is known on comparable traits among invertebrates (Diamond et al., 2023; but see: Piano et al., 2017).

Within the scientific literature on urban wildlife, insects have been in fact mostly neglected as targets, with higher attention being posed to vertebrates (Di Pietro et al., 2021). Nonetheless, insects represent a significant portion of wild species occurring within cities worldwide, beside playing key roles in trophic and pollination networks, that is, sustaining functioning ecosystems and their associated services (Losey & Vaughan, 2006; Steffan-Dewenter & Westphal, 2008). Moreover, the peculiar conditions found in many artificial (recreational) urban green spaces, such as the occurrence of large or senescent trees in historical parks and villas, may also provide unexpected profitable habitats even to highly specialised insects, as in the case of saproxylic beetles (Fattorini & Galassi, 2016; Horák, 2018). Conversely, species more strongly associated with habitat types that are rarely featured within anthropogenic green spaces, for example, natural or semi-natural grasslands and wetlands, may be at higher risk to become locally extinct following urbanisation (New, 2015).

Here we focus on Orthoptera, that is, crickets, grasshoppers and bush crickets, as a model group to test hypotheses on the relationship between species' traits and adaptability to urban environments, using the city of Rome, in Italy, as study area. European orthopterans are excellent models to study the long-term effects of land use changes, since they feature subtle and usually highly specific relationships with vegetation structure (Labadessa et al., 2015; Whiles & Charlton, 2006), are sensitive to anthropogenic modifications at several scales (Báldi & Kisbenedek, 1997; Labadessa & Ancillotto, 2022; Rácz et al., 2013) and their diversity includes species with diverging ecological needs and functional traits, for example, in terms of size, mobility, diet and habitat preferences (Moretti et al., 2013). Here we compare two Orthoptera faunal checklists from the urban area of Rome in the last decades, and predict that urban orthopterans' probability of persistence within urban areas will be biased according to specific sets of physiological, morphological and life-history traits. More specifically, and based on studies on other taxa—such as butterflies, birds and mammals (Callaghan et al., 2021; Fraissinet et al. 2023, Santini et al., 2019)—we predict that higher values of traits related to reproductive output and dispersal abilities may foster species' persistence in urban areas through time, while we conversely expect a negative effect of specialisation degree.

## MATERIALS AND METHODS

### Study area

We conducted our study in the metropolitan area of Rome, central Italy, the largest Italian city and one of the most ancient urban areas in

Europe, covering approximately 36,000 ha and hosting ca. 6 million inhabitants. The area is strongly dominated by built-up surfaces comprising sparse to high-density districts, yet is also densely interspersed by a network of green spaces (numbering 1798 public green areas, cumulatively covering 17,300 ha), including natural, semi-natural, recreational and agricultural areas. Climate is typically Mediterranean, with annual mean temperatures ranging from 18.9 to 31.7°C in summer to 2.8–11.7°C in winter, and precipitation is concentrated in autumn. Rome covered only 1400 ha and counted 200,000 inhabitants up to 1870s, yet most of its urban development occurred after World War II, as for many other Italian cities, so that most of the land use changes occurred between 1940 and 1960, and mainly consisted in the replacement of natural grasslands and shrublands with croplands and built-up areas. Subsequently, a more recent urban expansion occurred in the 1980–1990 decade, consisting in mostly unauthorised development (reviewed in: Zapparoli, 1997a, Zapparoli, 1997b). For this study, we considered the territory encompassed by the great ring road ('Grande Raccordo Anulare') as the focal study area, as in other studies targeting Rome's wildlife and urban landscape (Ancillotto et al., 2019; Di Pietro et al., 2021; Fattorini & Galassi, 2016).

### Orthoptera checklists

We compiled two comprehensive checklists of Orthoptera species occurring within the study area, namely one including data published in the 1990s and including records from the literature and from private and public collections, and one with exclusively recent records (2010–2022). The former was listed after the most updated checklist of insects available for Rome (Zapparoli, 1997b), integrated with data from the CKmap project ('Checklist and distribution of the Italian fauna'; Latella et al., 2007) and additional published records, excluding data dating back to before 1945. As such, this list mainly derives from non-systematic field sampling on all insect taxa, which took place in the 1950s and 1990s at specific locations within the study area and whose sampling effort is unknown. Within this checklist, 14 sites include data on orthopterans. The latter—more recent—checklist was instead compiled by conducting ad hoc repeated surveys in selected green areas ( $n = 22$ ) conducted in 2022 by adopting a mix of visual-acoustic and net-sweeping methods (Sperber et al., 2021), as well as opportunistically collected records by the authors and citizen scientists from the 'Rome's Orthoptera' project on the iNaturalist platform (<https://www.inaturalist.org/projects/ortotteri-di-roma-rome-s-orthoptera>, including records from 2010 to 2022). Specifically, we sampled at all localities for which at least one species was recorded in the first checklist, plus additional sites highly representative of Rome's urban biodiversity ( $N$  sites = 8); all sites were surveyed 2–6 times between May and October 2022, in order to decrease the possibility of false absences in the recent list. We refrained from conducting quantitative assessments of changes in the relative abundances of species present in the study area due to the lack of knowledge on the sampling effort and techniques adopted to compile the 1997 checklist. Nonetheless, we controlled for potential biases in Orthoptera species

detectability by specifically conducting field sampling in 2022 at the same sites mentioned in the checklist from 1997. Besides, in order to visualise the 2022 checklist completeness in terms of species recorded, we also checked the species accumulation curve by using the *specaccum* function in the *vegan* package for R (Oksanen et al., 2013), that is, assessing whether the number of species detected in the study area reached a plateau along the sampling sessions ( $n = 62$ ).

## Orthoptera traits

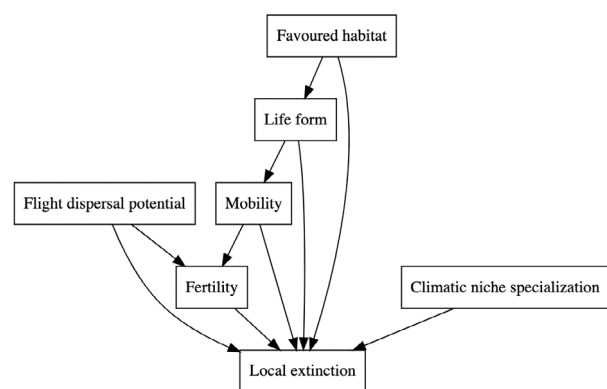
For each species featured within either of the compiled checklists, we retrieved a set of ecomorphological traits (Table S1 in Supplementary materials) that are known to potentially affect species' success in changing environments (e.g., Banaszak-Cibicka & Żmihorski, 2012). Specifically, we collected traits related to physiology (reproductive output, assessed as the numbers of eggs produced, Gossner et al., 2015), and morphology/movement abilities (flight dispersal potential, assessed as the ratio between forewing and body lengths; terrestrial mobility index, calculated as the ratio between hind femur and body lengths). All measurements were taken from Iorio et al. (2019) and represent maximum recorded values from individuals sampled in Italy. We also classified species according to their life form, by following Rácz et al. (2013), that is, as either chortobionta (grass dwelling), thamnobionta (shrub/herbaceous canopy-dwelling), geobionta (ground-dwelling) or geochortobionta (ground- and grass-dwelling), as well as according to their habitat preferences, extracted by species' habitat descriptions by Iorio et al. (2019), and reclassified into dry grasslands, wetlands (including wet grasslands), forest and generalist species. Additionally, we also assessed climatic niche specialisation by following an Environmental Niche Factorial Analysis (ENFA). For each species, we first extracted climate data at occurrence points as downloaded from the Global Biodiversity Information Facility ([www.gbif.org](http://www.gbif.org)), using a set of six a priori variables downloaded from Worldclim2 (Fick & Hijmans, 2017), with a 1-km (30 arc seconds) resolution, while climatic environment background was extracted by 5000 random points. For this testing, we used Italy as study area. Variables were those retained as most relevant in previous works on European orthopterans (Feldmeier et al., 2018; Labadessa & Ancillotto, 2022), that is, annual mean temperature (Bio01), isothermality (Bio03), mean temperature of driest quarter (Bio09), mean precipitation of driest month (Bio14), precipitation seasonality (Bio15) and precipitation of coldest quarter (Bio19).

Ecological Niche Factor Analysis (ENFA) was then conducted using the *CENFA* package in R (Rinnan & Lawler, 2019), using all occurrences retrieved. ENFA is a multivariate technique that summarises the environmental volume along two axes, namely marginality (M) and specialisation (S). Conventionally, S values  $>1$  indicate a specialised niche (Labadessa & Ancillotto, 2022). For our purposes, we extracted the latter as an indicator of climatic niche breadth for our set of species.

## Statistical analyses

We assessed both direct and indirect effects of ecomorphological traits upon species' persistence in the study area by following a structural equation modeling (SEM) approach, namely using path analysis as implemented by the *lavaan* package (Rosseel, 2012). For this analysis, we only retained species for which our sampling ensured an acceptable degree of certainty of species' occurrence, that is, we excluded taxa inhabiting underground sites, woodland leaf litters or that are myrmecophile, thus including only families Acrididae, Tettigoniidae and Tetrigidae ( $N = 63$ ). Path analysis is a technique that allows to test a priori hypotheses about causal relationships among selected variables (Wootton, 1994) by performing multiple regression tests to a set of pre-defined relationships. This approach thus allows to decompose and estimate the relative strengths of direct and indirect effects of variables upon a specific response of interest. The designed path in our case study included the effects of traits upon species' fate between the two checklists, coded as 1 (local extinction) or 0 (persistence) in the study area. Namely, to determine whether a species went locally extinct or not within the considered time interval, we assumed that (i) species found in 1997 and not in 2022 were genuinely extinct (an assumption justified by the direct search for species in their known locations as well as by following a more systematic approach than that from 1997), and (ii) species found in 2022 and not in 1997 represented false absences in the first checklist, that is, they are assumed to have already been present—but undetected—in the area. Consequently, we excluded any colonisation dynamics, thus not considering for this analysis the only species that has been expanding its range across Europe (including Italy) in recent years, that is, *Eyprepocnemis plorans* (Labadessa et al., 2018).

Relationships among the explaining variables were also tested, together with the indirect effects on species' probability of extinction, based on both published evidence and potential effects that may be expected (Figure 1). Overall model fit was assessed with a Chi-square ( $\chi^2$ ) goodness-of-fit test, with the root-mean-square error of



**FIGURE 1** Hypothesised relationships (black arrows) between ecomorphological traits of Orthoptera and species' probability of local extinction.

approximation index (RMSEA), and the comparative fit index (CFI). For all the tested relationships, we evaluated standardised coefficients and associated *p*-values, considering as significant those with values >|0.1| and <0.05, respectively.

## RESULTS

We retrieved evidence of occurrence for 85 Orthoptera species in Rome; from these, we excluded seven species whose geographical attribution is likely erroneous or doubtful (*n* = 3), have probably been misidentified (*n* = 2), are introduced (*n* = 1) or whose taxonomic status is unclear (*n* = 1), leading to a total of 78 species from 10 families (Acrididae: *n* = 31; Tettigoniidae: *n* = 28; Gryllidae: *n* = 7; Tetrigidae: *n* = 5; Oecanthidae: *n* = 2; Gryllotalpidae: *n* = 1; Mogoplistidae: *n* = 1; Myrmecophilidae: *n* = 1; Raphidophoridae: *n* = 1; Trigonidiidae: *n* = 1; see Table S2 in Supplementary materials for the full list of species within each checklist). A slight net decrease in richness was evident between the two checklists (from 68 species in 1997 to 54 in 2022); only 44 species were actually shared between the two lists, since 10 were newly detected in 2022, while 24 species went locally extinct in the time interval between the two checklists. The 2022 checklist proved to be satisfactorily complete in terms of numbers of detected species, since the species accumulation curve clearly reached a plateau well before our last sampling occasion, that is, we are confident that the 2022 checklist provides a genuine picture of the species present at the sampled locations (Figure S1 in Supplementary materials). Moreover, the retrieved 419 records from citizen scientists accounted for 48 species, only one of which was not detected by our field sampling (namely: the fossorial *Myrmecophilus myrmecophilus*), corresponding to <2.5% of the overall species richness from the 2022 checklist, further supporting the exhaustiveness of our sampling.

Overall, our SEM—built on a subset of species (*N* = 63)—fits well to data ( $\chi^2 = 0.10$ , *p* = 0.06; RMSEA < 0.1, CFI = 0.85), highlighting that the probability of extinction of Orthoptera is significantly affected by a set of functional traits that characterise the species found in the

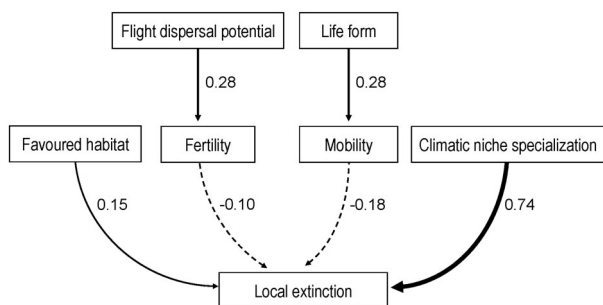
study area (Figure 2). Fertility and mobility both showed negative effects on the probability of extinction, with species that produce more eggs and are more mobile being less likely to disappear from the study area in the considered time interval (Figure 3a,b). Climatic niche specialisation showed the strongest—positive—effect on species' probability of extinction, featuring a regression coefficient > three times those of other significant predictors, and indicating that taxa that are more specialised were more likely to go locally extinct (Figure 3c). From a habitat perspective, species associated with wetlands (among Acrididae) and dry grasslands (among Acrididae and Tettigoniidae) were disproportionately likely to go extinct, if compared to those associated with forests or to generalist taxa (Figure 3d). Indirect effects that modulated some of these relationships also emerged, since we detected a significant positive effect of flight dispersal potential on fertility, indicating that more dispersive species also tend to produce more eggs. Moreover, species' life form also correlated with mobility, that is, thamnobionta showed higher potential mobility values than all other forms.

## DISCUSSION

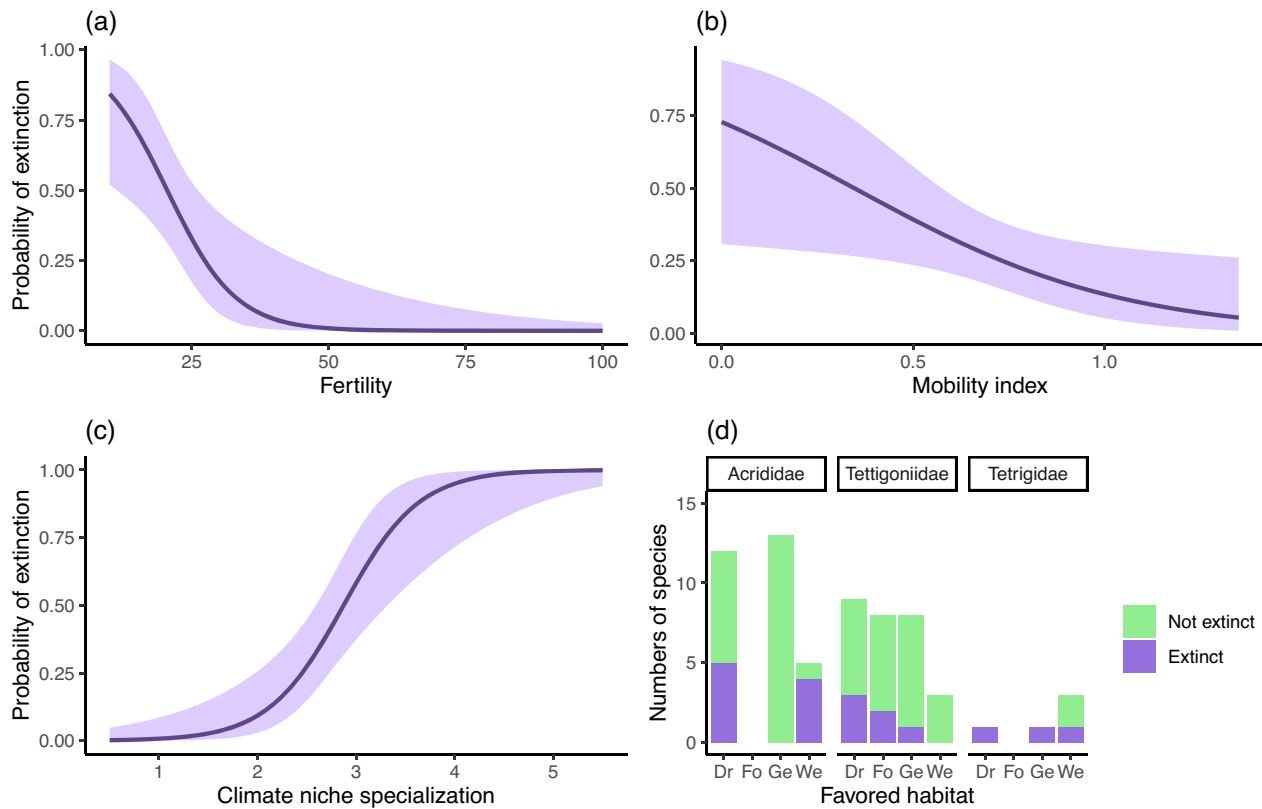
The study of urban assemblages and their variation in the last three decades revealed that local extinction of Orthoptera in urban areas is trait-biased, with significantly higher rates for species with low mobility and fertility, and narrower—more specialised—climatic niches.

The urban area of Rome is home to a rich community of orthopterans (numbering 68 and 54 species in 1997 and 2023, respectively), if compared to those recorded in the few urban areas systematically investigated in Europe so far (e.g., 21 species in Wien: Huchler et al., 2022; 25 species in Basel: Melliger et al., 2017). Such high biodiversity is not unusual for Rome, due to the high variety of green spaces still present within the urban matrix, all providing excellent opportunities to a high diversity of orthopterans, similarly to what is observed among other taxa (Ancillotto et al., 2019; Di Pietro et al., 2021; Fattorini & Galassi, 2016). Our temporal analysis though reveals that such high diversity of urban orthopterans is paired to relatively high levels of species erosion in the last decades, due to several apparent extinctions and, possibly, very few genuine faunal acquisitions. This result is also in agreement with those by Piano et al. (2020), who found poorer and more homogenised orthopteran communities at increasing degrees of built-up cover. Moreover, we highlight that most records from the first checklist we adopted as baseline, dating back to 1997, partially overlap with both development waves that occurred in Rome in the 20th century. As such, it is also possible that our first checklist was already deprived of more sensitive species that may have already gone extinct or decreased to low population sizes, as an immediate response to urbanisation. Since we cannot exclude this scenario, we disclose that our results may possibly indicate only mid-to-long-term responses of orthopterans to urbanisation.

The approach we adopted does not allow for quantitatively assessing assemblage changes in time, since methods used to compile the first checklist are not available and repeatable. Nonetheless, we are confident to have minimised the risk of recording false



**FIGURE 2** Path analysis explaining the probability of local extinction of Orthoptera (*n* species = 63) in the urban area of Rome (Italy) between 1997 and 2022, based on comparison of faunal checklists. Reported values for each relationship are standardised regression coefficients. Only coefficients with *p* < 0.05 are shown.



**FIGURE 3** Relationships between probability of extinction and ecomorphological traits of Orthoptera ( $n$  species = 63) in the urban area of Rome (Italy), between 1997 and 2022. Probability of extinction is calculated by generalised linear models with binomial error distribution, run on the comparison of checklists from 1997 and 2022; (a) fertility, approximated by the numbers of eggs produced per reproductive event; (b) mobility, as the ratio between hind femur length and total body length; (c) climate niche specialisation, assessed by Environmental Niche Factorial Analysis; (d) favoured habitat: Dr, dry grasslands; Fo, forests; Ge, generalist; We, wetlands and wet grasslands.

absences and interpret them as local extinctions by, for example, exhaustively sampling orthopterans in 2022. As such, the observed patterns may genuinely reflect actual ecological responses, rather than potential trait- or method-based biases in species' detectability. Even so, we still recommend caution in interpreting species' absences as genuine extinctions, since detecting populations occurring at very low densities may be challenging over such a large study area as ours (Watts et al., 2008), and should thus be considered as apparent extinctions only.

Species loss in Rome in the last decades was non-random among orthopterans, since probability of apparent extinction was influenced by a few key traits. Namely, climate niche specialisation played a major role in affecting whether species persisted or not in the study area. A key process in urban ecology is the so-called urban-heat-island (UHI) effect, that is, a set of environmental and structural conditions typical of cities, that leads to overall higher temperatures throughout the year, in comparison to similarly located natural environments (Arnfield, 2003). As a consequence of the UHI effect, temperature extremes during heatwaves, usually associated to droughts, are more frequent and intense in large urban areas than in the surrounding landscapes, potentially resulting as a major threat to urban populations, particularly in the case of species adapted to narrow environmental or climatic conditions (Maxwell et al., 2019; Ummenhofer & Meehl, 2017). Our approach did not allow us to identify the direct

causes of decline and extinction of species from our study area, so we cannot comment on whether the climatic niche measure we adopted actually captured a genuine climate-related response. Nonetheless, temperature patterns in Rome showed a significant trend in the last 20 years, with an estimated yearly increase of  $0.1^{\circ}\text{C}$  for both average and maximum temperatures, a value significantly higher than those measured in extra-urban areas nearby (Di Bernardino et al., 2022). Besides, Rome has also been classified among the top-ranking European cities at higher risk of heatwaves (Smid et al., 2019). Thermal stress may both directly and indirectly affect orthopterans, for example, by inducing vegetation changes (Welti et al., 2020), and significant distributional and compositional changes have been documented in floral assemblages in the study area (Fratarcangeli et al., 2022). Thus, we are confident that the decrease in narrow climatic-niche species from our study area in the last decades may represent a genuine response of orthopterans to the disproportionately pressing effects of climate change in urban areas. Noticeably, a decrease in specialisation degree at community level in response to urbanisation has also been documented in France (Penone et al., 2013), suggesting that the loss of specialised species is a consistent response to urbanisation by orthopteran assemblages. Moreover, climate niche—in terms of mean temperature within range—also proved as a key trait in classifying butterflies as either urban exploiters, tolerant or avoiders (Callaghan et al., 2021), suggesting a



consistently major role of temperature tolerance in shaping insect responses to urbanisation.

Reproductive output and mobility are also relevant traits that shape urban wildlife assemblages (Fenoglio et al., 2021), including orthopterans in our case study. Specifically, a visual inspection of the relationship between these traits and extinction reveals an increase in the probability of local disappearance for species laying <30 eggs per reproductive event, as well as featuring a mobility index <0.5, indicating that K-selected species and those with lower femur/body ratios (i.e., species assumed to be less mobile) are significantly at higher risk of extinction in urban areas. Both traits may be directly related to the maintenance of functional meta-population dynamics, particularly in highly unpredictable and fragmented environments such as cities, as also demonstrated for several mammalian orders (Santini et al., 2019), birds (Fraissinet et al., 2023) and insects (Fenoglio et al., 2021). These results also agree with other studies (Merckx et al., 2018; Piano et al., 2020) that highlighted the role of urbanisation in increasing community-weighted body size of orthopterans in comparison to non-urban assemblages. Urban areas are strongly characterised by the fragmentation of natural and semi-natural environments, yet also by highest rates of land use changes, due to renovation, abandonment and development. While many orthopterans may be well-suited to deal with land use changes in more natural contexts, for example, being able to colonise newly available habitats relatively quickly (e.g., Alignan et al., 2018), such ability may be significantly impaired in urban areas, particularly in the case of brachypterous and apterous species. As an example, the Italian endemic and flightless *Ephippiger zelleri* was considered as very common in the past decades in central Italy, also being recorded within several urban parks of Rome since the late 1990s (Zapparoli, 1997a; Zapparoli, 1997b), while it is now apparently absent from the study area and considered as Endangered within the European Red List of Orthoptera by IUCN (Hochkirch et al., 2016). Interestingly, mobility and fertility were also identified as key traits in shaping Orthoptera strategies to deal with environmental unpredictability in floodplain habitats (Dziocck et al., 2011), suggesting that reproductive outputs and dispersal abilities are consistently important for orthopterans in rapidly changing environments.

Beside species' mobility and fertility, association with different habitat types also influenced the probability of local extinction. Namely, orthopterans associated with wetlands and dry grasslands tended to disappear from the study area. Such an overall pattern across taxonomic groups was though most probably driven only by Acrididae and Tetrigidae in the case of wetlands, since none of the Tettigoniidae occurring in this habitat type went extinct in the considered time window. Both dry grasslands and wetlands are habitats at high risk of replacement in urban areas, due to their association with geomorphological and edaphic conditions that are also favourable for agricultural/pastoral reclamation and urban development (Labadessa & Ancillotto, 2023). Both these habitats are mostly disappearing at faster rates than others, such as forests, in cities worldwide (Kingsford et al., 2016), and are highly affected by small-scale management practices (e.g., mowing) that deeply affect the orthopteran assemblages they host (Huchler et al., 2022). In our specific case, the most recent

development in Rome included both urban development/expansion at the expense of formerly agricultural areas and reclamation of abandoned sites (Filibeck et al., 2016), the latter resulting in deeply modified floral assemblages that show lower suitability to orthopterans associated with dry grasslands. This is also evident in our study area, where at least one site featuring a large semi-natural grassland area in the 1990s was subsequently replaced by intensive cropland in the time interval between the two checklists, resulting in the current absence of suitable habitats to several species previously recorded (L. Ancillotto, pers. comm.). Namely, the low aesthetic appreciation by urbanites of spontaneous vegetation that characterises natural and semi-natural grasslands facilitates the replacement of such habitats with recreational green spaces (e.g., mowed and irrigated lawns) by land managers. Nonetheless, increasing awareness of biodiversity values among urbanites has been recently recorded across Europe, suggesting the potential for a change of paradigm in the management of urban green spaces (Fischer & Kowarik, 2020; Lampinen et al., 2021).

Ultimately, our results shed light on the relationship between insect diversity and urban environments, highlighting that local extinction risk of orthopterans in deeply modified environments, such as the large city where we conducted our study, is also shaped by species' characteristics. As such, specific functional traits should be taken into consideration when evaluating species' vulnerability to urbanisation. Our exercise represents an asset to future conservation assessments of orthopterans, as well as a useful—and easily repeatable—workflow for a better-informed planning and management of urban green spaces of wildlife-inclusive future cities. More specifically, our work highlights the potential value of local checklists and of resampling campaigns in disclosing ecological processes, evidencing which characteristics shape species' responses and, in turn, fostering prioritisation exercises for conservation.

## AUTHOR CONTRIBUTIONS

**Leonardo Ancillotto:** Conceptualization; data curation; formal analysis; visualization; writing – original draft; methodology; writing – review & editing. **Rocco Labadessa:** Conceptualization; data curation; visualization; writing – original draft; methodology; writing – review & editing.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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## REFERENCES

- Alignan, J.F., Debras, J.F. & Dutoit, T. (2018) Orthoptera prove good indicators of grassland rehabilitation success in the first French natural asset reserve. *Journal for Nature Conservation*, 44, 1–11. Available from: <https://doi.org/10.1016/j.jnc.2018.04.002>
- Ancillotto, L., Bosso, L., Salinas-Ramos, V.B. & Russo, D. (2019) The importance of ponds for the conservation of bats in urban landscapes. *Landscape and Urban Planning*, 190, 103607.
- Arnfield, A.J. (2003) Two decades of urban climate research: a review of turbulence, exchanges of energy and water, and the urban heat Island. *International Journal of Climatology*, 23, 1–26.
- Aronson, M.F.J., Lepczyk, C.A., Evans, K.L., Goddard, M.A., Lerman, S.B., MacIvor, J.S. et al. (2017) Biodiversity in the city: key challenges for urban green space management. *Frontiers in Ecology and the Environment*, 15, 189–196.
- Aronson, M.F.J., Nilon, C.H., Lepczyk, C.A., Parker, T.S., Warren, P.S., Cilliers, S.S. et al. (2016) Hierarchical filters determine community assembly of urban species pools. *Ecology*, 97, 2952–2963.
- Báldi, A. & Kisbenedek, T. (1997) Orthopteran assemblages as indicators of grassland naturalness in Hungary. *Agriculture, Ecosystems and Environment*, 66, 121–129.
- Banaszak-Cibicka, W. & Żmihorski, M. (2012) Wild bees along an urban gradient: winners and losers. *Journal of Insect Conservation*, 16, 331–343.
- Callaghan, C.T., Bowler, D.E. & Pereira, H.M. (2021) Thermal flexibility and a generalist life history promote urban affinity in butterflies. *Global Change Biology*, 27, 3532–3546.
- Di Bernardino, A., Iannarelli, A.M., Diémoz, H., Casadio, S., Cacciani, M., & Siani, A.M. (2022) Analysis of two-decade meteorological and air quality trends in Rome (Italy). *Theoretical and Applied Climatology*, 149, 291–307. Available from: <https://doi.org/10.1007/s00704-022-04047-y>
- Di Pietro, S., Mantoni, C. & Fattorini, S. (2021) Influence of urbanization on the avian species-area relationship: insights from the breeding birds of Rome. *Urban Ecosystem*, 24, 779–788.
- Diamond, S.E., Bellino, G. & Deme, G.G. (2023) Urban insect bioarks of the 21st century. *Current Opinion in Insect Science*, 57, 101028.
- Dziocck, F., Gerisch, M., Siebert, M., Hering, I., Scholz, M. & Ernst, R. (2011) Reproducing or dispersing? Using trait based habitat templet models to analyse orthoptera response to flooding and land use. *Agriculture, Ecosystems and Environment*, 145, 85–94.
- Fattorini, S. & Galassi, D.M.P. (2016) Role of urban green spaces for saproxylic beetle conservation: a case study of tenebrionids in Rome, Italy. *Journal of Insect Conservation*, 20, 737–745.
- Feldmeier, S., Schefczyk, L., Hochkirch, A., Lötters, S., Pfeifer, M.A., Heinemann, G. et al. (2018) Climate versus weather extremes: temporal predictor resolution matters for future rather than current regional species distribution models. *Biodiversity Research*, 24, 1047–1060.
- Fenoglio, M.S., Calviño, A., González, E., Salvo, A. & Videla, M. (2021) Urbanisation drivers and underlying mechanisms of terrestrial insect diversity loss in cities. *Ecological Entomology*, 46, 757–771.
- Fick, S.E. & Hijmans, R.J. (2017) Worldclim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, 37, 4302–4315.
- Filibeck, G., Petrella, P. & Cornelini, P. (2016) All ecosystems look messy, but some more so than others: a case-study on the management and acceptance of Mediterranean urban grasslands. *Urban Forestry & Urban Greening*, 15, 32–39.
- Fischer, J.D., Schneider, S.C., Ahlers, A.A. & Miller, J.R. (2015) Categorizing wildlife responses to urbanization and conservation implications of terminology. *Conservation Biology*, 29, 1246–1248.
- Fischer, L.K. & Kowarik, I. (2020) Connecting people to biodiversity in cities of tomorrow: is urban foraging a powerful tool? *Ecological Indicators*, 112, 106087.
- Fraissinet, M., Ancillotto, L., Migliozi, A., Capasso, S., Bosso, L., Chamberlain, D.E. et al. (2023) Responses of avian assemblages to spatiotemporal landscape dynamics in urban ecosystems. *Landscape Ecology*, 38, 293–305. Available from: <https://doi.org/10.1007/s10980-022-01550-5>
- Fratarcangeli, C., Fanelli, G., Testolin, R., Buffi, F. & Travaglini, A. (2022) Floristic changes of vascular flora in the city of Rome through grid-cell census over 23 years. *Urban Ecosystem*, 25, 1851–1864. Available from: <https://doi.org/10.1007/s11252-022-01293-w>
- Gandy, M. (2016) Unintentional landscapes. *Landscape Research*, 41, 433–440.
- Gossner, M.M., Simons, N.K., Achtziger, R., Blick, T., Dorow, W.H.O., Dziocck, F. et al. (2015) A summary of eight traits of coleoptera, Hemiptera, orthoptera and Araneae, occurring in grasslands in Germany. *Scientific Data*, 2, 1–9.
- Grilo, F., McPhearson, T., Santos-Reis, M. & Branquinho, C. (2022) A trait-based conceptual framework to examine urban biodiversity, socio-ecological filters, and ecosystem services linkages. *Npj Urban Sustainability*, 2, 32.
- Grimm, N.B., Faeth, S.H., Golubiewski, N.E., Redman, C.L., Wu, J., Bai, X. et al. (2008) Global change and the ecology of cities. *Science*, 319, 756–760.
- Hall, D.M., Camilo, G.R., Tonietto, R.K., Ollerton, J., Ahrné, K., Arduser, M. et al. (2017) The city as a refuge for insect pollinators. *Conservation Biology*, 31, 24–29.
- Hochkirch, A., Nieto, A., García Criado, M., Cáliz, M., Braud, Y., Buzzetti, F. M. et al. (2016) European Red List of Grasshoppers, Crickets and Bush-Crickets. 4.
- Horák, J. (2018) The role of urban environments for saproxylic insects. In: Ulyshen, M. (Ed.) *Saproxylic insects. Zoological monographs*, Vol. 1. Cham: Springer, pp. 835–846.
- Huchler, K., Pachinger, B. & Kropf, M. (2022) Management is more important than urban landscape parameters in shaping orthopteran assemblages across green infrastructure in a metropole. *Urban Ecosystem*, 26, 209–222. Available from: <https://doi.org/10.1007/s11252-022-01291-y>
- Iorio, C., Scherini, R., Fontana, P., Buzzetti, F.M., Kleukers, R., Odé, B., & Massa, B. (2019) *Grasshoppers and crickets of Italy: a photographic field guide to all the species*. WBA Project Srl, Italy.
- Kingsford, R.T., Basset, A. & Jackson, L. (2016) Wetlands: conservation's poor cousins. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 26, 892–916.
- Labadessa, R. & Ancillotto, L. (2022) A tale of two crickets: global climate and local competition shape the distribution of European *Oecanthus* species (orthoptera, Gryllidae). *Frontiers of Biogeography*, 14(4). <https://doi.org/10.21425/F5FBG57538>
- Labadessa, R. & Ancillotto, L. (2023) Small but irreplaceable: the conservation value of landscape remnants for urban plant diversity. *Journal of Environmental Management*, 339, 117907.
- Labadessa, R., Dura, T., Mascia, G., Pisconti, A., Rolli, E. & Wagner, W. (2018) First records of *Eyprepocnemis plorans plorans* in southeastern Italy (orthoptera: Acrididae). *Fragmenta Entomologica*, 50, 65–67. Available from: <https://doi.org/10.4081/fe.2018.288>
- Labadessa, R., Forte, L. & Mairota, P. (2015) Exploring life forms for linking orthopteran assemblage and grassland plant community. *Hacquetia*, 14, 24–33.

- Lampinen, J., Tuomi, M., Fischer, L.K., Neuenkamp, L., Alday, J.G., Bucharova, A., Cancellieri, L. et al. (2021) Acceptance of near-natural greenspace management relates to ecological and socio-cultural assigned values among European urbanites. *Basic and Applied Ecology*, 50, 119–131.
- Latella, L., Ruffo, S. & Stoch, F. (2007) The project CKmap (checklist and distribution of the Italian fauna) methods and informatical techniques. *Memorie del Museo Civico di Storia Naturale di Verona*, 17, 15–19.
- Losey, J.E. & Vaughan, M. (2006) The economic value of ecological services provided by insects. *Bioscience*, 56, 311–323.
- MacGregor-Fors, I., Escobar, F., Rueda-Hernández, R., Avendaño-Reyes, S., Baena, M., Bandala, V. et al. (2016) City “green” contributions: the role of urban greenspaces as reservoirs for biodiversity. *Forests*, 7, 146.
- Maxwell, S.L., Butt, N., Maron, M., McAlpine, C.A., Chapman, S., Ullmann, A. et al. (2019) Conservation implications of ecological responses to extreme weather and climate events. *Diversity and Distributions*, 25, 613–625.
- Melliger, R.L., Rusterholz, H.P. & Baur, B. (2017) Habitat- and matrix-related differences in species diversity and trait richness of vascular plants, orthoptera and lepidoptera in an urban landscape. *Urban Ecosystem*, 20, 1095–1107. Available from: <https://doi.org/10.1007/s11252-017-0662-5>
- Merckx, T., Souffreau, C., Kaiser, A., Baardsen, L.F., Backeljau, T., Bonte, D. et al. (2018) Body-size shifts in aquatic and terrestrial urban communities. *Nature*, 558, 113–116.
- Moretti, M., de Bello, F., Ibanez, S., Fontana, S., Pezzatti, G.B., Dzioc, F. et al. (2013) Linking traits between plants and invertebrate herbivores to track functional effects of land-use changes. *Journal of Vegetation Science*, 24, 949–962.
- New, T.R. (2015) *Insect conservation and urban environments*. Switzerland: Springer.
- Oksanen, J., Simpson, G.L., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R. et al. (2013) Package ‘vegan.’ Community Ecol Packag Version 2. 1–295.
- Penone, C., Kerbiriou, C., Julien, J.F., Julliard, R., Machon, N. & le Viol, I. (2013) Urbanisation effect on orthoptera: which scale matters? *Insect Conservation and Diversity*, 6, 319–327.
- Piano, E., De Wolf, K., Bona, F., Bonte, D., Bowler, D. E., Isaia, M. et al. (2017) Urbanization drives community shifts towards thermophilic and dispersive species at local and landscape scales. *Global Change Biology*, 23, 2554–2564.
- Piano, E., Souffreau, C., Merckx, T., Baardsen, L.F., Backeljau, T., Bonte, D. et al. (2020) Urbanization drives cross-taxon declines in abundance and diversity at multiple spatial scales. *Global Change Biology*, 2, 1196–1211.
- Planchuelo, G., Kowarik, I. & Von der Lippe, M. (2020) Endangered plants in novel urban ecosystems are filtered by strategy type and dispersal syndrome, not by spatial dependence on natural remnants. *Frontiers in Ecology and Evolution*, 8, 18.
- Rácz, I.A., Déri, E., Kisfali, M., Batiz, Z., Varga, K., Szabó, G. et al. (2013) Early changes of orthopteran assemblages after grassland restoration: a comparison of space-for-time substitution versus repeated measures monitoring. *Biodiversity and Conservation*, 22, 2321–2335.
- Rinnan, D.S. & Lawler, J. (2019) Climate-niche factor analysis: a spatial approach to quantifying species vulnerability to climate change. *Ecography*, 42, 1494–1503.
- Rosseel, Y. (2012) Lavaan: an R package for structural equation modeling. *Journal of Statistical Software*, 48, 1–36.
- Santini, L., González-Suárez, M., Russo, D., Gonzalez-Voyer, A., Hardenberg, A. & Ancillotto, L. (2019) One strategy does not fit all: determinants of urban adaptation in mammals. *Ecology Letters*, 22, 365–376.
- Smid, M., Russo, S., Costa, A.C., Granell, C. & Pebesma, E. (2019) Ranking European capitals by exposure to heat waves and cold waves. *Urban Climate*, 27, 388–402. Available from: <https://doi.org/10.1016/j.uclim.2018.12.010>
- Sperber, C.F., Zefa, E., de Oliveira, E.C., de Campos, L.D., Bolfarini, M.P., Fianco, M. et al. (2021) Measuring orthoptera diversity. In: Santos, J.-C. & Fernandes, G.W. (Eds.) *Measuring arthropod biodiversity*. Cham: Springer, pp. 257–287.
- Steffan-Dewenter, I. & Westphal, C. (2008) The interplay of pollinator diversity, pollination services and landscape change. *Journal of Applied Ecology*, 45, 737–741.
- Tryjanowski, P., Morelli, F. & Möller, A.P. (2020) Urban birds: urban avoiders, urban adapters, and urban exploiters. In: *The Routledge handbook of urban ecology*. Routledge, UK, pp. 399–411.
- Ummenhofer, C.C. & Meehl, G.A. (2017) Extreme weather and climate events with ecological relevance: a review. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 372, 20160135.
- Watts, C.H., Thornburrow, D., Green, C.J. & Agnew, W.R. (2008) Tracking tunnels: a novel method for detecting a threatened New Zealand giant weta (Orthoptera: Anostomatidae). *New Zealand Journal of Ecology*, 32, 92–97.
- Welti, E.A.R., Prather, R.M., Sanders, N.J., de Beurs, K.M. & Kaspari, M. (2020) Bottom-up when it is not top-down: predators and plants control biomass of grassland arthropods. *The Journal of Animal Ecology*, 89, 1286–1294. Available from: <https://doi.org/10.1111/1365-2656.13191>
- Whiles, M.R. & Charlton, R.E. (2006) The ecological significance of tallgrass prairie arthropods. *Annual Review of Entomology*, 51, 387–412.
- Wootton, J.T. (1994) Predicting direct and indirect effects: an integrated approach using experiments and path analysis. *Ecology*, 75, 151–165.
- Yang, D., Ye, C., Wang, X., Lu, D., Xu, J. & Yang, H. (2018) Global distribution and evolution of urbanization and PM<sub>2.5</sub> (1998–2015). *Atmospheric Environment*, 182, 171–178.
- Zapparoli, M. (1997a) Urban development and insect biodiversity of the Rome area, Italy. *Landscape and Urban Planning*, 38, 77–86. Available from: [https://doi.org/10.1016/S0169-2046\(97\)00020-0](https://doi.org/10.1016/S0169-2046(97)00020-0)
- Zapparoli, M. (1997b) *Insetti di Roma*. Roma: Palombi Editore.

## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**Figure S1.** Species accumulation curve of Orthoptera species detected in the study area (urban area of Rome, Italy) along sampling occasions ( $N = 62$ ).  $S$  = species richness.

**Table S1.** Description of ecomorphological traits of Orthoptera used for assessing species’ adaptability to urban environments.

**Table S2.** Orthoptera species from the urban area of Rome, as assessed by two checklists compiled in 1997 and 2022, respectively; X = species recorded; \* = excluded from trait-based analyses; species also recorded by citizen scientists.

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