TITLE

Urban refugia enhance persistence of an endemic keystone species facing a rapidly spreading invasive predator

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ABSTRACT

Urbanization shapes global biodiversity, often driving biodiversity loss and biotic homogenization. However, urban areas could paradoxically enhance conservation by acting as refugia for declining populations due to other global change components, such as biological invasions. Despite growing interest in the potential of urban areas to promote biodiversity conservation, the lack of robust empirical studies unveiling how urban refugia emerge and contribute to species persistence hinders our ability to leverage urban areas to minimize global biodiversity loss. In this study, we examined whether and how urban areas promote the persistence of a keystone Mediterranean island endemic lizard (*Podarcis pityusensis*) threatened by the invasive snake *Hemorrhois hippocrepis*. Using field transects and citizen science data, we found that while invasive snakes strongly drive local lizard extirpation, urbanization buffers this effect and supports local population persistence. Intensive snake trapping further revealed that urbanization acts as an ecological filter, hindering snake spread into urban centers. Finally, our population dynamics model shows that, contrary to a source-sink model, urban lizard populations can persist in the mid-term without the arrival of new individuals. Our findings effectively help uncover how urban areas can effectively act as refugia for threatened species, emphasizing their importance in global biodiversity conservation strategies.

INTRODUCTION

The destruction and fragmentation of natural ecosystems due to urbanization shapes patterns of biodiversity distribution worldwide [1,2]. In addition to habitat transformation, urbanization often entails the introduction of nonnative species, genetic isolation, or exposure to new diseases [3–5]. Altogether, these factors hinder biodiversity preservation of native biological communities and spur biotic homogenization across urban areas worldwide [6–8]. Paradoxically, however, urban areas could also effectively contribute to biological conservation when conditions in surrounding natural habitats become adverse [9].

The potential of urban areas to enhance biodiversity preservation has received considerable recent attention [10,11]. Urban habitats can for instance increase regional habitat heterogeneity and even promote phenotypic responses to different components of global change such as climate change or biological invasions [12–19]. An additional, intriguing way by which urban areas could contribute to global biodiversity conservation is by acting as refugia for species facing population declines in more natural surroundings [10,11]. The biotic or abiotic drivers of population decline in more natural areas could be buffered in these ‘urban refugia’, resulting in species ranges that are partially or completely restricted to these urban areas. Thus, urban areas are increasingly acknowledged as potential biodiversity reservoirs [9,20,21].

A number of recent studies have described patterns consistent with urban refugia. Plowes et al. [20] found that some urban residential areas in Texas had populations of the native fire ant species, *Solenopsis germinata*, while nearby natural habitats were occupied by the invasive species, *Solenopsis invicta*. They suggested that high vegetation cover or pest management in these urban areas might have limited the spread of the invasive species, thus creating urban refuges for the native ants. Another example can be found on the island of Hispaniola, where the endemic parrot *Psittacara chloropterus*, once common throughout the island [22], is currently absent from natural habitats [23]. It only persists in large urban areas where parrots are protected from hunting, further habitat destruction, and pet trafficking [24]. These valuable examples underscore the potential of urban areas to preserve endangered species, both against biotic [20,25] and abiotic threats [24,26].

Urban refugia could play a substantial role for future global biodiversity conservation because they may not only prevent local and global extinction of particular species [27], but rather also allow for their recovery and reintroduction if and when the threats in more natural habitats disappear. This possibility could enable the recovery of these species as well as the re-establishment of the ecological functions they play in the ecosystem [28]. This is crucial given that ecological interactions are essential to maintain ecosystem functioning as they hold the structure of and give stability to biological communities and ultimately sustain ecosystem services essential to human well-being [29–33]. In addition, the social dimension of urban refugia can help raise awareness for biodiversity conservation while leveraging umbrella species to safeguard entire biological communities [34–36].

Despite the potential of urban refugia to minimize biodiversity loss worldwide, however, essential questions regarding how urban refugia emerge remain poorly understood. Specifically, it is necessary to unravel the role of ecological filters that buffer the threats of surrounding natural habitats in urban areas [37]. Urban areas may for instance allow populations of native species to persist by preventing new predators to enter urban ecosystems where these native species thrive. Understanding how these filters work is essential to implement effective conservation strategies based on empirical data. In addition, apparent patterns of urban refugia could in fact emerge from source-sink dynamics from surrounding areas where urban areas worked as ecological traps. These sinks of biodiversity would not prevent population declines in the mid-term [38–40]. Our understanding of these questions is limited by the scarcity of studies moving beyond describing apparent patterns of urban refugia. Providing solid empirical evidence for how urban refuges emerge is crucial to assess their effectiveness as biodiversity reservoirs.

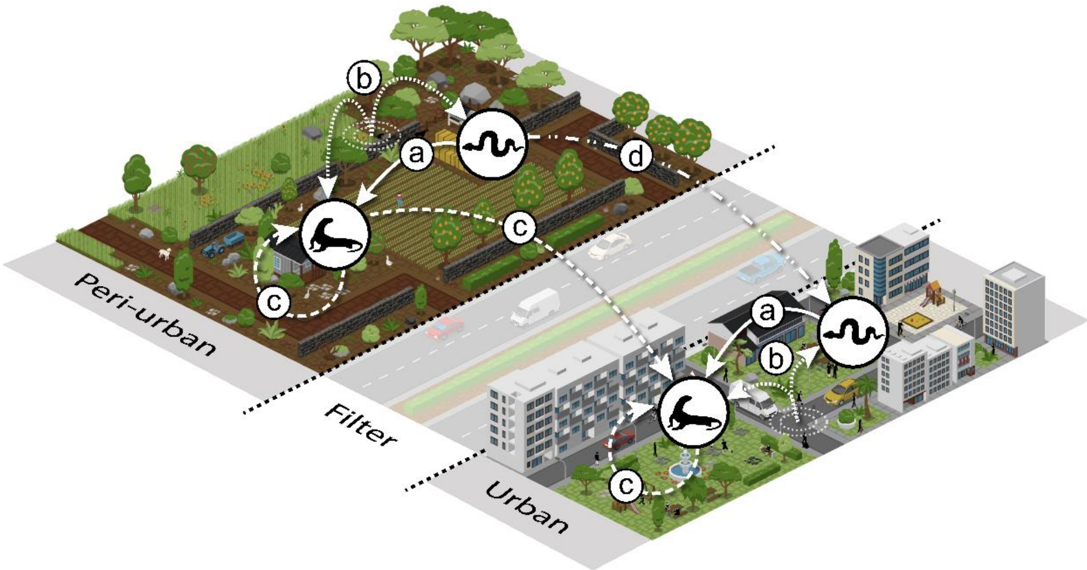

Figure 1: Conceptual diagram illustrating the main research questions addressed in this article. We investigate: a) the impact of the invasive predatory snake on the abundances of the Ibiza wall lizard in peri-urban (low urbanization) and urban (high urbanization) habitats, b) the effect of urbanization on the abundances of both the Ibiza wall lizard and the horseshoe whip snake, c) the population dynamics of the Ibiza wall lizard, and d) the potential role of urbanized areas as dispersal filters for the horseshoe whip snake.

To fill this gap, here we present a replicated study strictly designed to provide an empirical assessment of the effectiveness of urban refugia and to shed light into the processes behind these apparent patterns. We examine these questions to unravel whether and how urban refugia are enabling the persistence of the iconic Ibiza wall lizard *Podarcis pityusensis*, an endemic species facing extirpation due to the rapid spread of an invasive predator, the horseshoe whip snake *Hemorrhois hippocrepis*. Specifically, we quantify the effect of the presence of the invasive snake on the abundance and extirpation of the endemic lizard in urban and peri-urban areas. In parallel, we tackle the effect of urbanization on both species, use empirical trapping data to characterize if urbanization acts as a dispersal filter for the invasive horseshoe whip snake, and use modelling techniques to test for the existence of source-sink dynamics in urban lizard populations (Fig. 1).

METHODS

Study system

The Ibiza wall lizard (*Podarcis pityusensis*) is a lacertid lizard endemic to the islands of Ibiza and Formentera in the Balearic Islands, Spain [41,42]. This species is the only native terrestrial vertebrate species found during the recent evolutionary history of these islands. These lizards therefore evolved in the absence of terrestrial predators. Consequently, Ibiza wall lizards express a docile and relatively non-skittish behaviour, with little fear of humans, low levels of vigilance, and low aggression [43,44]. Ibiza wall lizards are very generalists and known to inhabit all sorts of habitats including forested, agricultural, and coastal areas with a preference for dry rock walls [41,42], to fully urbanized areas [45]. Being a successful urban dweller, together with its tame behaviour and colourful appearance, has led this species of lizard to become a beloved cultural icon of these islands [46,47].

In 2003, the horseshoe whip snake (*Hemorrhois hippocrepis*) was first detected in Ibiza [48–51]. This snake was introduced from the Iberian Peninsula via the importation of olive trees for gardening purposes [48,49]. Horseshoe whip snakes are characterized by an active foraging strategy and a preference for Mediterranean rocky environments, actively seeking for prey in natural or man-made walls [52]. The diet of the horseshoe whip snake is mainly composed of small mammals and reptiles, with juveniles feeding almost exclusively on reptiles while adults also prey on small mammals [53,54].

Consequently, since their accidental introduction in 2003 the snakes have spread rapidly across the island of Ibiza [50,51]. This spread has led to a sharp decline and even local extirpation of Ibiza wall lizard populations from the eastern half of the island, where the first individuals of the horseshoe whip snake arrived, to the west, where natural populations of the lizard can still be found in the absence of snakes [51,55,56]. In Ibiza, wall lizards represent a large proportion (57%) of prey items of horseshoe whip snakes [47]. Ibiza wall lizards are good urban dwellers and observational evidence suggests their presence in invaded areas might be restricted to urban areas. Together with the fact that both invaded and non-invaded areas in Ibiza include both urban and natural habitats, this system provides a unique opportunity to empirically examine whether and how urban areas are effectively acting as urban refugia.

Study design

We selected 18 localities across the island of Ibiza to investigate the role of these urban areas as possible refugia for the Ibiza wall lizard. We selected all urban areas that had existed as urban nuclei for the longest time, thus discarding recently built urbanizations. In each of these 18 localities we selected 4 urban points and 4 peri-urban points (Fig. 2). We considered as urban points all those habitats potentially good for the Ibiza wall lizard that were found within the urban matrix such as flowerbeds with rocks and vegetation, or dry-stone walls with vegetation (Fig. S1). To select peri-urban sites, we chose the closest vegetated dry-stone wall found around a random point located near unpaved roads and fields surrounding the sampled urban area (Fig. S2). We did not conduct any census on paved roads. Each of the points considered were selected in an attempt to choose a potentially optimal habitat for the Ibiza wall lizard. In total, we established 144 sampling points (i.e. 18 sites X 2 habitat types X 4 replicates). At each of these sampling points, we conducted standardized 3-minute active visual encounter survey censuses. During each census, we noted the total number of Ibiza wall lizard individuals detected both on dry-stone walls and in the surrounding vegetation. We conducted the surveys from a safe distance from focal animals and without disturbing the environment (i.e. we did not lift stones or shake vegetation to find lizards). We conducted the censuses on sunny days between May 1st and July 22nd, 2022, between 9:00 and 15:00, matching the highest activity period of this species [57]. We conducted a minimum of 2 censuses per sampling point (three in some cases), a total of 312 censuses conducted (Table S1).

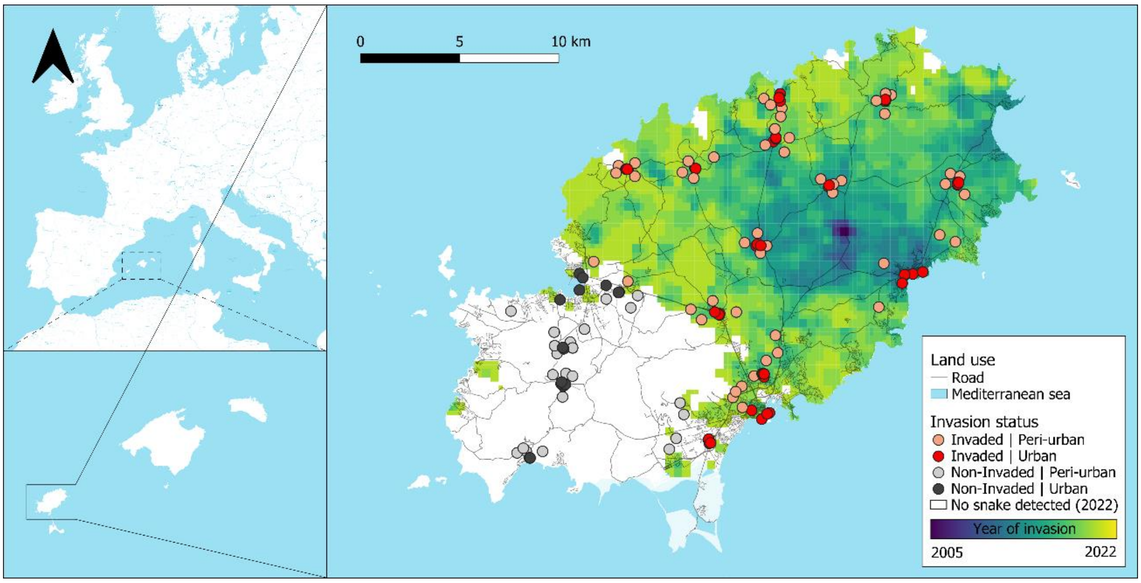

Figure 2: Map of the 144 sampling sites on Ibiza, Spain, distinguishing between urban (dark colors) and peri-urban (light colors) areas. Red marks correspond to invaded sites while grey marks represent non-invaded sites as of summer 2022. The map also includes a colour scale indicating the interpolated year of invasion by the horseshoe whip snake across the island.

Using citizen science data to build a snake establishment map

To identify the year snakes arrived at each sampling point, we created a map with the area occupied by the horseshoe whip snake from 2003 to 2023. To do this, we compiled a total of 5270 records of captures or sighting records of the horseshoe whip snake from 2003 to 2023. Data came from COFIB's horseshoe whip snake capture records (n = 2771, from 2016 to 2023, https://recuperacionfaunabaleares.es), data in Montes et al. [50] (n = 1291, from 2008 to 2018), an app integrating citizen snake observations (*Línea verde*, n = 904, from 2022 to 2023, https://www.lineaverdeeivissa.com), roadkills (n = 77, from 2021 to 2022, own data), iNaturalist (n = 14, from 2016 to 2023, https://www.inaturalist.org), and from an online survey we conducted in 2023 to local people regarding the year in which they detected for the first time a snake in their house (n = 213, from 2003 to 2023, own data). Then, we used QGis [58] (QGIS.org, 2023), to identify those records far from the invasion core that did not have any other records in the surrounding area in the following years. We considered these records as either location errors or secondary translocations that did not persist over time, and thus removed them from this establishment database (n = 45 observations). The remaining records were projected onto a 500 x 500m matrix superimposed on the island of Ibiza. We labelled each 500 x 500m cell with the year of the oldest snake record found in each cell. Then, using the QGIS Convex Hull tool, we created a polygon that encapsulated all online survey locations indicated by the island residents as snake-free (n = 90). All unlabelled cells that were located within this polygon were identified as "non-invaded". The remaining unlabelled cells were left unlabelled. Lastly, we performed an IDW (Inverse Distance Weighting) interpolation based on the year of invasion assigned to each 500 x 500m cell using the IDW interpolation QGis tool, with a P-parameter of 3.0 and a pixel size of 250m. We categorized each of the 144 sampling points as "invaded" or "non-invaded" depending on whether each point was located over the snake-invaded interpolated area between 2005 and 2022 (invaded) or not (non-invaded).

Urbanization index

To calculate the 'urbanization index' for each sampling point, we downloaded a .TIF file containing the 2021 satellite categorization of Ibiza's habitats at a 10m resolution [59] (Fig. S3). Using the R package '*raster'* [60,61], we draw a 50m radius area around each of the 144 sampling points and computed the percentage of 10 x 10m cells categorized as "Build up" found within each 50m radius area. The resulting percentages represented the 'urbanization index' of each sampling point, ranging 0 (not-urbanised) to 1 (fully urbanised, i.e. 100% impervious surface) (Fig. S4-S7).

Statistical analysis

Given the large number of zeros in our lizard census data (67.63%), we performed overdispersion and zero-inflation tests using the R package '*performance*' [60,62]. The results of the overdispersion test on an initial Generalized Linear Mixed Model (GLMM) following a Poisson distribution obtained using the R package '*glmmTMB*' [60,63] revealed no overdispersion in our data (Pearson's $\chi 2 = 197.92$, $p > 0.99$). The zero-inflation test revealed that our initial GLMM Poisson model did not correctly estimate the number of zeros (predicted/observed number of zeros = 0.92, tolerance = 1 ± 0.05), indicating a possible zero-inflation. Therefore, we modelled our data using zero-inflated Poisson regression. This type of regression assumes that the excess of zeros in our data would be caused by a different process than the process modelling the count data, so the two processes can be modelled independently. The explanatory variables considered for both parts of the model (Poisson part and zero-inflated part) were 'year of invasion' and 'urbanization index'. 'Year of invasion' was calculated as the normalized number of years that the snake has been present, based on the interpolated snake establishment map, at each sampling point, ranging from 0 (not invaded) to 1 (oldest invaded sampling site). Statistical models also included locality and sampling point as random factors, with sampling point nested within locality. To extract and visualize the results from these analyses, we used the R package ‘*sjPlot’* [60,64]. Additionally, we used the R package ‘*stats*’ [60] to perform a one-way ANOVA test and a post hoc Tukey’s HSD test to look for differences in the total number of lizards observed among the different treatments. Finally, we performed a spatial autocorrelation analysis using the R packages ‘*DHARMa’* [60,65] and ‘*pgirmess’* [60,66], which determined there was no spatial patterns in our data influencing the results (DHARMa Moran's I test, observed = -0.053, expected = -0.007, sd = 0.033, p = 0.17).

Urban filtering

We also conducted an exhaustive trapping procedure (51 traps baited with life mice to which snakes could not access) during the months of May to September of 2022 to quantify the role of urban areas as potential filters for the dispersal of snakes and their chances to become established in these areas. With this aim, we delimited three successive 1.5km^2 urban areas within the city of Ibiza, separated from each other by major roads. These three areas were thus ordered sequentially from less to more urbanized to detect snake movements between invaded peri-urban areas to nearby urban areas. In each of the delimited areas, we tallied the total number of snakes captured. We used the R package ‘*stats*’ [60] to perform a one-way ANOVA test and a post hoc Tukey’s HSD test to look for differences in the number of snakes captured between the three considered areas.

Modelling source-sink dynamics in urban refugia

Finally, we examined the key hypothesis that urban areas might actually act as sinks rather than refuges for native lizard populations. With this aim, we conducted simulations to model population dynamics of urban and peri-urban lizard populations under different levels of predation pressure. The simulation is divided into two parts. The first part is dedicated to simulating the population dynamics of a closed population of lizards. The second part models the effects of various mortality sources, both intrinsic and extrinsic, on this same closed population.

At the start of the simulation, a typical population of lizards from undisturbed environments is simulated. With each iteration (corresponding to one year), the simulated lizard population sequentially undergoes a mortality episode due to anthropogenic factors (e.g. predation by cats, roadkills), a mortality episode due to the presence or absence of snakes in the habitat, which is modulated by the degree of urbanization of the habitat, and a density-dependent mortality episode. Once all this external mortality has occurred, the model moves to the part dedicated to simulating the population dynamics of a closed population of lizards. Episodes of mortality due to senescence and population stochasticity follow, after which the surviving individuals reproduce and lay eggs, from which new individuals will hatch and form the next generation. Finally, an immigration episode occurs, in which individuals from outside the simulated population are introduced into the next generation. The simulation progresses generation by generation until the maximum number of projection years is reached. Each year, the population size of each simulation is analyzed under each invasion regime. For a detailed description of all parameters and steps included in the model, please refer to the 'Source-sink dynamic model description' section in the Supplementary materials.

RESULTS

The maximum number of lizards observed in a single census was 14. This corresponds to an urban site located within the city of Ibiza, located within the snake-invaded area range (mean = 1.07, sd = 2.70). The highest number of lizards observed in peri-urban sites in snake-invaded areas was 5 (mean = 0.30, sd = 0.88). For non-invaded sites, the highest number of lizards observed in urban sites was 11 (mean = 1.98, sd = 2.33), whereas we observed a maximum of 9 lizards in peri-urban sites (mean = 1.11, sd = 1.70, Fig. 3). The one-way ANOVA test revealed significant differences in the total number of lizards observed among the different treatments ($F_{3,\ 308}$ = 7.40, p < 0.001, Table S2). Post-hoc Tukey's HSD test indicated significant differences between invaded urban and invaded peri-urban environments (p = 0.034, CI = [0.04, 1.51], Table S2), and non-invaded urban and invaded peri-urban environments (p < 0.001, CI = [0.74, 2.62], Table S2). The proportion of censuses with zero lizard sightings within the snake-invaded area was 69.5% in urban sites and 84.6% in peri-urban sites. In non-invaded areas, the proportion of censuses with zero sightings was 34.4% in urban sites, and 46.7% in peri-urban sites.

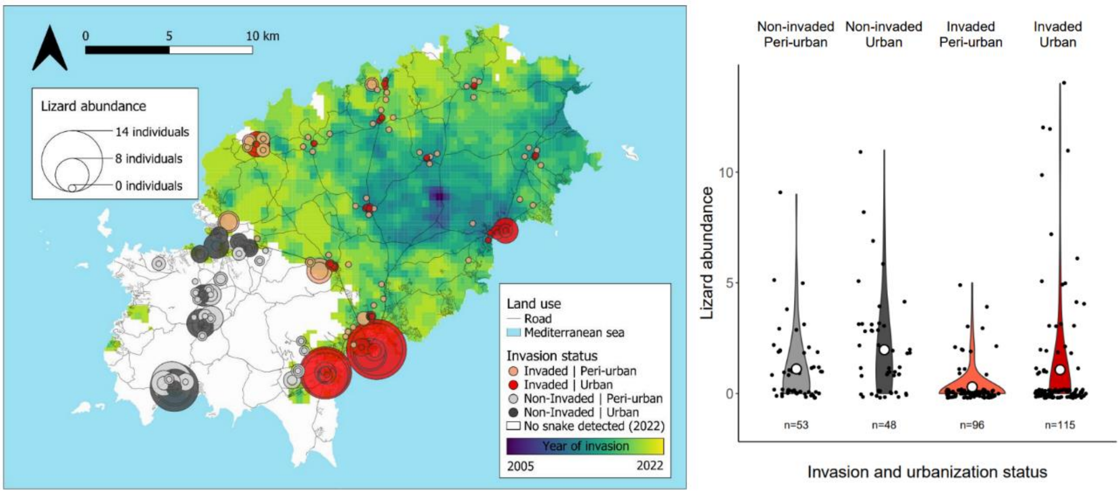

Figure 3: Maximum number of Ibiza wall lizard individuals observed per sampling point (n=144 points) across the 18 sampled towns of the island of Ibiza, represented by the diameter of the circle. The colour of the circles indicates the invasion and urbanization status of each site. The map also displays a colour scale representing the interpolated year in which the horseshoe whip snake became established across the island (left). Violin plot showing the total number of lizards observed in each of the 312 censuses performed. The white circle represents the mean number of lizards observed per treatment (right).

The GLMM results following the zero-inflated Poisson regression can be divided into two parts: one that explains the role of the explanatory variables in modelling the distribution of the excess of zeros (i.e. local lizard extirpation; zero-inflated part) and one that explains the role of the explanatory variables in explaining the distribution of the count values (i.e. relative local lizard abundance; Poisson part). The zero-inflated part of the model shows that both ‘urbanization index’ (odds ratio = -1.82, CI = [-3.50, -0.14], $\chi 2$ = 4.52, $p < 0.001$) and ‘year of invasion’ (odds ratio = 4.53, CI = [2.09, 6.76], $\chi 2$ = 15.76, $p < 0.001$, Fig. 4, Table 1) have a significant effect in explaining the excess of zeros observed in our data (i.e. no lizards detected). The Poisson part of the model indicates that both ‘urbanization index’ (odds ratio = 0.75, CI = [0.06, 1.44], χ^2 = 4.48, $p < 0.05$) and ‘year of invasion’ (odds ratio = -2.68, CI = [-4.73, -0.64], χ^2 = 6.60, $p < 0.05$, Fig. 4, Table 1) also have a significant effect on local relative lizard abundance (the count part of the model).

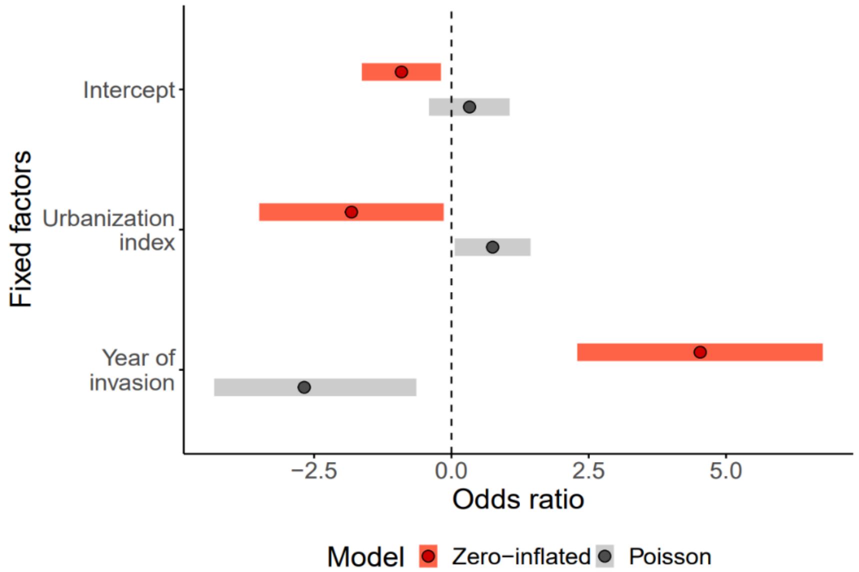

Figure 4: Results of the Generalized Linear Mixed Model (GLMM) testing the effects of the ‘year of invasion’ and ‘urbanization index’ on the presence-absence (zero-inflated model) and abundance (Poisson model) of Ibiza wall lizard individuals. The figure displays the odds ratio for each fixed factor predictor (x-axis) included in the GLMM. The dark dot indicates the mean odds ratio value, while the box shows the 95% confidence interval. The vertical dashed line denotes the null value.

In our snake trapping procedure to test the urban filter hypothesis, we captured 62 snakes in the outer area (mean = 3.44 snakes/trap, sd = 3.18) and 13 in the intermediate area (mean = 1.63 snakes/trap, sd = 1.41), while no snakes were captured in the inner area (Fig. 5). Overall, there were significant differences between groups in the number of snakes captured (one-way ANOVA test, $F_{2, 38}$ = 9.94, $p < 0.001$). This significance emerges from different number of captured snakes between the outer area and the inner area (Tukey’s HSD test for multiple comparisons, $p < 0.001$, CI = [-5.33, -1.55]) whereas differences between the outer area and the intermediate area ($p = 0.14$) or between the intermediate area and the inner area ($p = 0.22$) did not reach significance.

Table 1: GLMM results on the effects of year of invasion and urbanization index on the presence-absence (a) and abundance (b) of Ibiza wall lizard individuals.

(a) Presence-absence of lizards (Zero-inflated model)			
Variable	Odds ratio [95% CI]	χ^2	p
(Intercept)	-0.91 [-1.63, -0.19]		0.014
Urbanization index	-1.82 [-3.50, -0.14]	4.52	0.033
Year of invasion	4.53 [2.29, 6.76]	15.76	< 0.001
(b) Abundance of lizards (Poisson model)			
Variable	Odds ratio [95% CI]	χ^2	p
(Intercept)	0.33 [-0.41, 1.06]		0.385
Urbanization index	0.75 [0.06, 1.44]	4.48	0.034
Year of invasion	-2.68 [-4.73, -0.64]	6.60	0.010
Random effects			
σ^2	0.81		
τ_{00}	$0.33_{Site:Town}$		
	0.76_{Town}		
ICC	0.57		
Marginal R^2	0.24		
Conditional R^2	0.68		
AICc	686.36		

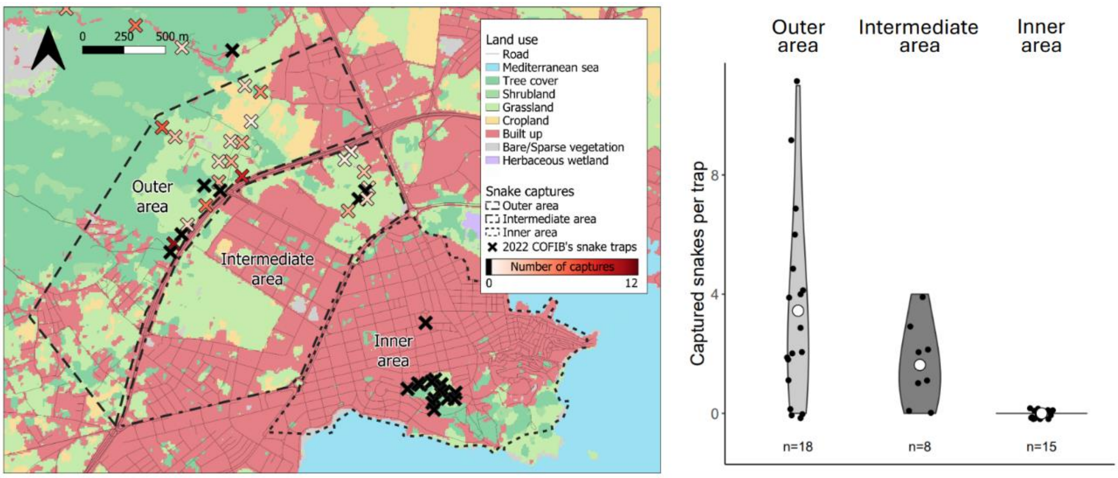

Figure 5: Map of the city of Ibiza showing 2022 snake traps location. Trap locations were divided into 3 areas of 1.5km^2 each. The colour of the symbol used to mark trap locations indicates the number of snakes captured in each trap during the period the trap was active, with black corresponding to 0 captures and shades of red for increasing capture numbers for each trap (left). Number of captures per trap for each of the three 1.5km^2 areas, with a white dot indicating the mean number of captures (right).

Finally, our population dynamics model, used to examine the potential existence of source-sink dynamic in urban areas revealed that current abundances in invaded urban environments can only be explained by the existence of an urban refugia effect. Low to moderate levels of mortality due to anthropogenic activities allow lizards in urban areas to maintain stable population numbers without the need for external individuals to immigrate into these habitats when anthropogenic activities affect lizard survival weakly (Fig. 6a-c) or moderately (Fig. 6d-e), only becoming eventually extirpated when such mortality is very high (Fig. 6f). The presence of snakes disrupts these stable dynamics (Fig. 6g-l). When anthropogenic activities are moderate, snakes cause a rapid decline in lizard numbers and lead to the local extirpation of these populations (Fig. 6g-i). This accelerated population decline is, however, mitigated by increased urbanization. Relatively high urbanization scores allow population persistence despite the presence of snakes in the surrounding areas (Fig. 6j-l). These results reject the hypothesis that urban areas could be acting as ecological traps for lizard populations; urban areas are not acting as biodiversity sinks. This result underscores that urban areas can serve as effective refugia against the accelerated decline of native populations, at least in the mid-term.

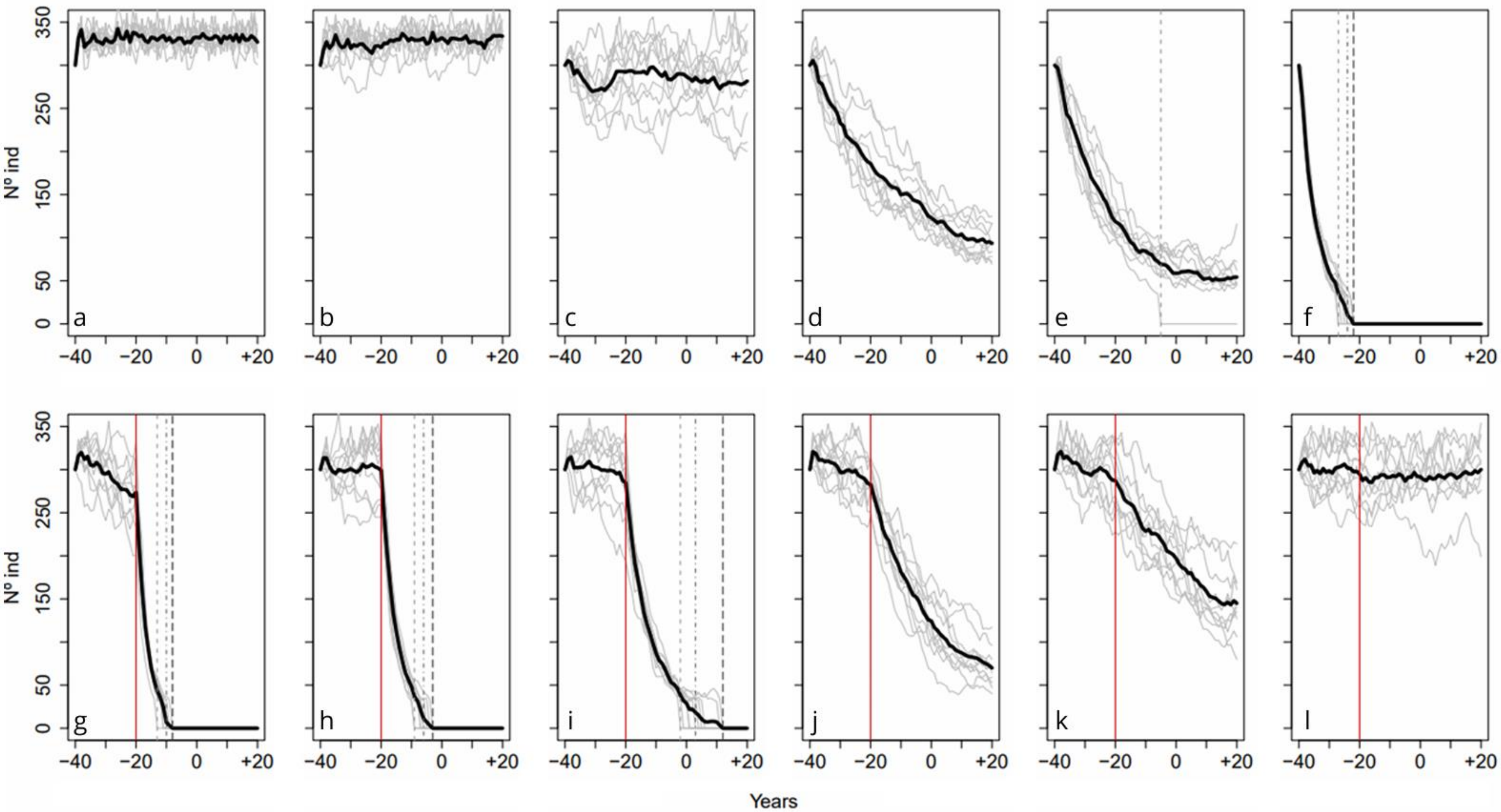

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Figure 6: Effect of the mortality derived from anthropogenic factors (top row) and urbanization index (bottom row) on a simulated population of Ibiza wall lizards over time. On the X-axis, 0 represents the present; the past is depicted to the left, and the model's future projection is shown to the right. The Y-axis represents the total number of living individuals in the lizard population. In the top row, the negative effect of anthropogenic factors progressively increases (e = 0.05, 0.075, 0.1, 0.125, 0.15, 0.25), with no snake introduction at any point. In the bottom row, the effect of anthropogenic factors is fixed at e = 0.1, and snake predation pressure is fixed at s = 0.25, exclusively modifying the urbanization index (u = 0.0, 0.25, 0.5, 0.8, 0.9, 1.0) following empirically measured urbanization index distribution of our sites (Fig. S7). Grey lines represent individual simulations (n = 10), and the black line shows the average of these simulations. The vertical red line indicates the year of snake introduction, and the vertical grey lines indicate the year in which the first simulated population becomes virtually extinct (short, dashed light grey line), the year in which half of the populations are virtually extinct (short, dashed medium grey line), and the time all populations become virtually extinct (long, dashed dark grey line). A population is considered virtually extinct when fewer than 10% of the carrying capacity of individuals remain alive.

DISCUSSION

Despite their enormous implications for global biodiversity conservation, whether and how urban refugia can effectively promote population persistence remains poorly understood. To tackle this question, we integrated exhaustive field data from free ranging native prey and trapping of their invasive predators with citizen science data and modelled urban population dynamics. Altogether, our results provide empirical demonstration that urban areas are effectively enhancing survival of the keystone Ibiza wall lizard, a keystone species from a delicate Mediterranean ecosystem.

Before the arrival of the horseshoe whip snake to the island of Ibiza in the early 2000s, Ibiza wall lizards were abundant throughout the island, both in natural and urban habitats [41,42]. Since then, this situation changed dramatically across the island with snake-free habitat rapidly shrinking every year [47,50,51]. Results from our GLMMs suggest that the presence of invasive snakes has significantly reduced Ibiza wall lizard abundances across the island. More specifically, the longer the snake has been established in a specific area, the greater is the effect on the lizard populations (Fig. 1a). The effect of 'year of invasion' on the zero-inflated part of the model is significantly positive. This implies that the time since the establishment of snakes in an area is positively associated with the proportion of censuses with zero lizard observations compared to the proportion of zeroes expected by a simple Poisson distribution (Fig. 4, Table 1). On the other hand, the effect of the variable 'year of invasion' on the Poisson part of the model is significantly negative, revealing that the longer the snake has been established, the lower the number of lizards counted per census (Fig. 4, Table 1).

In this uncertain scenario, nonetheless, urban areas seem to offer some hope. Although Ibiza wall lizard populations seem to be declining at an alarmingly rate, urban Ibiza wall lizard populations seem to be coping well with this situation (Fig. 1b). Ibiza wall lizard abundances in large urban areas are in fact among the highest in the island, despite snakes having long been established in the surrounding peri-urban areas (Fig. 3). The results obtained from the GLMM support these findings. The effect of the variable ‘urbanization index’ on the zero-inflated part of the model is significantly negative. As urbanization index increases, the proportion of zeroes observed (i.e., censuses with zero lizard observations) decreases with respect the total number of zeroes expected by a Poisson distribution (Fig. 4, Table 1). On the other hand, in the Poisson part of the model, the effect of ‘urbanization index’ on the number of lizards observed is significantly positive, meaning that the number of lizards observed increases with urbanization index (Fig. 4, Table 1). Our results provide long-needed empirical evidence that urbanization can favour species that are otherwise threatened in more natural surrounding habitats. These patterns are consistent with patterns observed across taxa in different areas of the planet [20,24–26,67]. Whether these patterns emerge from a filter that differentially affects native prey from their invasive predators, however, still remains an open question.

Ecological filters as a driver of urban refugia

A crucial open question to understand how urban refugia emerge remains the role of ecological filters. Ecological filters can limit the establishment of populations of invasive predators in habitats that are potentially suitable for them. One example of ecological filter is the dispersal or expansion filter, which restricts the movement of dispersing individuals from one area to another [37,68]. Here we investigated the possibility that roads act as dispersal filters for invasive snakes in search of new territories [20,69]. Although the horseshoe whip snake can sometimes exploit urban habitats [53,54], heavily trafficked roads could limit their ability to colonize these areas. The results of our analyses on the number of snakes captured in every delimited 1.5km^2 area within the city of Ibiza reveal significant differences between the outermost part of the city and the inner part of the city. As the habitat gets increasingly urbanised, and the number of roads and vehicles increase, the number of snakes captured progressively decreased to zero. This suggests a filtering process along the peri-urban to urban transition (Fig. 1d).

Another urban filter that may contribute to the emergence of urban refugia is the interaction filter. In urban environments, other species may interact differently with the invasive predators than with their native species. Snakes have been absent from Ibiza in recent evolutionary times. Thus, citizens had never seen snakes on the island until the recent invasion [48,49] and do not tolerate 2their presence due to either environmental concerns [70] or fear [71,72]. With the expansion of the invasion, Ibiza administrations implemented several pest detection and control measures (COFIB, ‘Línea verde’, ‘Amics de la Terra Eivissa’). Consequently, snakes in Ibiza are more easily detected and culled in urbanized areas, where more people reside, than in peri-urban areas [73,74]. Meanwhile, the colourful appearance and tame behaviour of Ibiza wall lizards have turned them into a beloved species that is in fact a cultural icon of the island [46,47]. As a result, Ibiza wall lizards have long maintained good population numbers in urban areas [56]. This interaction filter, coupled with the dispersal challenges posed by the dispersal filter, likely contributes significantly to the persistence of endemic lizards in urban areas despite the rapid snake expansion [37,47,50,51].

These combined filtering effects explain why larger urban areas seem to act as more effective refugia for the Ibiza wall lizard than smaller ones. For instance, the number of lizards observed in the main city of Ibiza is the highest compared to other urban and peri-urban sites (Fig. 3). As urban areas expand and their urbanization index increases, the likelihood of detecting lizards in their optimal urban habitats also rises (Fig. 4, Table 1). With this expansion, the number of roads acting as barriers and the number of people capable of detecting snakes also increases, providing enhanced protection for the lizard populations and supporting their persistence in larger urban areas, consistent with previous studies [2,75].

Source sink dynamics and ecological traps

A crucial question to shed light on the biological relevance of urban refugia is to ensure that patterns apparently consistent with urban refugia are not in fact acting as ecological traps. If this happened, urban areas may not be able to maintain stable populations in the longer term and therefore they would ultimately act as biodiversity sinks [2,75]. For an urban area to be considered an urban refuge, the species with its distribution range restricted to these urban areas should benefit from either greater resource accessibility [76–78], environmental stability [26,79], or protection against multiple threats [80,81] compared to their natural distribution. In contrast, ecological traps could emerge if individuals in urban areas in fact had lower fitness than their conspecifics present in surrounding natural habitats [82,83]. This could happen as a consequence of factors such as predation, pollution or diseases [38,82–84]. Therefore, urban refugia should allow the maintenance of stable populations without the need of individuals immigrating from peri-urban areas. Long-term population persistence is however uncertain in the current context of rapid environmental change. Conditions that may initially allow for the establishment of urban refugia might change over time due to new management practices [38,85] or as a consequence of unpredictable climatic events [83], turning these urban refugia into ecological traps.

In this study, we used a modelling approach based on field and published data to formally test the hypothesis that urban areas in Ibiza are effectively maintaining population numbers in the absence of immigration from surrounding areas under distinct mortality pressures and varying degrees of urbanization. Results indicate that when mortality rates from anthropogenic activities are low to moderate urban populations are viable without the need for external immigration (Fig. 1c and 6a-e). These findings support the idea that urban areas are not acting as ecological traps but rather as urban refugia. However, a high mortality rate due to anthropogenic activities could potentially turn these urban refuges into ecological traps [2] (Fig. 6f). Therefore, adequate management of these refuges must be prioritized to enhance population persistence [8,38]. On the other hand, stable urban populations under low to moderate anthropogenic mortality rates are rapidly destabilized and succumb to local extirpation with the introduction of the invasive snake (Fig. 6g-i). While urban areas can serve as refugia, if the urbanization index of these areas is not sufficiently high, the protection they offer to lizard populations is insufficient to prevent local extirpation (Fig. 6j-l). Otherwise, the introduction of the snake turns these urban areas into biodiversity sinks.

Species conservation and management strategies in urban refugia

The number and extension of green areas with native vegetated area and dry-stone walls should be increased to promote lizard population persistence in urban habitats, as suggested for other species [85,86]. Outside these optimal habitats, Ibiza wall lizards in urban areas are still vulnerable to other threats such as road mortality or predation by other opportunistic urban predators like cats, seabirds, or kestrels [43,87,88]. In addition, a low connectivity between these optimal habitats commonly hinders their long-term viability [68,89]. A management strategy to enhance connectivity between Ibiza wall lizard urban populations could be the creation of ecological corridors between urban parks [90]. This strategy, paradoxically, could be a disaster in some cases, such as for the Ibiza wall lizards. The creation of ecological corridors could in fact serve as an opportunity for snakes that manage to enter these urban areas to establish urban populations. Although uncommon, snake sightings occur within Ibiza's urban areas [55]. This possibility underscores that management practices in urban refugia should be finely tailored to the ecology of the species that aims to be protected. Otherwise, some common management practices could in fact help transform these urban refugia into biodiversity sinks [37,38,91].

Independently, investment in pest control measures, citizen awareness, and participation in biodiversity monitoring should reduce the possibility that urban refugia become ecological traps [73,74,92]. If ecological corridors exist, the capture effort along these corridors should be prioritized. In addition, the role of citizens can also be crucial in maintaining the effectiveness of urban refugia. Raising awareness about the cultural, ecological, and evolutionary heritage of targeted species is a key step to involve citizens in conservation practices. Citizens can contribute for example by setting traps, reporting snake sightings, or reporting the status of urban lizard populations. The development of digital tools such as apps or websites for reporting these events to wildlife management entities could encourage citizen participation in the conservation of this species [1,73,74,92,93]. These measures of citizen participation already exist in Ibiza and citizen science data has proven essential for the present study.

The importance of urban refugia for the functioning of biological communities and preservation of culture

Urban refugia can play a significant role in biodiversity preservation in two distinct ways. Firstly, our study provides empirical evidence that urban areas can act as shelters, enabling the mid-term persistence of species populations that are rapidly declining in surrounding natural landscapes [10,27,94]. Once the causes of decline are mitigated, for example by the removal of invasive predators, urban populations could become crucial for management strategies like reintroduction programs [28].

Secondly, urban refugia are vital for preserving the functionality of entire native biological communities. This is especially true when these refugia effectively protect populations of keystone species, which influence ecological interactions that sustain the structure and stability of their communities [29–33]. The global extirpation of keystone species has had dramatic cascading effects on the functioning of biological communities [33,95–97], and this can happen rapidly with the introduction of novel predators [19,98,99]. Degradation of ecosystem functionality can result in the loss of ecosystem services essential for human civilization [31,32]. For example, the generalist Ibiza wall lizard regulates arthropod populations through predation and also serves as an important pollinator and seed disperser [100–102]. Conserving these endemic keystone species also means preserving part of the local culture. Therefore, iconic species such as the Ibiza wall lizard can serve as umbrella species preserving ecological interactions that ensure the resilience of biological communities [34–36].

Invasive snakes wreak havoc on island communities worldwide. For example, the California kingsnake *Lampropeltis californiae* on the island of Gran Canaria (Spain) has led to the local extirpation of the Gran Canaria giant lizard *Gallotia stehlini* and a significant decline in the populations of Gran Canaria skink *Chalcides sexlineatus* and Boettger's gecko *Tarentola boettgeri*, all three are endemic to the island of Gran Canaria [103]. On the island of Guam, the accidental introduction of the brown tree snake in the 1940s led to the extinction of various endemic bird species, as well as a species of bat, and a snail [25,104,105]. Management of these invasive species has proven extremely challenging worldwide and whether and how urban refugia can offer hope in such scenarios has remained virtually unknown. Future research will be fundamental to unravel if the mid-term persistence of urban animal populations translates into management strategies that effectively enhance their re-establishment in natural surroundings after the mitigation of the threats that decimated them.

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Authors Contribution

MVG: Writing – original draft (equal); Writing – Review & Editing (lead); Formal Analysis (lead); Methodology (equal). **SM:** Writing – original draft (equal); Methodology (equal). **GC:** Conceptualization (equal); Methodology (equal); Formal Analysis (equal); **VC:** Methodology (equal); Resources (lead). **OL:** Conceptualization (equal); Writing – Review & Editing (equal); Formal Analysis (equal); Methodology (equal).

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