TITLE

Urban refugia enhance persistence of an endangered endemic keystone lizard threatened by the rapid spread of an invasive predator

LIST OF AUTHORS

Marc Vez-Garzón [a,b]*, Sandra Moreno [a]*, Guillem Casbas [a,b], Victor Colomar [c], Oriol Lapiedra [a]

* Both authors contributed extensively to this work

INSTITUTIONAL AFFILIATIONS

[a] Centre for Ecological Research and Forestry Applications (CREAF), Catalonia, Spain
[b] Autonomous University of Barcelona (UAB), Catalonia, Spain
[c] Consortium for the Recovery of Fauna of the Balearic Islands (COFIB), Government of the Balearic Islands, Santa Eugènia, Balearic Islands, Spain

CONTACT INFORMATION

Oriol Lapiedra as corresponding author: o.lapiedra@creaf.uab.cat

ABSTRACT

Urbanization shapes global patterns of biodiversity. While often driving biodiversity loss and biotic homogenization, urban areas could paradoxically act as refugia for species threatened by other global change drivers, such as biological invasions. Despite growing interest in their conservation potential, a 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. Here, we examined whether and how urban areas promote the persistence of a keystone, endangered endemic Mediterranean island lizard (*Podarcis pityusensis*) threatened by a rapidly spreading invasive snake (*Hemorrhois hippocrepis)*. By integrating field transects, citizen science data, snake trapping, and population dynamics models, we show that invasive snakes drive rapid lizard extirpation in natural areas, but urbanization buffers this effect, enabling local persistence. Intensive snake trapping revealed that urbanization hinders snake spread, acting as an ecological filter. Finally, population dynamics models show that, contrary to a source-sink model, urban lizard populations can persist in the mid-term under sustained predation pressure without requiring an influx of new individuals from surrounding areas. Our findings provide empirical evidence of 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 (McKinney, 2002, 2008). In addition to habitat transformation, urbanization often entails the introduction of non-native species, genetic isolation of populations, or their exposure to new diseases (Dickman, 1996; Fusco et al., 2021; Sol et al., 2013). Altogether, these factors hinder biodiversity preservation of native biological communities and spur biotic homogenization across urban areas worldwide (Faeth et al., 2011; McKinney & Lockwood, 1999; Piano et al., 2020). Paradoxically, however, urban areas could also effectively contribute to biological conservation when conditions in surrounding natural habitats become adverse (Spotswood et al., 2021).

The potential of urban areas to enhance biodiversity preservation has received considerable recent attention (Gentili et al., 2023; Lokatis et al., 2023). 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 (Alberti et al., 2017; Campbell-Staton et al., 2020; Lapiedra, 2018; Lapiedra et al., 2017; Lowry et al., 2013; Sage, 2020; Sih, 2013; Wong & Candolin, 2015). 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 (Gentili et al., 2023; Lokatis et al., 2023). 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 (Plowes et al., 2007; Rebolo-Ifrán et al., 2017; Spotswood et al., 2021).

A number of recent studies have described patterns consistent with urban refugia. Plowes et al. (2007) 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 refugia for the native ants. Similarly, on the island of Hispaniola the endemic parrot *Psittacara chloropterus*, once common throughout the island (Wetmore & Swales, 1931), is currently absent from natural habitats (Kirwan et al., 2019). It only persists in large urban areas where parrots are protected from hunting, further habitat destruction, and pet trafficking (Luna et al., 2018). These valuable examples underscore the potential of urban areas to preserve endangered species, both against biotic (Plowes et al., 2007; Savidge, 1987) and abiotic threats (Luna et al., 2018; Rutz, 2008).

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 (Ives et al., 2016), 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 (Hale & Koprowski, 2018). 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 (Jordán, 2009; Montoya & Raffaelli, 2010; Sanders et al., 2013; Tylianakis et al., 2008; Valiente-Banuet et al., 2015). In addition, the social dimension of urban refugia can help raise awareness for biodiversity conservation while leveraging umbrella species to safeguard entire biological communities (Branton & Richardson, 2011; Mekonnen et al., 2022; Roberge & Angelstam, 2004).

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 (Aronson et al., 2016). 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. Additionally, the apparent patterns of urban refugia could actually result from source-sink dynamics, where surrounding natural areas act as sources, continuously supplying individuals to urban zones that function as ecological traps. These sinks of biodiversity would not prevent population declines in the mid-term (Hale & Swearer, 2016; Sousa et al., 2019; Zuñiga-Palacios et al., 2021). 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 refugia emerge is crucial to assess their effectiveness as biodiversity reservoirs.

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 being rapidly extirpated due to predation by a rapidly spreading invasive predator, the horseshoe whip snake *Hemorrhois hippocrepis*. The effects of this invasive predator to native lizards have been extremely severe (Montes et al., 2022). Consequently, the IUCN recently reassessed the conservation status of the Ibiza wall lizard from 'Near Threatened' to 'Endangered' as a direct result of this expansion (IUCN, 2025). Here, we quantify how the arrival of the invasive snake shapes the abundance and extirpation of the endemic lizard across an urbanization gradient. In parallel, we use 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 (Salvador, 2015; Salvador & Pérez-Mellado, 1984). 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 behavior, with little fear of humans, low levels of vigilance, and low aggression (Cooper et al., 2014; Cooper & Pérez-Mellado, 2010). 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 (Salvador, 2015; Salvador & Pérez-Mellado, 1984), to fully urbanized areas (Carretero et al., 1995). Being a successful urban dweller, together with its tame behavior and colorful appearance, has led this species of lizard to become a beloved cultural icon of these islands (Dappen et al., 2009; Hinckley et al., 2017).

In 2003, the horseshoe whip snake (*Hemorrhois hippocrepis*) was first detected in Ibiza (Álvarez et al., 2010; Hinckley et al., 2017; Montes, 2021; Montes et al., 2022; Silva-Rocha et al., 2018). This snake was introduced from the Iberian Peninsula via the importation of olive trees for gardening purposes (Álvarez et al., 2010; Silva-Rocha et al., 2018). 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 (Pleguezuelos, 1989). 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 (Pleguezuelos & Moreno, 1999; Vericad-Coromina & Escarré-Esteve, 1976).

Consequently, since their accidental introduction around 2003, horseshoe whip snakes have rapidly spread across the island of Ibiza (Montes, 2021; Montes et al., 2022). This expansion has caused a severe decline in Ibiza wall lizard populations, with complete local extirpations tightly following the geographical expansion of the invasion front. In contrast, natural populations of the lizard still persist in the westernmost regions of the island, where snakes have not yet established (COFIB, 2022; Montes et al., 2022; Pérez-Cembranos & Pérez-Mellado, 2022). Ibiza wall lizards make up 57% of the snakes' diet in Ibiza (Hinckley et al., 2017). Consequently, the IUCN the conservation status of the Ibiza wall lizard recently escalated by two levels, from 'Near Threatened' to 'Endangered' (IUCN, 2025). However, these lizards are also highly adaptable to urban environments (Carretero et al., 1995), and observational evidence suggests that in snake-invaded areas, their presence is largely restricted to intensively urbanized habitats. Given that both invaded and non-invaded regions contain a mix of urban and natural habitats, this system offers a unique opportunity to empirically examine whether urban areas are effectively acting as refugia for this keystone, endangered endemic species.

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 four urban points and four 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 suitable habitat for the Ibiza wall lizard. In total, we established 144 sampling points (i.e. 18 sites × 2 habitat types × 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 (Pérez-Mellado & Salvador, 1981). We conducted a minimum of two censuses per sampling point (three in some cases), a total of 312 censuses conducted (Table S1).

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. (2021) (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 (2023) (n = 14, from 2016 to 2023), 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 (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 500×500m matrix superimposed on the island of Ibiza. We labelled each 500×500m 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 Inverse Distance Weighting (IDW) interpolation based on the year of invasion assigned to each 500×500m 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) (Table S1).

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 (Zanaga et al., 2021) (Fig. S3). Using the R package '*raster*' (Hijmans et al., 2023; R Core Team, 2023), we drew a 50m radius area around each of the 144 sampling points and computed the percentage of 10×10m 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*' (Lüdecke et al., 2021; R Core Team, 2023). The results of the overdispersion test on an initial Generalized Linear Mixed Model (GLMM) following a Poisson distribution obtained using the R package '*glmmTMB*' (Magnusson et al., 2017; R Core Team, 2023) revealed no overdispersion in our data (Pearson's $\chi^2 = 193.59$, $p > 0.99$). 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 (Poisson part and zero-inflated part) of the best model were 'years from invasion', 'urbanization index', and the interaction between these two variables. The variable 'years from 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. We constructed multiple models using different combinations of these variables and selected the best model based on the lowest AICc, ensuring a minimum difference of two AICc points from the next best model (Table S2). To extract and visualize the results from these analyses, we used the R package ‘*sjPlot’* (Lüdecke, 2021; R Core Team, 2023). We also performed a spatial autocorrelation analysis using the R packages ‘*DHARMa’* (Hartig, 2019; R Core Team, 2023) and ‘*pgirmess’* (Giraudoux, 2013; R Core Team, 2023), which determined there was no spatial patterns in our data influencing the results (DHARMa Moran's I test, observed = 0.022, expected = -0.007, sd = 0.033, p = 0.37).

Urban filtering

In order to quantify the role of urban areas as potential filters for the dispersal of snakes and their chances to become established in these areas we 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 across an increasing urbanization gradient separated by heavily trafficked roads. 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. Specifically, we placed 18 traps in the outer (less urbanized) area, 8 in the intermediate area, and 15 in the inner (most urbanized) area. In each of the delimited areas, we tallied the total number of snakes captured. We used the R package ‘*stats*’ (R Core Team, 2023) 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 refugia for native lizard populations. With this aim, we conducted simulations to model the population dynamics of lizard populations under varying levels of urbanization and different degrees of predation pressure.

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 these external mortality events have occurred, the model proceeds to simulate the population dynamics of a closed population of lizards. This part of the model simulates mortality due to senescence and population stochasticity, 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. 3a and 3b). 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 (Fig. 3b).

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 ‘urbanization index’ (odds ratio = 7.02, CI = [1.79, 12.26], $\chi^2_{1,\,0.05} = 6.92$, $p < 0.01$), ‘years from invasion’ (odds ratio = 27.73, CI = [12.22, 43.25], $\chi^2_{1,\,0.05} = 12.28$, $p < 0.001$), and the interaction between these two variables (odds ratio = -26.92, CI = [-43.14, -10.69], $\chi^2_{1,\,0.05} = 10.57$, $p < 0.01$, Fig. 4a, Table S3) 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 only ‘urbanization index’ (odds ratio = 1.52, CI = [0.76, 2.29], $\chi^2_{1,\,0.05} = 15.34$, $p < 0.001$) has a significant effect on local relative lizard abundance. ‘Years from invasion’ (odds ratio = 0.97, CI = [-2.39, 4.33], $\chi^2_{1,\,0.05} = 0.32$, $p = 0.57$) and the interaction between ‘years form invasion’ and ‘urbanization index’ (odds ratio = -3.17, CI = [-7.32, 0.97], $\chi^2_{1,\,0.05} = 2.25$, $p = 0.13$, Fig. 4a, Table S3) were not significant.

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. 5a and 5b). 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 ($p = 0.14$, CI = [-4.11, 0.48]) or between the intermediate area and the inner area ($p = 0.22$, CI = [-3.99, 0.23]) did not reach significance.

Finally, we used a population dynamics model to examine the potential existence of source-sink dynamic in urban areas. This model revealed that current abundances in urban environments surrounded by snake-invaded areas can only be explained by the existence of an urban refugia effect. When anthropogenic mortality is low to moderate, urban lizard populations can remain stable without requiring immigration from external sources (Fig. 6a-e), only reaching local extirpation when anthropogenic mortality levels become very high (Fig. 6f). However, the presence of invasive snakes disrupts these stable dynamics (Fig. 6g-l). Under low and moderate anthropogenic pressure, snakes drive a rapid population decline and leads to local extirpation (Fig. 6g-i). Notably, increasing urbanization mitigates this effect. Higher urbanization levels allow lizards to persist despite snake presence in surrounding areas (Fig. 6j-l). These findings refute the hypothesis that urban areas act as ecological traps or biodiversity sinks. Instead, our results highlight that urban environments can represent effective refugia, at least in the mid-term, sheltering native lizard populations from the devastating effect of new top predators.

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 models of urban population dynamics. Altogether, our results provide empirical evidence that urban areas are enhancing survival of the keystone Ibiza wall lizard, a keystone species from a delicate Mediterranean island ecosystem.

Before the arrival of the horseshoe whip snake in the early 2000s, Ibiza wall lizards were abundant in natural and urban habitats throughout the island (Pérez-Cembranos & Pérez-Mellado, 2022; Salvador, 2015; Salvador & Pérez-Mellado, 1984). This situation changed dramatically following the rapid progression of the invasion year by year (Hinckley et al., 2017; Montes, 2021; Montes et al., 2022). Results from our GLMMs show 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 ‘years from 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. 4a, Table S3). On the other hand, the effect of the variable ‘years from invasion’ on the Poisson part of the model was not significant, indicating that relative lizard abundances are not affected by how long the snake has been present in the area (Fig. 4a, Table S3).

In this disturbing scenario for the long-term persistence of Ibiza wall lizards, nonetheless, urban areas offer some hope. Despite the alarming general population declines, urban populations are coping better with this situation (Fig. 1b). In fact, lizard abundances in large urban areas are among the highest on the island, despite snakes having long been established in the surrounding peri-urban areas (Fig. 3a and 3b). 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 positive, indicating that, in non-invaded areas, increasing urbanization initially leads to more censuses with zero lizard observations. This suggests a potential negative effect of urbanization on lizard presence (Fig. 4a and 4b, Table S3). However, this factor interacts with ‘years from invasion’, and as the invasion progresses, the influence of urbanization on the number of censuses with zero observations changes. Specifically, the interaction between ‘urbanization index’ and ‘years from invasion’ reduces the impact of ‘years from invasion’ on the number of zeroes observed, particularly when the invasion has progressed significantly, leading to fewer zero counts in invaded urban areas compared to less urbanized areas (Fig. 4b). This suggests that while urbanization alone may initially contribute to slightly higher numbers of censuses with no lizards, intensively urban areas become crucial refugia as the invasion progresses, buffering urban lizard populations from the impact of the invasive snake.

Finally, the 'urbanization index' is significantly positive in the Poisson part of the model, meaning that relative lizard abundances are higher in more urbanized sites (Fig. 4a, Table S3). The absence of a clear effect of snake presence on lizard densities could be due to the drastic nature of the snake's impact: rather than gradually reducing lizard numbers, snake predation appears to drive populations to local extinction within a short time frame (Fig. 4b). This pattern further supports the idea that urban lizard populations persist in certain suitable areas within the city such as parks or small vegetated areas where they can reach high densities. These results provide long-needed empirical evidence that urbanization can favor 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 (Chester & Robson, 2013; Luna et al., 2018; Plowes et al., 2007; Rutz, 2008; Savidge, 1987).

Ecological filters as drivers 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 (Aronson et al., 2016; Baguette et al., 2013). Here we investigated the possibility that urban areas and their surrounding roads act as dispersal filters for invasive snakes in search of new territories (Coffin, 2007; Plowes et al., 2007). For instance, although the horseshoe whip snake can sometimes exploit urban habitats (Pleguezuelos, 1989; Pleguezuelos & Moreno, 1999; Vericad-Coromina & Escarré-Esteve, 1976), 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 urbanized, 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. 1b and 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 (Álvarez et al., 2010; Hinckley et al., 2017) and do not tolerate their presence due to either environmental concerns (Montes et al., 2015) or fear (da Silva et al., 2021; Öhman & Mineka, 2003). As a result, both governmental initiatives (COFIB, 'Línea verde') and independent citizen-led efforts (e.g., 'Amics de la Terra Eivissa', https://amicsdelaterraeivissa.org) have implemented pest detection and control measures. Consequently, snakes in Ibiza are more easily detected and culled in urbanized areas, where more people reside, than in peri-urban areas (Chandler et al., 2017; Sewell & Parr, 2017). Meanwhile, the colorful appearance and tame behavior of Ibiza wall lizards have turned them into a beloved species that is in fact a cultural icon of the island (Dappen et al., 2009; Hinckley et al., 2017). As a result, Ibiza wall lizards have long maintained good population numbers in urban areas (Pérez-Cembranos & Pérez-Mellado, 2022). 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 (Aronson et al., 2016; Hinckley et al., 2017; Montes, 2021; Montes et al., 2022) (Fig. 1b).

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. 3a and 3b). As urbanization intensifies, it seems to provide a more effective protection to lizard populations (Fig. 4a and 4b, Table S3). The expansion of urban areas leads to increased traffic and more people capable of detecting and potentially removing snakes. These create an ecological filter that reduces predation pressure. This protection allows lizard populations to maintain high densities in suitable urban habitats, supporting the role of urban areas as refugia (Gentili et al., 2023; McKinney, 2008).

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 (Cooper et al., 2021; McKinney, 2008). For an urban area to be considered an urban refugia, the species with its distribution range restricted to these urban areas should benefit from either greater resource accessibility (Hollander et al., 2013; Sun et al., 2020; Williams et al., 2006), environmental stability (Emlen, 1966; Rebolo-Ifrán et al., 2017), or protection against multiple threats (Brown, 1988; Jordan et al., 1997) 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 (Battin, 2004; Robertson & Hutto, 2006). This could happen as a consequence of factors such as predation, pollution or diseases (Battin, 2004; Boal & Mannan, 1999; Hale & Swearer, 2016; Robertson & Hutto, 2006). 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 (Aronson et al., 2017; Hale & Swearer, 2016) or as a consequence of unpredictable climatic events (Robertson & Hutto, 2006), 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 refugia into ecological traps (Cooper et al., 2021; McKinney, 2008) (Fig. 6f). Therefore, adequate management of these refugia must be prioritized to enhance population persistence (Hale & Swearer, 2016; Piano et al., 2020). 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 (Aronson et al., 2017; Hostetler et al., 2011). Outside these suitable 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 (Castilla & Labra, 1998; Cooper & Pérez-Mellado, 2010; Li et al., 2014). In addition, low connectivity between these suitable habitats commonly hinders their long-term viability (Baguette et al., 2013; Mumby & Hastings, 2008). A management strategy to enhance connectivity between Ibiza wall lizard urban populations could be the creation of ecological corridors between urban parks (Huang et al., 2021). However, while this strategy is generally beneficial for biodiversity conservation, in the case of Ibiza wall lizards, it could have unintended negative consequences. These corridors could facilitate the spread of invasive snakes into urban refugia, ultimately jeopardizing lizard populations. Although uncommon, snake sightings occur within Ibiza’s urban areas (COFIB, 2022), highlighting the risk of inadvertently aiding the predator’s expansion. 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 (Aronson et al., 2016; Hale & Swearer, 2016; Turrini & Knop, 2015).

To prevent ecological corridors from turning urban refugia into ecological traps, active pest control measures, citizen awareness, and participation in biodiversity monitoring are essential (Callaghan et al., 2020; Chandler et al., 2017; Crain et al., 2014; Sewell & Parr, 2017). If ecological corridors are stablished, targeted capture efforts along these corridors should be prioritized to prevent snake establishment. Additionally, citizen engagement can play a crucial role in maintaining the effectiveness of urban refugia. Raising awareness about the cultural, ecological, and evolutionary significance of Ibiza wall lizards is a key step to fostering public involvement in conservation efforts. 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 (Callaghan et al., 2020, 2020; Crain et al., 2014; McKinney, 2002; Sewell & Parr, 2017). In fact, such citizen science initiatives are already in place in Ibiza and have proven essential for the present study.

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

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 three endemic lizards on the island of Gran Canaria (Piquet et al., 2022). 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 (Fritts & Rodda, 1998; IUCN, 2025; Savidge, 1987). Management of these invasive species has proven extremely challenging worldwide. Although the potential role of urban refugia in this ecological context has remained largely unknown, they could play a significant role in biodiversity preservation in two different ways. Firstly, our study provides empirical evidence that urban areas can act as shelters, enabling the mid-term persistence of populations that are rapidly declining in surrounding natural landscapes (Aronson et al., 2014; Gentili et al., 2023; Ives et al., 2016; Luna et al., 2018). Future research will be fundamental to design and implement management strategies promoting the persistence of urban animal populations in ways that facilitate their re-establishment in natural surroundings. Efforts such as reintroduction programs (Hale & Koprowski, 2018), however, need to take place after the mitigation of the threats that decimated these populations (e.g. the removal of invasive predators).

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 (Jordán, 2009; Montoya & Raffaelli, 2010; Sanders et al., 2013; Tylianakis et al., 2008; Valiente-Banuet et al., 2015). The global extirpation of keystone species has had dramatic cascading effects on the functioning of biological communities (Bregman et al., 2015; Cerini et al., 2023; MacDougall et al., 2013; Valiente-Banuet et al., 2015), and this can happen rapidly with the introduction of novel predators (Lapiedra et al., 2024; Peller & Altermatt, 2024; Sage, 2020). Degradation of ecosystem functionality can result in the loss of ecosystem services essential for human civilization (Montoya & Raffaelli, 2010; Sanders et al., 2013). For example, the generalist Ibiza wall lizard regulates arthropod populations through predation and also serves as an important pollinator and seed disperser (Grzywacz et al., 2014; Traveset, 1995). 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 (Branton & Richardson, 2011; Mekonnen et al., 2022; Roberge & Angelstam, 2004).

REFERENCES

Alberti, M., Correa, C., Marzluff, J. M., Hendry, A. P., Palkovacs, E. P., Gotanda, K. M., Hunt, V. M., Apgar, T. M., & Zhou, Y. (2017). Global urban signatures of phenotypic change in animal and plant populations. *Proceedings of the National Academy of Sciences*, *114*(34), 8951–8956. https://doi.org/10.1073/pnas.1606034114

Álvarez, C., Mateo, J. A., Oliver, J., & Mayol, J. (2010). Los ofidios ibéricos de introducción reciente en las Islas Baleares. *Boletín de La Asociación Herpetológica Española, 21*, 126–131.

Aronson, M. F. J., La Sorte, F. A., Nilon, C. H., Katti, M., Goddard, M. A., Lepczyk, C. A., Warren, P. S., Williams, N. S. G., Cilliers, S., Clarkson, B., Dobbs, C., Dolan, R., Hedblom, M., Klotz, S., Kooijmans, J. L., Kühn, I., MacGregor-Fors, I., McDonnell, M., Mörtberg, U., … Winter, M. (2014). A global analysis of the impacts of urbanization on bird and plant diversity reveals key anthropogenic drivers. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1780), 20133330. https://doi.org/10.1098/rspb.2013.3330

Aronson, M. F. J., Nilon, C. H., Lepczyk, C. A., Parker, T. S., Warren, P. S., Cilliers, S. S., Goddard, M. A., Hahs, A. K., Herzog, C., Katti, M., La Sorte, F. A., Williams, N. S. G., & Zipperer, W. (2016). Hierarchical filters determine community assembly of urban species pools. *Ecology*, *97*(11), 2952–2963. https://doi.org/10.1002/ecy.1535

Aronson, M. F., Lepczyk, C. A., Evans, K. L., Goddard, M. A., Lerman, S. B., MacIvor, J. S., Nilon, C. H., & Vargo, T. (2017). Biodiversity in the city: Key challenges for urban green space management. *Frontiers in Ecology and the Environment*, *15*(4), 189–196. https://doi.org/10.1002/fee.1480

Baguette, M., Blanchet, S., Legrand, D., Stevens, V. M., & Turlure, C. (2013). Individual dispersal, landscape connectivity and ecological networks. *Biological Reviews*, *88*(2), 310–326. https://doi.org/10.1111/brv.12000

Battin, J. (2004). When Good Animals Love Bad Habitats: Ecological Traps and the Conservation of Animal Populations. *Conservation Biology*, *18*(6), 1482–1491. https://doi.org/10.1111/j.1523-1739.2004.00417.x

Boal, C. W., & Mannan, R. W. (1999). Comparative Breeding Ecology of Cooper's Hawks in Urban and Exurban Areas of Southeastern Arizona. *The Journal of Wildlife Management*, *63*(1), 77. https://doi.org/10.2307/3802488

Branton, M., & Richardson, J. S. (2011). Assessing the Value of the Umbrella-Species Concept for Conservation Planning with Meta-Analysis. *Conservation Biology*, *25*(1), 9–20. https://doi.org/10.1111/j.1523-1739.2010.01606.x

Bregman, T. P., Lees, A. C., Seddon, N., MacGregor, H. E. A., Darski, B., Aleixo, A., Bonsall, M. B., & Tobias, J. A. (2015). Species interactions regulate the collapse of biodiversity and ecosystem function in tropical forest fragments. *Ecology*, *96*(10), 2692–2704. https://doi.org/10.1890/14-1731.1

Brown, J. S. (1988). Patch use as an indicator of habitat preference, predation risk, and competition. *Behavioral Ecology and Sociobiology*, *22*(1), 37–47. https://doi.org/10.1007/BF00395696

Callaghan, C. T., Ozeroff, I., Hitchcock, C., & Chandler, M. (2020). Capitalizing on opportunistic citizen science data to monitor urban biodiversity: A multi-taxa framework. *Biological Conservation*, *251*, 108753. https://doi.org/10.1016/j.biocon.2020.108753

Campbell-Staton, S. C., Winchell, K. M., Rochette, N. C., Fredette, J., Maayan, I., Schweizer, R. M., & Catchen, J. (2020). Parallel selection on thermal physiology facilitates repeated adaptation of city lizards to urban heat islands. *Nature Ecology & Evolution*, *4*(4), 652–658. https://doi.org/10.1038/s41559-020-1131-8

Carretero, M. A., Llorente, G. A., Santos, X., & Montori, A. (1995). Características reproductoras de una población introducida de *Podarcis pityusensis*. *Revista Española de Herpetología*, *9*, 93–102.

Castilla, A. M., & Labra, A. (1998). Predation and spatial distribution of the lizard *Podarcis hispanica atrata*: An experimental approach. *Acta Oecologica*, *19*(2), 107–114. https://doi.org/10.1016/S1146-609X(98)80014-3

Cerini, F., Childs, D. Z., & Clements, C. F. (2023). A predictive timeline of wildlife population collapse. *Nature Ecology & Evolution*, *7*(3), 320–331. https://doi.org/10.1038/s41559-023-01985-2

Chandler, M., See, L., Copas, K., Bonde, A. M. Z., López, B. C., Danielsen, F., Legind, J. K., Masinde, S., Miller-Rushing, A. J., Newman, G., Rosemartin, A., & Turak, E. (2017). Contribution of citizen science towards international biodiversity monitoring. *Biological Conservation*, *213*, 280–294. https://doi.org/10.1016/j.biocon.2016.09.004

Chester, E. T., & Robson, B. J. (2013). Anthropogenic refuges for freshwater biodiversity: Their ecological characteristics and management. *Biological Conservation*, *166*, 64–75. https://doi.org/10.1016/j.biocon.2013.06.016

Coffin, A. W. (2007). From roadkill to road ecology: A review of the ecological effects of roads. *Journal of Transport Geography*, *15*(5), 396–406. https://doi.org/10.1016/j.jtrangeo.2006.11.006

COFIB. (2022). *Control de especies invasoras en las Pitiusas*. COFIB.

Cooper, D. S., Wood, E. M., Katz, N. D., Superfisky, K., Osborn, F. M., Novoselov, A., Tarczynski, J., & Bacasen, L. K. (2021). Large Cities Fall Behind in "Neighborhood Biodiversity." *Frontiers in Conservation Science*, *2*. https://doi.org/10.3389/fcosc.2021.734931

Cooper, W. E., & Pérez-Mellado, V. (2010). Island tameness: Reduced escape responses and morphological and physiological antipredatory adaptations related to escape in lizards. *Islands and Evolution*, 231–253.

Cooper, W. E., Pyron, R. A., & Garland, T. (2014). Island tameness: Living on islands reduces flight initiation distance. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1777), 20133019. https://doi.org/10.1098/rspb.2013.3019

Crain, R., Cooper, C., & Dickinson, J. L. (2014). Citizen Science: A Tool for Integrating Studies of Human and Natural Systems. *Annual Review of Environment and Resources*, *39*(1), 641–665. https://doi.org/10.1146/annurev-environ-030713-154609

da Silva, M. X. G., Braga-Pereira, F., da Silva, M. C., de Oliveira, J. V., de Faria Lopes, S., & Alves, R. R. N. (2021). What are the factors influencing the aversion of students towards reptiles? *Journal of Ethnobiology and Ethnomedicine*, *17*(1), 35. https://doi.org/10.1186/s13002-021-00462-z

Dappen, N., Losin, N., & Pérez Mellado, V. (2009). *The symbol: Wall lizards of Ibiza & Formentera*.

Dickman, C. R. (1996). Impact of exotic generalist predators on the native fauna of Australia. *Wildlife Biology*, *2*(3), 185–195. https://doi.org/10.2981/wlb.1996.018

Emlen, J. M. (1966). The Role of Time and Energy in Food Preference. *The American Naturalist*, *100*(916), 611–617. https://doi.org/10.1086/282455

Faeth, S. H., Bang, C., & Saari, S. (2011). Urban biodiversity: Patterns and mechanisms. *Annals of the New York Academy of Sciences*, *1223*(1), 69–81. https://doi.org/10.1111/j.1749-6632.2010.05925.x

Fritts, T. H., & Rodda, G. H. (1998). The role of introduced species in the degradation of island ecosystems: A Case History of Guam. *Annual Review of Ecology and Systematics*, *29*(1), 113–140. https://doi.org/10.1146/annurev.ecolsys.29.1.113

Fusco, N. A., Pehek, E., & Munshi-South, J. (2021). Urbanization reduces gene flow but not genetic diversity of stream salamander populations in the New York City metropolitan area. *Evolutionary Applications*, *14*(1), 99–116. https://doi.org/10.1111/eva.13025

Gentili, R., Quaglini, L. A., Galasso, G., Montagnani, C., Caronni, S., Cardarelli, E., & Citterio, S. (2023). Urban refugia sheltering biodiversity across world cities. *Urban Ecosystems*. https://doi.org/10.1007/s11252-023-01432-x

Giraudoux, P. (2013). *pgirmess: Data analysis in ecology* [Computer software].

Grzywacz, D., Stevenson, P. C., Mushobozi, W. L., Belmain, S., & Wilson, K. (2014). The use of indigenous ecological resources for pest control in Africa. *Food Security*, *6*(1), 71–86. https://doi.org/10.1007/s12571-013-0313-5

Hale, R., & Swearer, S. E. (2016). Ecological traps: Current evidence and future directions. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1824), 20152647. https://doi.org/10.1098/rspb.2015.2647

Hale, S. L., & Koprowski, J. L. (2018). Ecosystem-level effects of keystone species reintroduction: A literature review. *Restoration Ecology*, *26*(3), 439–445. https://doi.org/10.1111/rec.12684

Hartig, F. (2019). *DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models* [Computer software].

Hijmans, R. J., Van Etten, J., Cheng, J., Mattiuzzi, M., Sumner, M., Greenberg, J. A., ..., & Hijmans, M. R. J. (2023). *raster: Geographic Data Analysis and Modeling* [Computer software].

Hinckley, A., Montes, E., Ayllón, E., & Pleguezuelos, J. M. (2017). The fall of a symbol? A high predation rate by the introduced horseshoe whip snake *Hemorrhois hippocrepis* paints a bleak future for the endemic Ibiza wall lizard *Podarcis pityusensis*. *European Journal of Wildlife Research*, *63*(1), 13. https://doi.org/10.1007/s10344-016-1068-z

Hollander, F. A., Titeux, N., & Van Dyck, H. (2013). Habitat-dependent prey availability and offspring provisioning explain an ecological trap in a migratory bird. *Functional Ecology*, *27*(3), 702–709. https://doi.org/10.1111/1365-2435.12077

Hostetler, M., Allen, W., & Meurk, C. (2011). Conserving urban biodiversity? Creating green infrastructure is only the first step. *Landscape and Urban Planning*, *100*(4), 369–371. https://doi.org/10.1016/j.landurbplan.2011.01.011

Huang, X., Wang, H., Shan, L., & Xiao, F. (2021). Constructing and optimizing urban ecological network in the context of rapid urbanization for improving landscape connectivity. *Ecological Indicators*, *132*, 108319. https://doi.org/10.1016/j.ecolind.2021.108319

IUCN. (2025). *The IUCN red list of threatened species*.

Ives, C. D., Lentini, P. E., Threlfall, C. G., Ikin, K., Shanahan, D. F., Garrard, G. E., Bekessy, S. A., Fuller, R. A., Mumaw, L., Rayner, L., Rowe, R., Valentine, L. E., & Kendal, D. (2016). Cities are hotspots for threatened species. *Global Ecology and Biogeography*, *25*(1), 117–126. https://doi.org/10.1111/geb.12404

Jordán, F. (2009). Keystone species and food webs. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*(1524), 1733–1741. https://doi.org/10.1098/rstb.2008.0335

Jordan, F., Bartolini, M., Nelson, C., Patterson, P. E., & Soulen, H. L. (1997). Risk of predation affects habitat selection by the pinfish *Lagodon rhomboides* (Linnaeus). *Journal of Experimental Marine Biology and Ecology*, *208*(1–2), 45–56. https://doi.org/10.1016/S0022-0981(96)02656-1

Kirwan, G. M., Levesque, A., Oberle, M., & Sharpe, C. J. (2019). *Birds of the West Indies*. Lynx Edicions.

Lapiedra, O. (2018). Urban Behavioral Ecology: Lessons from Anolis Lizards. *Integrative and Comparative Biology*. https://doi.org/10.1093/icb/icy109

Lapiedra, O., Chejanovski, Z., & Kolbe, J. J. (2017). Urbanization and biological invasion shape animal personalities. *Global Change Biology*, *23*(2), 592–603. https://doi.org/10.1111/gcb.13395

Lapiedra, O., Morales, N., Yang, L. H., Fernández-Bellon, D., Michaelides, S. N., Giery, S. T., Piovia-Scott, J., Schoener, T. W., Kolbe, J. J., & Losos, J. B. (2024). Predator-driven behavioural shifts in a common lizard shape resource-flow from marine to terrestrial ecosystems. *Ecology Letters*, *27*(1), e14335. https://doi.org/10.1111/ele.14335

Li, B., Belasen, A., Pafilis, P., Bednekoff, P., & Foufopoulos, J. (2014). Effects of feral cats on the evolution of anti-predator behaviours in island reptiles: Insights from an ancient introduction. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1788), 20140339. https://doi.org/10.1098/rspb.2014.0339

Lokatis, S., Jeschke, J. M., Bernard-Verdier, M., Buchholz, S., Grossart, H., Havemann, F., Hölker, F., Itescu, Y., Kowarik, I., Kramer-Schadt, S., Mietchen, D., Musseau, C. L., Planillo, A., Schittko, C., Straka, T. M., & Heger, T. (2023). Hypotheses in urban ecology: Building a common knowledge base. *Biological Reviews*, *98*(5), 1530–1547. https://doi.org/10.1111/brv.12964

Lowry, H., Lill, A., & Wong, B. B. M. (2013). Behavioural responses of wildlife to urban environments. *Biological Reviews*, *88*(3), 537–549. https://doi.org/10.1111/brv.12012

Lüdecke, D., Ben-Shachar, M., Patil, I., Waggoner, P., & Makowski, D. (2021). performance: An R Package for Assessment, Comparison and Testing of Statistical Models. *Journal of Open Source Software*, *6*(60), 3139. https://doi.org/10.21105/joss.03139

Lüdecke, Daniel. (2021). *sjPlot: Data visualization for statistics in social science* [Computer software]. R Foundation for Statistical Computing.

Luna, Á., Romero-Vidal, P., Hiraldo, F., & Tella, J. L. (2018). Cities may save some threatened species but not their ecological functions. *PeerJ*, *6*, e4908. https://doi.org/10.7717/peerj.4908

MacDougall, A. S., McCann, K. S., Gellner, G., & Turkington, R. (2013). Diversity loss with persistent human disturbance increases vulnerability to ecosystem collapse. *Nature*, *494*(7435), 86–89. https://doi.org/10.1038/nature11869

Magnusson, A., Skaug, H., Nielsen, A., Berg, C., Kristensen, K., Maechler, M., van Bentham, K., Sadat, N., Bolker, B., & Brooks, M. (2017). *glmmTMB: Generalized Linear Mixed Models using Template Model Builder* [Computer software].

McKinney, M. L. (2002). Urbanization, Biodiversity, and Conservation: The impacts of urbanization on native species are poorly studied, but educating a highly urbanized human population about these impacts can greatly improve species conservation in all ecosystems. *BioScience*, *52*(10), 883–890.

McKinney, M. L. (2008). Effects of urbanization on species richness: A review of plants and animals. *Urban Ecosystems*, *11*(2), 161–176. https://doi.org/10.1007/s11252-007-0045-4

McKinney, M. L., & Lockwood, J. L. (1999). Biotic homogenization: A few winners replacing many losers in the next mass extinction. *Trends in Ecology & Evolution*, *14*(11), 450–453. https://doi.org/10.1016/S0169-5347(99)01679-1

Mekonnen, A., Fashing, P. J., Chapman, C. A., Venkataraman, V. V., & Stenseth, N. Chr. (2022). The value of flagship and umbrella species for restoration and sustainable development: Bale monkeys and bamboo forest in Ethiopia. *Journal for Nature Conservation*, *65*, 126117. https://doi.org/10.1016/j.jnc.2021.126117

Montes, E. (2021). *Natural history and impacts of an invasive snake: The horseshoe whip snake, Hemorrhois hippocrepis (Linnaeus, 1758), on Ibiza*. Universitat de València.

Montes, E., Estarellas, J., Ayllón, E., Carretero, M. Á., Feriche, M., Hernández, P. L., & Pleguezuelos, J. M. (2015). Dades preliminars del projecte pilot de control de serps a l'illa d'Eivissa. *Monogr Soc Hist Nat Balear*, *20*, 455-464.

Montes, E., Kraus, F., Chergui, B., & Pleguezuelos, J. M. (2022). Collapse of the endemic lizard *Podarcis pityusensis* on the island of Ibiza mediated by an invasive snake. *Current Zoology*, *68*(3), 295–303. https://doi.org/10.1093/cz/zoab022

Montoya, J. M., & Raffaelli, D. (2010). Climate change, biotic interactions and ecosystem services. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1549), 2013–2018. https://doi.org/10.1098/rstb.2010.0114

Mumby, P. J., & Hastings, A. (2008). The impact of ecosystem connectivity on coral reef resilience. *Journal of Applied Ecology*, *45*(3), 854–862. https://doi.org/10.1111/j.1365-2664.2008.01459.x

Öhman, A., & Mineka, S. (2003). The Malicious Serpent: Snakes as a Prototypical Stimulus for an Evolved Module of Fear. *Current Directions in Psychological Science*, *12*(1), 5–9. https://doi.org/10.1111/1467-8721.01211

Peller, T., & Altermatt, F. (2024). Invasive species drive cross-ecosystem effects worldwide. *Nature Ecology & Evolution*, *8*(6), 1087–1097. https://doi.org/10.1038/s41559-024-02380-1

Pérez-Cembranos, A., & Pérez-Mellado, V. (2022). *Estado de conservación de los reptiles endémicos de las Islas Baleares 2021-2022*.

Pérez-Mellado, V., & Salvador, A. (1981). Actividad y termorregulación estival de *Podarcis pityusensis* BOSCÀ, 1883 (Saura: Lacertidae) en Ibiza y Formentera. *Amphibia-Reptilia*, *2*(2), 181–186. https://doi.org/10.1163/156853881X00221

Piano, E., Souffreau, C., Merckx, T., Baardsen, L. F., Backeljau, T., Bonte, D., Brans, K. I., Cours, M., Dahirel, M., Debortoli, N., Decaestecker, E., De Wolf, K., Engelen, J. M. T., Fontaneto, D., Gianuca, A. T., Govaert, L., Hanashiro, F. T. T., Higuti, J., Lens, L., … Hendrickx, F. (2020). Urbanization drives cross-taxon declines in abundance and diversity at multiple spatial scales. *Global Change Biology*, *26*(3), 1196–1211. https://doi.org/10.1111/gcb.14934

Piquet, J. C., Maestresalas, B., & López-Darias, M. (2022). Coupling phenotypic changes to extinction and survival in an endemic prey community threatened by an invasive snake. *Scientific Reports*, *12*(1), 18249. https://doi.org/10.1038/s41598-022-22583-5

Pleguezuelos, J. M. (1989). Distribución de los reptiles en la provincia de Granada (SE Península Ibérica). *Doñana, Acta Vertebrata*, *16*(1), 15–44.

Pleguezuelos, J. M., & Moreno, M. (1999). Alimentación de *Coluber hippocrepis* en el SE de la Península Ibérica. *Amphibia-Reptilia*, *11*, 325–337.

Plowes, R. M., Dunn, J. G., & Gilbert, L. E. (2007). The urban fire ant paradox: Native fire ants persist in an urban refuge while invasive fire ants dominate natural habitats. *Biological Invasions*, *9*(7), 825–836. https://doi.org/10.1007/s10530-006-9084-7

QGIS.org. (2023). *QGIS Geographic Information System* (Version 3.28) [Computer software].

R Core Team. (2023). *R: A Language and Environment for Statistical Computing* [Computer software].

Rebolo-Ifrán, N., Tella, J. L., & Carrete, M. (2017). Urban conservation hotspots: Predation release allows the grassland-specialist burrowing owl to perform better in the city. *Scientific Reports*, *7*(1), 3527. https://doi.org/10.1038/s41598-017-03853-z

Roberge, J.-M., & Angelstam, P. (2004). Usefulness of the Umbrella Species Concept as a Conservation Tool. *Conservation Biology*, *18*(1), 76–85. https://doi.org/10.1111/j.1523-1739.2004.00450.x

Robertson, B. A., & Hutto, R. L. (2006). A framework for understanding ecological traps and an evaluation of existing evidence. *Ecology*, *87*(5), 1075–1085. https://doi.org/10.1890/0012-9658(2006)87[1075:affuet]2.0.co;2

Rutz, C. (2008). The establishment of an urban bird population. *Journal of Animal Ecology*, *77*(5), 1008–1019. https://doi.org/10.1111/j.1365-2656.2008.01420.x

Sage, R. F. (2020). Global change biology: A primer. *Global Change Biology*, *26*(1), 3–30. https://doi.org/10.1111/gcb.14893

Salvador, A. (2015). *Lagartija de las Pitiusas – Podarcis pityusensis (Boscá, 1883)*. Enciclopedia Virtual de Los Vertebrados Españoles.

Salvador, A., & Pérez-Mellado, V. (1984). The amphibians and reptiles of the Pityusic Islands. In H. Kuhbier, J. A. Alcover, & C. Guerau d'Arellano Tur (Eds.), *Biogeography and Ecology of the Pityusic Islands* (Vol. 52, pp. 429–439). Springer Netherlands. https://doi.org/10.1007/978-94-009-6539-3_20

Sanders, D., Sutter, L., & van Veen, F. J. F. (2013). The loss of indirect interactions leads to cascading extinctions of carnivores. *Ecology Letters*, *16*(5), 664–669. https://doi.org/10.1111/ele.12096

Savidge, J. A. (1987). Extinction of an Island Forest Avifauna by an Introduced Snake. *Ecology*, *68*(3), 660–668. https://doi.org/10.2307/1938471

Sewell, J., & Parr, J. (2017). Citizen sentinels: The role of citizen scientists in reporting and monitoring invasive non-native species. In *Citizen science for coastal and marine conservation* (pp. 59–76). Routledge.

Sih, A. (2013). Understanding variation in behavioural responses to human-induced rapid environmental change: A conceptual overview. *Animal Behaviour*, *85*(5), 1077–1088. https://doi.org/10.1016/j.anbehav.2013.02.017

Silva-Rocha, I., Montes, E., Salvi, D., Sillero, N., Mateo, J. A., Ayllón, E., Pleguezuelos, J. M., & Carretero, M. A. (2018). *Herpetological History of the Balearic Islands: When Aliens Conquered These Islands and What to Do Next* (pp. 105–131). https://doi.org/10.1007/978-3-319-74986-0_5

Sol, D., Lapiedra, O., & González-Lagos, C. (2013). Behavioural adjustments for a life in the city. *Animal Behaviour*, *85*(5), 1101–1112. https://doi.org/10.1016/j.anbehav.2013.01.023

Sousa, R., Nogueira, J. G., Lopes-Lima, M., Varandas, S., & Teixeira, A. (2019). Water mill canals as habitat for *Margaritifera margaritifera*: Stable refuge or an ecological trap? *Ecological Indicators*, *106*, 105469. https://doi.org/10.1016/j.ecolind.2019.105469

Spotswood, E. N., Beller, E. E., Grossinger, R., Grenier, J. L., Heller, N. E., & Aronson, M. F. J. (2021). The Biological Deserts Fallacy: Cities in Their Landscapes Contribute More than We Think to Regional Biodiversity. *BioScience*, *71*(2), 148–160. https://doi.org/10.1093/biosci/biaa155

Sun, K., Yu, W., Jiang, J., Richards, C., Siemann, E., Ma, J., Li, B., & Ju, R. (2020). Mismatches between the resources for adult herbivores and their offspring suggest invasive *Spartina alterniflora* is an ecological trap. *Journal of Ecology*, *108*(2), 719–732. https://doi.org/10.1111/1365-2745.13277

Traveset, A. (1995). Seed dispersal of *Cneorum tricoccon* L. (Cneoraceae) by lizards and mammals in the Balearic islands. *Acta Oecologica*, *16*(2), 171–178.

Turrini, T., & Knop, E. (2015). A landscape ecology approach identifies important drivers of urban biodiversity. *Global Change Biology*, *21*(4), 1652–1667. https://doi.org/10.1111/gcb.12825

Tylianakis, J. M., Didham, R. K., Bascompte, J., & Wardle, D. A. (2008). Global change and species interactions in terrestrial ecosystems. *Ecology Letters*, *11*(12), 1351–1363. https://doi.org/10.1111/j.1461-0248.2008.01250.x

Valiente-Banuet, A., Aizen, M. A., Alcántara, J. M., Arroyo, J., Cocucci, A., Galetti, M., García, M. B., García, D., Gómez, J. M., Jordano, P., Medel, R., Navarro, L., Obeso, J. R., Oviedo, R., Ramírez, N., Rey, P. J., Traveset, A., Verdú, M., & Zamora, R. (2015). Beyond species loss: The extinction of ecological interactions in a changing world. *Functional Ecology*, *29*(3), 299–307. https://doi.org/10.1111/1365-2435.12356

Vericad-Coromina, J. R., & Escarré-Esteve, A. (1976). Datos de alimentación de ofidios en el levante sur ibérico. *Mediterránea. Serie de Estudios Biológicos*, *1*, 3–32. https://doi.org/10.14198/MDTRRA1976.1.01

Wetmore, A., & Swales, B. H. (1931). The birds of Haiti and the Dominican Republic. *Bulletin of the United States National Museum*, *155*, i–483. https://doi.org/10.5479/si.03629236.155.i

Williams, N. S. G., McDonell, M. J., Phelan, G. K., Keim, L. D., & Van Der Ree, R. (2006). Range expansion due to urbanization: Increased food resources attract Grey-headed Flying-foxes (*Pteropus poliocephalus*) to Melbourne. *Austral Ecology*, *31*(2), 190–198. https://doi.org/10.1111/j.1442-9993.2006.01590.x

Wong, B. B. M., & Candolin, U. (2015). Behavioral responses to changing environments. *Behavioral Ecology*, *26*(3), 665–673. https://doi.org/10.1093/beheco/aru183

Zanaga, D., Van De Kerchove, R., Daems, D., De Keersmaecker, W., Brockmann, C., Kirches, G., Wevers, J., Cartus, O., Santoro, M., Fritz, S., Lesiv, M., Herold, M., Tsendbazar, N. E., Xu, P., Ramoino, F., & Arino, O. (2021). *ESA WorldCover 10 m 2021 v200*.

Zuñiga-Palacios, J., Zuria, I., Castellanos, I., Lara, C., & Sánchez-Rojas, G. (2021). What do we know (and need to know) about the role of urban habitats as ecological traps? Systematic review and meta-analysis. *Science of The Total Environment*, *780*, 146559. https://doi.org/10.1016/j.scitotenv.2021.146559

FIGURES

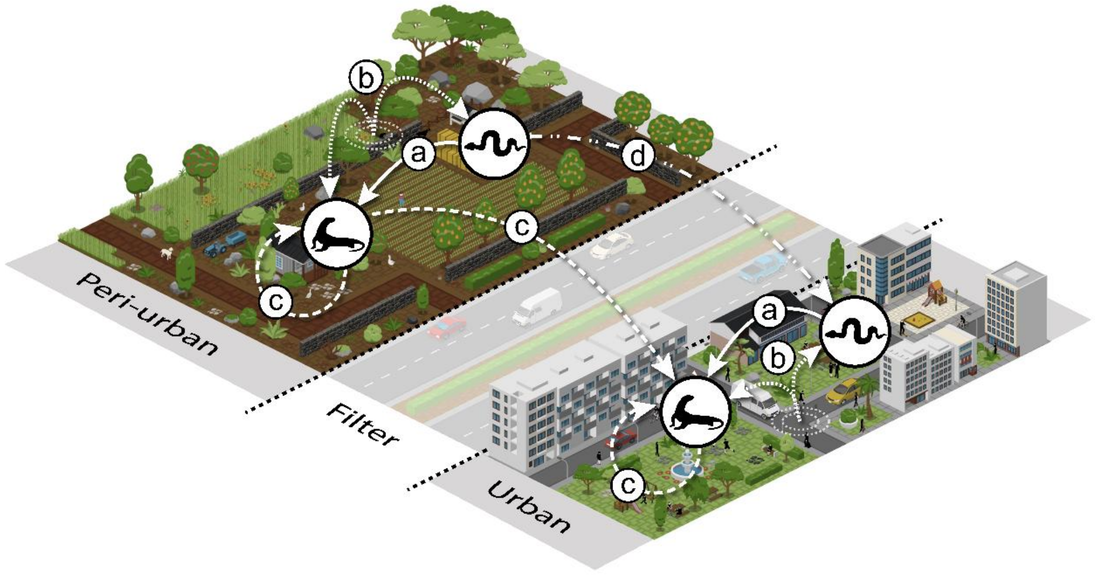

Figure 1: Conceptual diagram illustrating our examination of: (a) the impact of the invasive predatory snake on the abundances of the Ibiza wall lizard across a gradient of increasing urbanization from peri-urban (low urbanization) to highly urbanized habitats; (b) the effect of urbanization on the abundances of both the Ibiza wall lizard and the horseshoe whip snake along this gradient; (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.

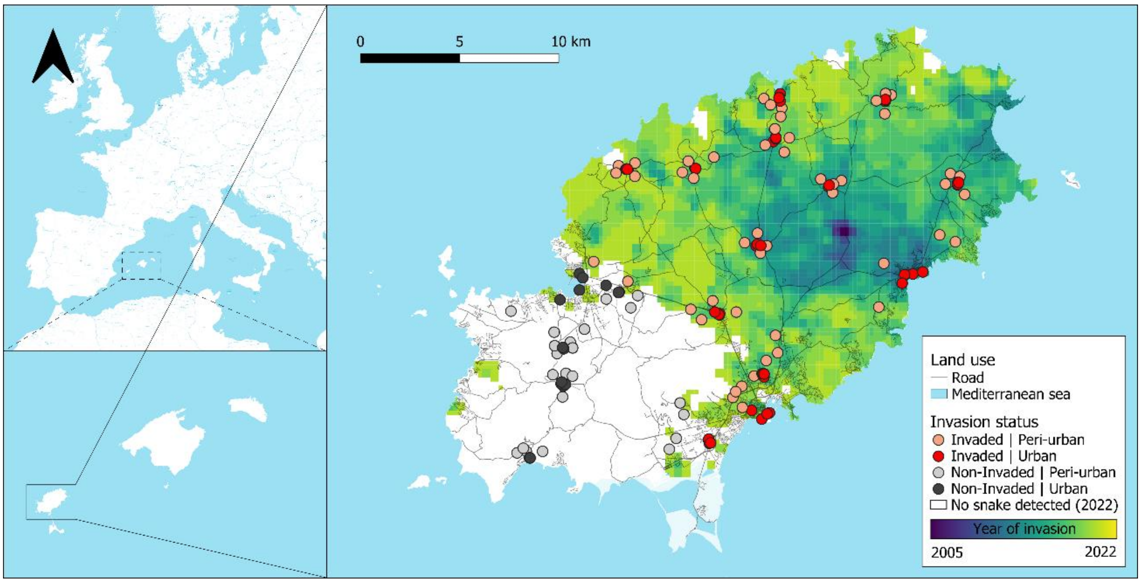

Figure 2: Map of the 144 sampling sites on Ibiza, Spain, distinguishing between urban (dark colors) and peri-urban (light colors) areas. Red marks correspond to invaded sites while grey marks represent non-invaded sites as of summer 2022. The map also includes a color scale indicating the interpolated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

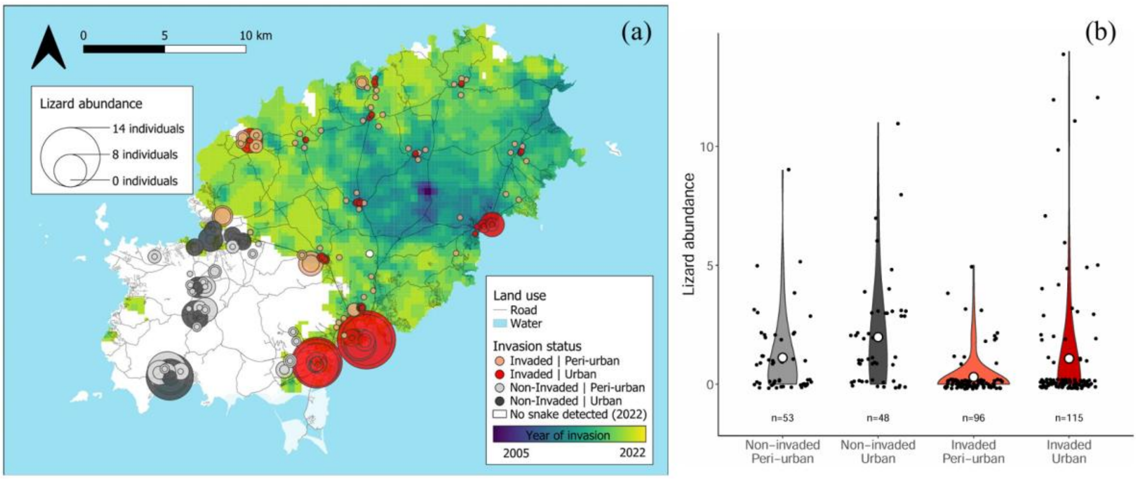

Figure 3: (a) Maximum number of Ibiza wall lizard individuals observed per sampling point (n=144 points) across the 18 sampled towns of the island of Ibiza, represented by the diameter of the circle. The color of the circles indicates the invasion and urbanization status of each site. The map also displays a color scale representing the interpolated year in which the horseshoe whip snake became established across the island. (b) 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.

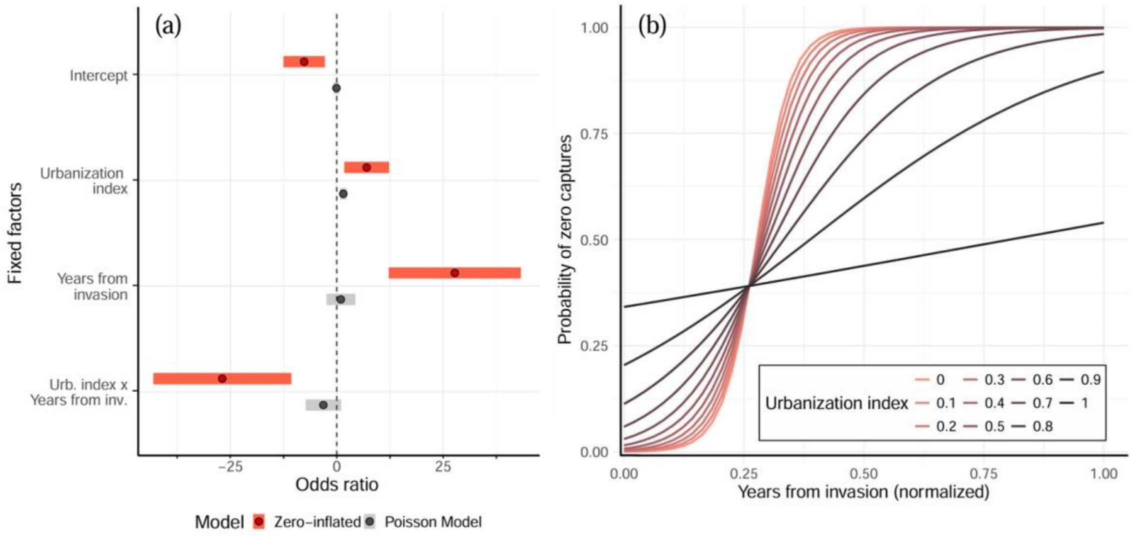

Figure 4: (a) Results from a Generalized Linear Mixed Model (GLMM) testing the effects of 'urbanization index', 'years from invasion', and the interaction between these two variables on the presence-absence (zero-inflated model) and abundance (Poisson model) of Ibiza wall lizard individuals. The figure displays the odds ratio for each fixed factor predictor (x-axis) included in the GLMM. Dark dots indicates mean odds ratio values, while colored boxes shows the 95% confidence interval. The vertical dashed line denotes the null value. (b) Effect of urbanization and invasion time on the probability of zero observations. The probability of recording zero lizard observations increases as more time has passed since the invasion (higher values on the x-axis). However, this effect is modulated by urbanization levels: in highly urbanized areas (darker lines), the probability of zero observations is lower compared to less urbanized areas (lighter red lines), suggesting that urban environments effectively buffer local lizard extirpations. These probabilities were derived from the zero-inflated component of the GLMM, incorporating invasion time, urbanization level, and their interaction as explanatory variables.

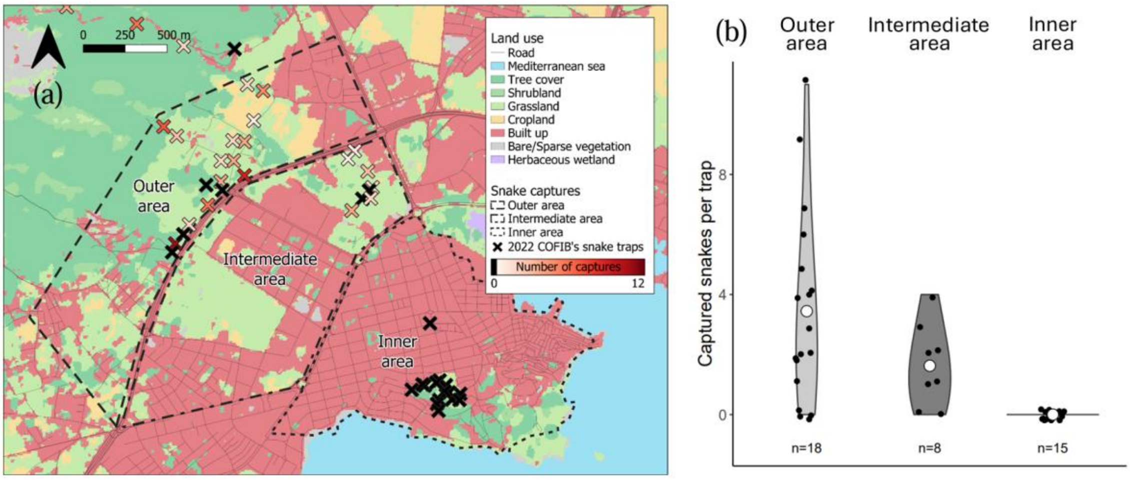

Figure 5: (a) Map of snake trap locations around the city of Ibiza in 2022. Trap locations were divided into three areas of 1.5km^2, each trap represented by a cross symbol. The color of these crosses indicates the number of snakes captured in each trap during the period the trap was active, with black corresponding to zero captures and darker shades of red indicating increasing capture numbers for each trap. (b) Number of captures per trap for each of the three 1.5km^2 areas, with a white dot indicating the mean number of captures per treatment.

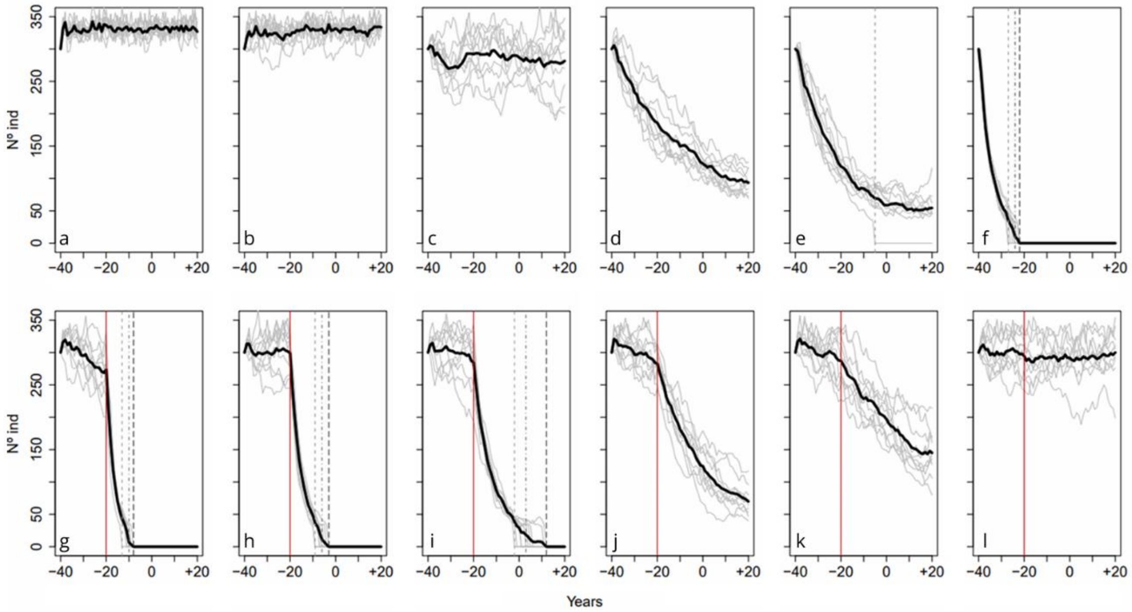

Figure 6: Effect of the mortality derived from anthropogenic factors (top row) and urbanization index (bottom row) on a simulated population of Ibiza wall lizards over time. On the X-axis, 0 represents the present; the past is depicted to the left, and the model's future projection is shown to the right. 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. Immigration of individuals from outside the simulated population is set to 0 in these simulations.