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Real-time invasion dynamics reveal the drivers of predator spread and prey extirpation on an island

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Non-native predators profoundly restructure island biological communities worldwide, yet their management is hindered by limited empirical understanding of the dynamics of predator spread and prey extirpation. Here, we integrate two decades of field surveys, citizen-science records and standardized transects to reconstruct the invasion of the snake *Hemorrhois hippocrepis* on Ibiza and its impact on the endangered, endemic lizard *Podarcis pityusensis*. We found a marked acceleration in range expansion despite intensified culling, evidence for the transition from establishment to spread stages of this invasion. Spatially explicit invasion maps combined with citizen reports of lizard disappearance show a nonlinear acceleration in the interval from predator arrival to local prey extirpation, shortening from over 10 years in early-invaded areas to 3 years in recently invaded areas. The observed patterns are consistent with density-dependent predator pressure, which generates a wave-like, rapidly advancing invasion front evidenced by declining snake body condition and reduced efficiency of snake captures in long-invaded areas. Our study empirically confirms theoretical predictions of nonlinear spread and impact dynamics and highlights how citizen science can crucially help documenting early invasion stages. Effectively incorporating the nonlinear dynamics of invasions into conservation strategies is urgent to mitigate invasion-driven transformations of fragile island ecosystems worldwide.

1. Introduction

Islands worldwide have become hotspots of biodiversity loss [1–5]. Biological invasions, and invasive predators in particular, are the leading cause of this global phenomenon, having driven numerous local extirpations and global extinctions across island ecosystems worldwide [4–8]. These biotic losses often result in irreversible functional and phylogenetic erosion in island biological communities [9,10], with cascading effects on ecosystem services [2,11–13]. Managing invasive predators on islands is, therefore, an urgent priority for global biodiversity conservation in an era of rapid environmental changes [4]. Yet effective management of invasive predators is largely limited by a lack of empirical data on key aspects of predator invasion dynamics [14,15].

A major gap to effectively respond to the global threat of non-native predators remains to disentangle the temporal dynamics of the spread and impact of predator invasions [16,17]. Because much of the damage to native communities occurs during the spread stage [5], understanding the transition from establishment to spread is critical to tackle invasion progression [18].

Reconstructing the fine-scale temporal dynamics of invasive predator spread requires analysing long-term empirical datasets including extensive observations of the transition between the establishment and the spread stage of the invasion [19]. Consequently, studies uncovering both the dynamics and consequences of this transition in natural systems are scarce mostly due to the difficulty to track invasions in their early invasion stages as they unfold [20]. Indeed, data on the impact of alien predators often become available only once it is pervasive and after predators are widespread [1,21]. Invasive predators are often not conspicuous and difficult to detect in the absence of ongoing local biodiversity tracking systems in the newly invaded area. This is especially true for snake invasions, with their commonly secretive behaviour often obscuring patterns of establishment and spread [22]. Consequently, snake invasions often wreak havoc in native biological communities worldwide [21,23–28].

A complementary unresolved, critical question in invasion biology is to untangle the dynamics of native species decline and extirpation following the spread of invasive predators. However, reliable data on this process are scarce, since it requires high-quality data on prey dynamics before, during and after the arrival of invasive predators. Only by explicitly linking the range expansion of invasive predators to robust long-term data on the decline, range contraction or local extirpation of their native prey can we fully understand the dynamics of this process [29]. However, empirical studies coupling these two processes remain scarce and focused on post-impact scenarios (as highlighted by [4]). Untangling the real-time impact dynamics of invasive predators on native prey has, therefore, become a global conservation priority to guide targeted conservation actions to minimize biodiversity loss [28,30] and preserve ecosystem functioning, particularly on islands [4,11,25].

To address this question, we leveraged a rare opportunity to study predator spread and prey extirpation in real time. In the Mediterranean island of Ibiza, the rapidly spreading invasive horseshoe whip snake (*Hemorrhois hippocrepis*) is extirpating the endangered endemic Ibiza wall lizard (*Podarcis pityusensis*) [26,27]. By integrating two decades of data from more than 5000 geo-referenced snake captures and lizard observations on Ibiza with standardized field transects and different sources of citizen science data, here we first characterize the spatial and temporal progression of the invasive snake's range, with a particular focus in untangling the transition between establishment and spread stages. We then examine if there is a tight temporal association between predator arrival and local extirpation of the endemic lizard. Then, we assess how these dynamics change over time by characterizing the acceleration of extirpation as a stronger invasion front develops. Finally, we examine whether and how food depletion is linked to lower predator abundance at the core of the invasion as well as to the emergence of an invasion front. Our findings provide new insights into both the patterns and processes of invasive predator spread dynamics as well as the rapid extirpation of endemic species that have wide implications for conservation and management of worldwide island biodiversity under global change.

2. Methods

(a) Study system and invasion history

The study was conducted on the island of Ibiza (572.6 km^2), located in the Balearic archipelago (western Mediterranean). Ibiza is characterized by a heterogeneous landscape dominated by Mediterranean shrublands, pine forests and semi-abandoned agricultural areas, prime habitat for both the invasive predator and its endemic prey [31,32].

The invasion of the horseshoe whip snake was first confirmed in 2003, when an individual emerged from the hollow trunk of an ornamental olive tree imported from mainland Spain [33]. From this very localized introduction point, the species spread rapidly across the island, reaching 83.36% of its surface by 2023 despite sustained management efforts (figure 1) [27,34].

The horseshoe whip snake is a diurnal, non-venomous colubrid native to North Africa and the Iberian Peninsula. It is a ground-dwelling, active predator that thrives on Mediterranean shrublands and agricultural areas, with lizards representing an important part of their diet in their native range [35]. In Ibiza, the Ibiza wall lizard constitutes a major prey item, representing more than 55% of its diet [26].

The endemic Ibiza wall lizard is, on the other hand, an icon of local culture, and plays a key ecological role as an insect consumer, pollinator and seed disperser [26,36]. Having evolved in the absence of native snake predators, it exhibits marked island tameness, which makes it particularly vulnerable to predation [37]. Its rapid decline in Ibiza following the snake invasion has led to its recent classification as endangered by the IUCN [38].

(b) Mapping invasion spread through time

To reconstruct the spatiotemporal dynamics of the horseshoe whip snake invasion in Ibiza, we compiled a comprehensive dataset of snake occurrence records spanning two decades (see electronic supplementary material, table S1), using empirical snake occurrence records (yielding almost 6000 snake capture records, electronic supplementary material, figure S1) and citizen science observations. Empirical snake occurrence data were obtained from long-term trapping campaigns associated with the eradication programme (n = 4394), roadkill detections (n = 77) and previously published records (n = 1271) [27]. This dataset was complemented with citizen science observations. Thanks to the human innate predisposition to respond strongly against snakes [39] and the herpeto-phobic attitude of many Mediterranean cultures [37], residents often clearly recall their first encounter with a snake. These reports provided valuable temporal and spatial coverage for reconstructing the early stages of the invasion. These included structured in-person surveys with rural residents (n = 60), responses to an online questionnaire (n = 172) and validated observations submitted to iNaturalist (n = 14).

In parallel, we incorporated 120 reports of snake absence provided by local observers. While such reported absences may reflect either true absence or a non-detection, these records provided a useful reference to delineate the limits of the

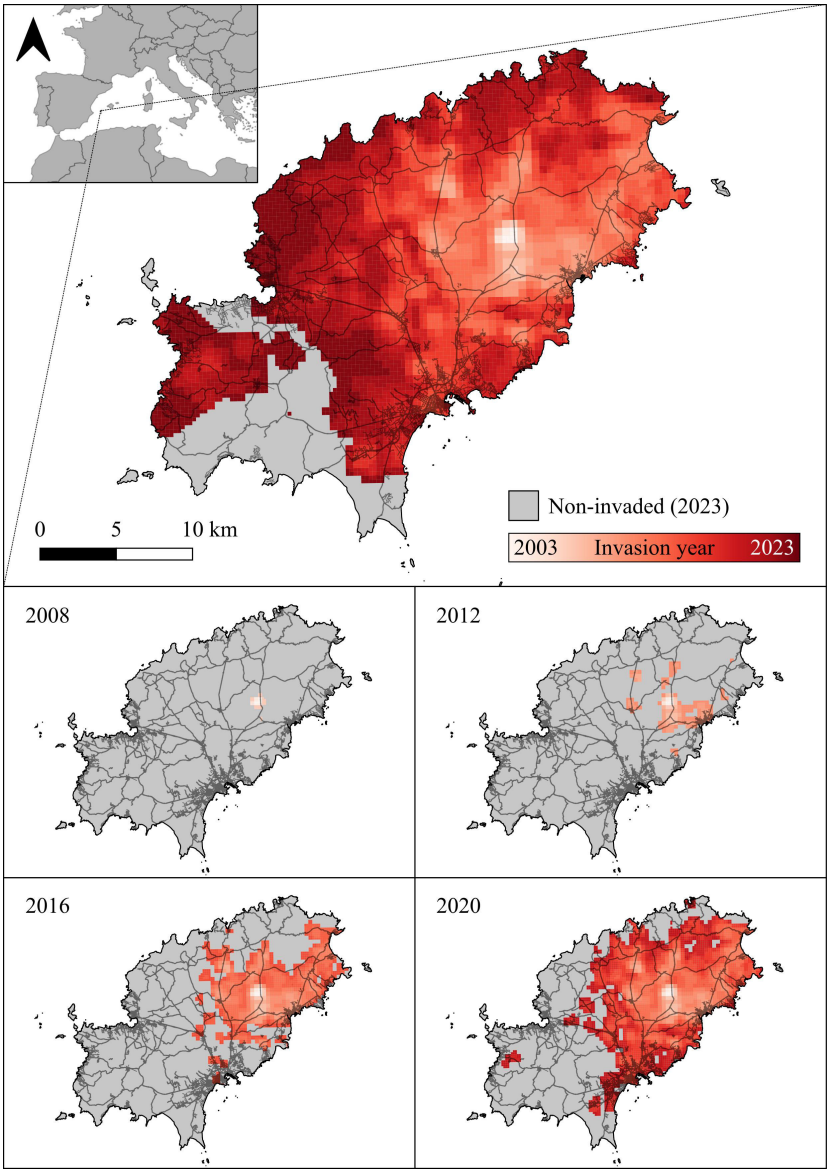

Figure 1. Chronology of snake invasion across Ibiza as reconstructed using empirical and citizen science data. The panel shows the estimated year of the horseshoe whip snake presence across the island. Warmer colours indicate earlier invasion years. Grey cells represent areas without confirmed invasion as of 2023 (top). Bottom panels show detailed invasion fronts at four key time points (2008, 2012, 2016 and 2020).

invasion front through time. We treated them conservatively as provisional absences unless contradicted by alternative sources considered to be more reliable, such as confirmed captures or roadkills. Reports with conflicting dates or vague spatial information were excluded. Additionally, to improve detection at the invasion front, sentinel traps were deployed in areas without confirmed snake presence, providing additional information on early colonization dynamics.

All spatial analyses were conducted in QGIS 3.28. Each georeferenced snake occurrence point was buffered with a 500 m radius and overlaid onto a 500 × 500 m grid covering the entire island. Each grid cell was assigned the earliest year of confirmed snake presence, resulting in a temporal invasion year map that covered 79.8% of the island's 500 × 500 m grid cells (n = 1987 grid cells with invasion data out of a total of 2493). To estimate the invasion year in unsampled areas and to reduce spatial discontinuities, we applied an inverse distance weighting (IDW) interpolation (p = 5).

To quantify uncertainty on the invasion year estimates, we implemented a bootstrap approach. We generated 100 resampled datasets from the full occurrence dataset and repeated the same interpolation workflow to each replicate, producing a set of alternative invasion surfaces. For every grid cell, we obtained a distribution of inferred invasion years, and calculated summary statistics, including the mean (figure 1), minimum and maximum invasion years (electronic supplementary material, figure S1), as well as the width of the 95% confidence intervals (electronic supplementary material, figure S2). These values were used to define three alternative invasion scenarios: mean (central estimate), fast (minimum) and conservative (maximum).

Finally, to provide a more ecologically meaningful assessment of invasion extent in relation to suitable habitat, we quantified habitat-specific detection rates using trapping data from 2016 to 2025. For each habitat type (forest versus non-forest) and year, we calculated the proportion of traps capturing at least one snake during the active trapping season, restricting analyses to areas already reached by the invasion front (electronic supplementary material, table S2, electronic supplementary material, figure S3).

(c) Quantifying expansion dynamics

To quantify invasion dynamics, we first calculated the cumulative area invaded annually by extracting the total area classified as invaded from the rasterized invasion map (figure 2C). We distinguished between contiguous expansion from the introduction point (primary invasion) and spatially disjunct occurrences (secondary translocation), which might have resulted from accidental human-driven translocations.

To characterize the spatial progression of the invasion front, we defined 16 cardinal and intercardinal axes radiating from the introduction point (electronic supplementary material, figure S4). For each axis and year, we calculated the distance reached by the primary invasion front from the introduction point. To obtain a robust estimate of the front position, we defined the invasion front as the 95th percentile of the distribution of distances within each direction-year combination. This approach reduces the influence of extreme observations and avoids overestimating expansion due to isolated outliers. We excluded from each yearly estimate of expansion those axes that had reached the coastline the previous year and therefore could not expand further.

We then calculated the annual invasion front for each direction, as well as the mean front position across all directions. To assess the robustness of these patterns, the analysis was performed using the three bootstrap-derived invasion scenarios (mean, fast and conservative), thereby incorporating uncertainty on the invasion year estimation.

Finally, to detect temporal changes in expansion rate, we fitted segmented regression models to the mean annual invasion front trajectory using the R package *segmented* [40]. Breakpoints were estimated iteratively, allowing the identification of distinct expansion phases characterized by different rates of expansion (figure 2A; electronic supplementary material, figure S4).

(d) Timing local lizard disappearance across the invasion

To evaluate the impact of snake invasion on the endemic Ibiza wall lizard, we estimated the time elapsed between snake arrival and local lizard extirpation. Extirpation dates were obtained from two complementary sources: structured citizen science surveys conducted across rural households and repeated field surveys. As a tame, well-known, and culturally iconic species [26,34], its disappearance could be reconstructed using local knowledge gathered through structured citizen science surveys [41] complemented by standardized field transects.

Citizen surveys yielded 358 responses, of which 219 were excluded because lizards were still reported as present and 35 were excluded due to time inconsistencies or missing data, resulting in 104 valid records. As for the repeated field surveys, we actively searched for lizards in locations that were frequently visited by us or other research or monitoring projects. A total of 18 sites were surveyed repeatedly across 2 years (2022 and 2025) until lizards were no longer detected.

For each record, we calculated the time lag between the estimated year of snake arrival and the last confirmed lizard observation. We tested whether this time lag varied as a function of invasion timing using linear regression. (figure 2B).

(e) Assessing prey depletion along the invasion

To investigate the role of prey depletion in shaping the invasion dynamics, we used four complementary analyses. First, we evaluated changes in snake body condition across the invasion gradient. A total of 1505 snakes from 2022 and 2023 were measured from snout–vent length (SVL) and body mass. Body condition was calculated as the residuals of a log–log regression of body mass against SVL. We then tested whether body condition declined with increasing time since invasion (electronic supplementary material, table S3; figure 3*b*).

Second, we assessed changes in lizard abundance using standardized visual encounter surveys conducted at 18 sites both in 2022 and 2025. The surveys followed fixed transects along traditional drystone walls in semi-abandoned Mediterranean agricultural landscapes. During each survey, lizards were recorded only when observed within a 3 m band directly facing the wall. For each site and year, we used the maximum number of lizards recorded across repeated visits as a relative abundance estimate. This design allowed direct comparison of lizard populations across invasion stages (figure 3C).

Third, we quantified snake trapping efficiency as the number of snakes captured per trap-day while the traps were active (April to November), using data from 4981 geo-referenced traps deployed across the island between 2016 and 2023 (4 176 631 trap-days in total). We modelled trapping efficiency as a function of years since invasion using a zero-inflated mixed-effects model implemented in the *glmmTMB* [42] and *performance* R packages [43], allowing us to separately model the probability of zero captures and the capture rate when snakes were present (electronic supplementary material, table S4; figure 3A). Model assumptions, including residual distribution, overdispersion, zero inflation and overall model fit, were assessed using the performance package.

Finally, to directly link predator and prey dynamics, we analysed the relationship between snake trapping efficiency and lizard abundance across 22 sites with consistent sampling across years. Predator pressure was quantified as the mean number of snakes captured per trap-day across five traps per site, whereas prey abundance was estimated from standardized transect counts. This relationship was analysed both across all sites and restricted to sites where lizards were still present (electronic supplementary material, figure S5).

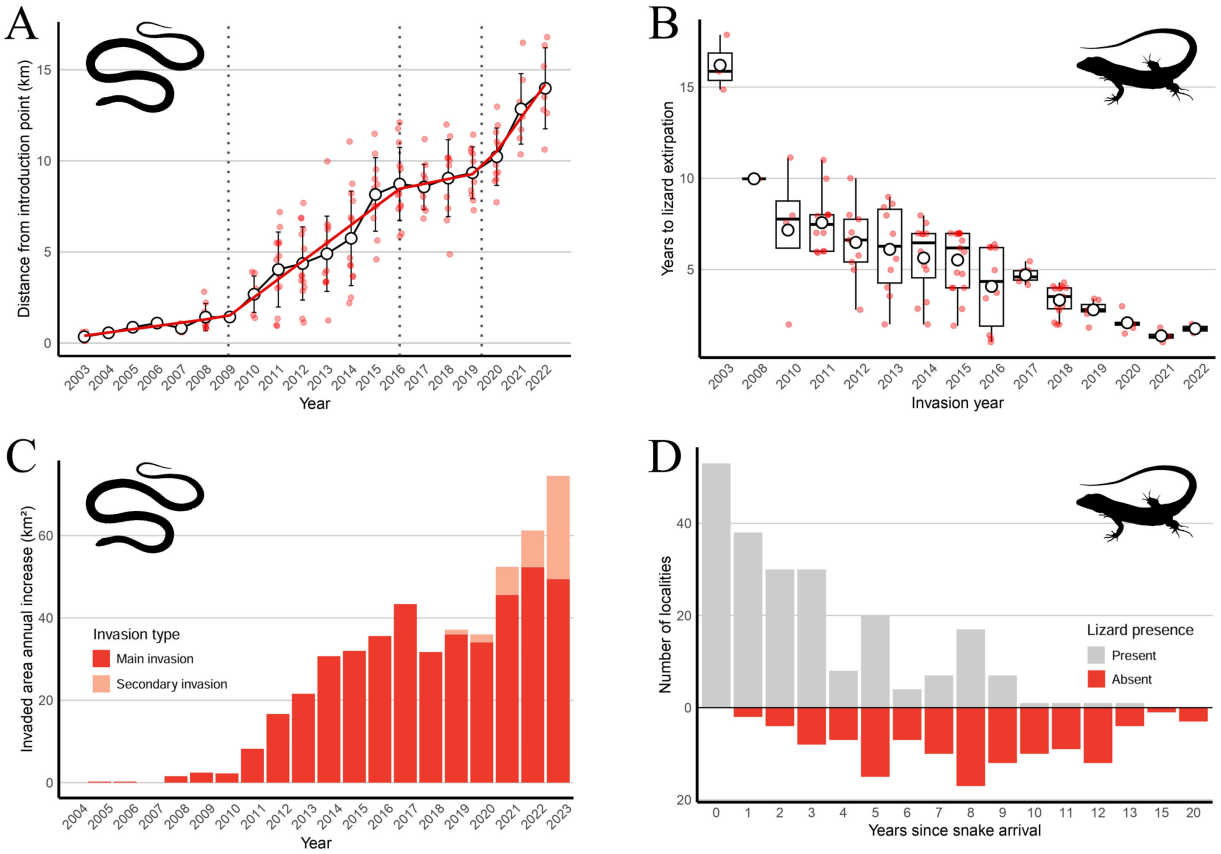

Figure 2. Spatiotemporal dynamics of the snake invasion and associated lizard extirpation patterns in Ibiza. (A) Distance from the introduction point over time along 16 cardinal directions, showing nonlinear acceleration in range expansion. Dotted vertical lines indicate breakpoints separating invasion stages. The solid red line indicates the mean slope of each invasion phase, and the solid grey line, the polynomic adjustment. (B) Relationship between year of snake arrival and time to local lizard extirpation. (C) Cumulative area invaded by snakes (km^2) from 2003 to 2023, differentiating between primary invasion (dark) and secondary translocation (light) (D) Histogram of time since snake arrival in all surveyed grid cells, differentiating sites where lizards are still present (grey) versus extirpated (red).

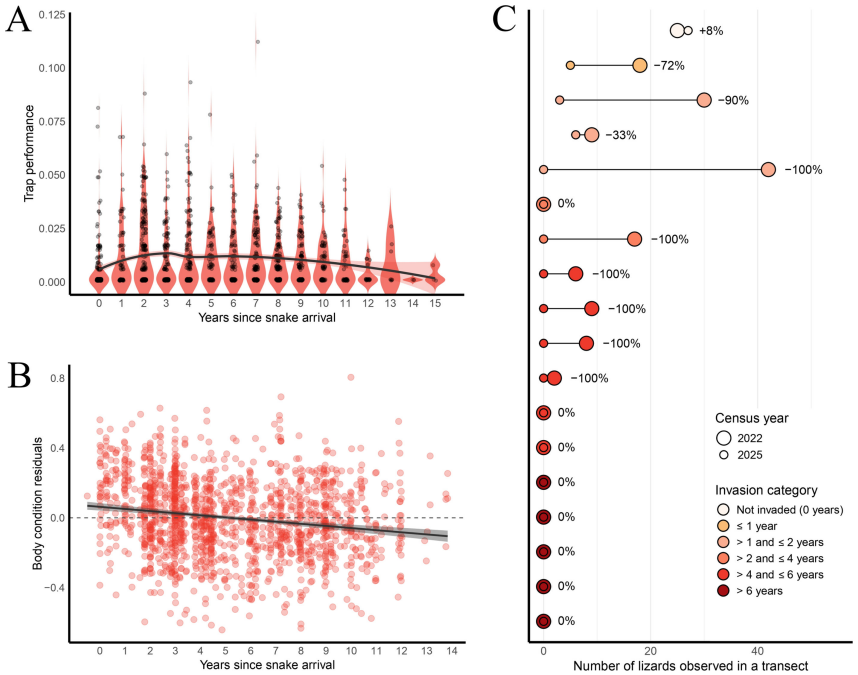

Figure 3. Evidence for prey depletion and associated effects of prolonged snake invasion. (A) Trap performance (captures per trap-day) plotted against the number of years since snake arrival. (B) Body condition of snakes, represented as the residuals of the log(mass) ~ log(SVL), plotted against years since snake arrival. (C) Lizard abundance per transect showing changes between the 2022 and 2025 surveys across invasion categories reflected by the size of the circles. Colour indicates the number of years since snake arrival at each site (as of 2025). Lines connect data points from the same site across years.

3. Results

(a) Spatial reconstruction and uncertainty

The reconstructed invasion map indicates that snakes occupied 83.4% of Ibiza by 2023 (figure 1). The invasion proceeded predominantly through contiguous expansion from the introduction point, although secondary, spatially disjunct occurrences were also detected (figure 2C).

Bootstrap analyses revealed low uncertainty in invasion-year estimates. The width of the 95% confidence interval did not exceed 0.56 years across the island, and uncertainty was spatially limited to small, scattered clusters rather than concentrated in specific regions (electronic supplementary material, figure S2). Interpolated cells represented only 3.6% of the total grid, indicating that the invasion reconstruction was largely supported by empirical observations.

Snake detection rates varied slightly across habitat types, with lower capture probability in forested areas compared to non-forest habitats (quasibinomial GLM: $\beta = -0.207 \pm 0.091$ s.e., $p = 0.049$). However, this difference was only significant in a subset of years, as this difference was only detected in 2016, 2019 and 2025 after Benjamini–Hochberg correction for multiple tests (electronic supplementary material, table S2 and figure S3).

(b) Nonlinear expansion dynamics and invasion phases

The analysis of the invasion front progression across 16 cardinal directions revealed strongly nonlinear expansion dynamics (figure 2A; electronic supplementary material, figure S4). The segmented regression analysis identified three significant breakpoints at 2008.94 ± 0.62, 2016.00 ± 0.72, and 2019.38 ± 0.45 years, defining four distinct phases of invasion.

During the initial establishment phase (2003–2008.9), expansion was slow and not significantly different from zero (0.18 ± 0.11 km year^{-1}, 95% CI = [−0.05–0.41]). This phase was followed by a marked acceleration between 2008.9 and 2016.0, with expansion rates increasing to 0.99 ± 0.08 km year^{-1} (95% CI = [0.81–1.17]). A transient slowdown occurred between 2016.0 and 2019.4, during which expansion rates decreased to 0.27 ± 0.20 km year^{-1} (95% CI = [−0.16–0.70]), potentially associated with landscape barriers such as major road infrastructure [44]. Finally, a second phase of rapid expansion was detected after 2019.4, with rates reaching 1.85 ± 0.31 km year^{-1} (95% CI = [1.17–2.52]).

Notably, the two main expansion phases (2008.9–2016.0 and post-2019.4) showed clearly distinct slopes, with minimal overlap between their confidence intervals, indicating a significant increase in expansion rate in the most recent phase. This renewed acceleration occurred despite a substantial increase in culling effort, transitioning from 223 traps in 2018 to over 1200 after 2021, suggesting that management actions did not significantly alter large-scale invasion dynamics.

These temporal patterns were consistent across bootstrap-derived invasion scenarios (electronic supplementary material, figures S14), indicating that the inferred expansion dynamics are robust to uncertainty in invasion-year estimation.

Specifically, the pattern of snake expansion through time best fits a polynomic function adjustment (F-statistic = 756.5, d.f. = 193, $p < 0.001$, $R^2 = 0.8857$).

(c) Acceleration of lizard extirpation

Lizard extirpation closely followed snake arrival across all sites. On average, lizard populations disappeared 5.18 ± 2.99 years after snake establishment. However, this time lag decreased significantly over the course of the invasion ($\beta = -0.66 \pm 0.04$ s.e., $p < 0.001$, $R^2 = 0.66$; figure 2B).

Early in the invasion (2003–2011), extirpation occurred after approximately 8.9 ± 3.78 years. This period mostly corresponds to the establishment phase and the beginning of the spread phase of the snake invasion. For sites invaded between 2012 and 2015, the average time to lizard extirpation was 5.03 ± 1.87 years. Finally, in more recently invaded areas (2016–2019), lizard populations disappeared within approximately 3.19 ± 1.45 years. Overall, time to extirpation decreased significantly with invasion timing ($\beta = -0.66 \pm 0.04$ s.e., $p < 0.001$), indicating a progressive acceleration of lizard disappearance across the invasion timeline (figure 2B).

(d) Evidence for prey depletion and the emergence of a wave-like invasion pattern

Multiple lines of evidence indicate strong prey depletion in long-invaded areas. Snake body condition declined significantly with time since invasion ($\beta = -0.0449 \pm 0.0062$ s.e., $p < 0.001$, $R^2 = 0.033$; figure 3B), suggesting reduced resource availability at the invasion core.

Consistent with this pattern, lizard abundance declined sharply across the invasion gradient. Visual surveys, based on repeated standardized transects across 18 sites (77 transects in total; mean length = 332 ± 111 m; total surveyed area = 17 319 m^2), revealed an average reduction of 84.05% in lizard counts between 2022 and 2025 in sites where lizards were initially present. In 2022, sites represented different invasion stages (7 already invaded with no lizards, 5 with lizards but no snakes and 6 with both species), whereas by 2025 all sites had been invaded and only 4 out of 18 retained lizard populations (figure 3C).

Snake trapping efficiency declined significantly with increasing time since invasion, both in terms of the probability of capture and the number of captures per trap-day (electronic supplementary material, table S4; figure 3A). The zero-inflated component revealed a strong increase in the probability of zero captures with time since invasion ($\beta = -1.58$, 95% CI = [−2.32–−0.84], $\chi^2 = 17.60$, $p < 0.001$), indicating that traps were increasingly likely to yield no captures in long-invaded areas. Similarly,

the conditional (Gamma) component showed a significant decline in capture rates where snakes were present ($\beta = -0.31$, 95% CI: [−0.54– −0.07, $\chi^2 = 6.56$, $p = 0.010$), reflecting reduced trapping efficiency over time. These results indicate a consistent decline in both snake occurrence and capture rates with increasing invasion age, suggesting reduced predator abundance or activity in long-invaded areas.

Finally, at the site level, lizard abundance was negatively associated with snake trapping efficiency ($\beta = -0.51 \pm 0.14$ s.e., $p = 0.0006$; electronic supplementary material, figure S5). This relationship remained significant when analyses were restricted to sites where lizards were still present, confirming the robustness of this pattern.

Taken together, these results indicate that prey depletion plays a central role in shaping invasion dynamics. In long-invaded areas, reduced prey availability is associated with lower snake body condition and decreased capture efficiency, suggesting declining predator performance. In contrast, high prey availability at the invasion front supports higher predator densities and continued expansion.

This spatial structure generates a wave-like invasion dynamic, in which the leading edge of the invasion drives range expansion while the core becomes progressively depleted.

4. Discussion

Overwhelming evidence shows that predator invasions are global drivers of island biodiversity loss (e.g. [2–6,8,11–13,23,45]). However, our lack of understanding of key aspects of their invasion dynamics is a major stumbling block hindering their effective management worldwide [14–17,45]. Indeed, a major challenge to disentangle the dynamics of invasive-predator–native-prey interactions as they unfold has been to compile detailed real-time, replicated empirical data of this process [46]. Our study empirically links the spatiotemporal dynamics of invasive predator spread to the collapse of an endemic prey species on an island, offering new insights into the processes driving biodiversity loss in fragile insular ecosystems worldwide.

By reconstructing the 20 year progression of the horseshoe whip snake invasion in Ibiza, we help fill key gaps in understanding the dynamics of biological invasions. Specifically, we show how predator spread has led to the rapid collapse of an endemic keystone species and associate the emergence of an invasion front to a rapid resource depletion driven by the invasive predator itself. These findings contribute to identify the drivers of the transition from invasion establishment to spread, as well to accurately characterize the temporal dynamics of native species collapse following predator arrival.

(a) Unraveling the dynamics of invasive predator spread

Our study shows a high-resolution reconstruction of the invasion dynamics of the horseshoe whip snake on the Mediterranean island of Ibiza (figure 1; electronic supplementary material, figure S1). By integrating long-term culling records, citizen science observations and standardized field transects (electronic supplementary material, table S1), we identified a critical transition from the establishment phase to a rapid spread phase, marked by a sharp acceleration in geographical expansion despite intensified culling efforts (figure 2A; electronic supplementary material, figure S4). This transition aligns with theoretical models that predict nonlinear invasion dynamics and underscores the importance of early detection and intervention in managing invasive species [14,18]. We detected a deceleration of the invasion around 2017, which can likely be attributable to the invasion front reaching the main traffic artery of the island (figures 1 and 2A; electronic supplementary material, figure S4). This interpretation is consistent with previous studies showing that snakes exhibit behavioural avoidance of roads, which act as partial barriers to movement and reduce dispersal across the landscape, thereby slowing the progression of invasion fronts [47–49]. The occurrence of secondary translocation event ahead of the main invasion front suggests that human-mediated transport within the island may also contribute to the spread, allowing the invasion to advance beyond the limits of continuous expansion (figures 1 and 2C).

Identifying the transition between establishment and spread can be crucial for informing management strategies, as it represents a window of opportunity where containment and eradication efforts are most likely to succeed. Our findings emphasize the need for continuous monitoring and adaptive management approaches that can respond swiftly to changes in invasion dynamics, particularly through early action before the spread phase begins.

(b) Linking predator spread to native species collapse

A central result of our study is the characterization of the temporal lag between predator establishment and prey extirpation, which consistently shortens over time. This indicates that the impact of the invasive predator intensifies as the invasion advances. The delay between snake establishment and lizard disappearance declined from around a decade in early invaded sites to less than 3 years in recent ones in a period of just over 10 years (figure 2B–D). These findings support theoretical predictions of nonlinear and density-dependent invasion impacts [1,50], but empirical confirmation of these dynamics has remained limited. Our results show how these processes play out in real time, highlighting the urgent need to intervene during the early stages of predator establishment before accelerated collapse becomes inevitable.

The spread dynamics of an invasion are not temporally or spatially static phenomena. Rather, they are emergent outcomes of how populations respond to the ecological conditions they experience [29]. The accelerated invasion dynamics observed in our study system can result from different, non-mutually exclusive ecological processes. One possibility is that growing predator densities intensify per capita pressure on native prey populations, rapidly driving them below viability thresholds. Another factor is the ecological naivety of island prey to novel predators, which results in ineffective antipredator responses and little

behavioural adjustment over short timescales. In addition, predators might be rapidly plastically or evolutionary adapting to new conditions in their invasive range, thereby becoming more efficient predators for the native fauna. Combined, these factors highlight the vulnerability of island biota to predation-driven collapse if invasive predators are not rapidly and effectively managed [4,30].

(c) The global threat of invasive snakes

Invasive snakes have emerged as major drivers of biodiversity loss on islands, where they have become extremely efficient invasive predators [23,24,28,51]. This can be explained in part by the fact that snakes can survive for extended periods of time with little food uptake [52]. This buffers small population size stochastic events such as Allee effects [53], which is an important cause of local extinction of non-native species arriving to novel areas [50,54]. Our findings from Ibiza resonate with other documented cases worldwide. For instance, the introduction of the brown tree snake (*Boiga irregularis*) to Guam led to the extirpation of most native forest bird species, resulting in cascading ecological effects, including disrupted seed dispersal and altered forest composition [11]. Similarly, the Burmese python (*Python bivittatus*) in Florida's Everglades has caused severe declines in mammal populations, with some species experiencing reductions of over 90% [24]. In the Canary Islands, the California kingsnake (*Lampropeltis californiae*) has decimated endemic reptile populations on Gran Canaria, with reductions exceeding 90% for some species, leading to significant ecological imbalances [28]. These examples underscore the profound and often irreversible impacts invasive snakes can have on island ecosystems. Our study adds to this body of evidence by demonstrating the rapid and accelerating effects of snake invasions on native prey species, emphasizing the need for vigilant biosecurity measures and rapid response strategies to prevent similar outcomes in other vulnerable regions.

(d) Invasion fronts and their resource-driven expansion

We also provide evidence that prey depletion behind the invasion front may contribute to both the structure and accelerated spread of the invasion. Declines in trapping efficiency and snake body condition in long-invaded areas suggest that food resources, including the endemic lizard, become depleted as the invasion proceeds (figure 3A–B). This supports the idea that invasive snakes are not only expanding opportunistically but also are being ecologically pushed forward by the degradation of foraging conditions in already colonized habitats. Such resource-driven invasion fronts represent a self-reinforcing mechanism of spatial spread and ecological disruption, in line with the predictions of consumer–resource models [55].

These findings have clear management implications. Control measures focusing solely on suppressing predator abundance in long-invaded areas may not be sufficient to limit predator spatial spread or conserve threatened prey. Instead, adaptive strategies that anticipate and intercept invasion fronts, ideally during the transition from establishment to spread, may be more effective in minimizing impacts. This is particularly relevant given that the final wave of expansion in Ibiza occurred despite a tenfold increase in trapping effort, highlighting the difficulty of halting invasion momentum once underway.

(e) The value of citizen science in tracking invasions

Our study also demonstrates the critical role that citizen science can play in reconstructing invasion histories and documenting biodiversity impacts in real time. In many regions, especially on islands, professional monitoring networks are sparse or absent. In such contexts, data provided by local residents, landowners and nature enthusiasts can offer a valuable complement to formal scientific monitoring [41]. This data can be especially useful in the case of iconic species such as the Ibiza wall lizard [26,34]. Indeed, beyond their informational value, these observations also reflect strong local concern and cultural attachment to this iconic declining species, which can be effectively used to provide empirical data critical to support conservation interventions. Citizen observations of lizard disappearances aligned closely with our field data, validating the reliability of such participatory approaches (figures 2B–D and 3C). This underscores the potential of citizen science as a cost-effective and scalable tool for monitoring invasive species and their impacts, particularly in regions where resources for extensive fieldwork may be limited [56].

(f) The importance of untangling invasion dynamics to protect native biodiversity in a rapidly changing planet

The dynamics we document in Ibiza illustrate how rapidly invasive species can restructure ecological communities, especially on islands where native species often lack the tools to effectively respond to them [57]. More broadly, our findings emphasize the importance of integrating dynamic invasion processes, including feedbacks between resource availability, predator capture performance and expansion dynamics, into biodiversity conservation planning. Indeed, our results contribute to a growing recognition that understanding the tempo of biological invasions is as critical as understanding their spatial extent. This is particularly urgent in a rapidly changing world, where global trade continues to increase the frequency and ecological footprint of biological invasions [3,17,58,59].

By elucidating the transition from establishment to rapid spread and documenting the acceleration of prey extirpation, we highlight critical phases where management interventions on predator invaders worldwide can be most effective. The acceleration of both range expansion and ecological impact in our study system suggests that windows for effective intervention may be narrower than previously assumed. Therefore, management strategies that prioritize early detection and rapid intervention are essential to confront the growing threat of invasive predators [14,17,29]. These insights are particularly relevant for island

ecosystems, which are hotspots of biodiversity disproportionately affected by the negative impact of invasive species [3,5]. Our findings underscore the necessity of integrating invasion dynamics into conservation planning and policy-making to mitigate the impacts of invasive predators and preserve ecosystem services in the current scenario of rapid global environmental change.

Ethics. All field procedures involving Podarcis pityusensis were conducted under permit CEP 05/2024 issued by the Direcció General de Medi Natural i Gestió Forestal (Govern de les Illes Balears) to Oriol Lapiedra González. The permit authorized the capture, handling and non-lethal tissue sampling of lizards for scientific purposes. Snake capture data were obtained from the official monitoring and control programme conducted by the Consortium for the Recovery of Fauna of the Balearic Islands (COFIB), under the authority of the Government of the Balearic Islands.

Data accessibility. All data, GIS layers and R scripts supporting the findings of this study are available from the Zenodo [60].

Supplementary material is available online [61].

Declaration of AI use. The authors used generative artificial intelligence tools solely to assist with improving R code implementation for statistical analyses and for minor language editing, including spelling and grammar corrections. All scientific analyses, interpretation of results, and the writing of the manuscript were performed by the authors, who take full responsibility for the content of this article.

Authors' contributions. G.C.P.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, resources, visualization, writing—original draft, writing—review and editing; M.V.-G.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, resources, visualization, writing—original draft, writing—review and editing; E.M.: investigation, resources, supervision, writing—review and editing; V.C.: investigation, resources, supervision, writing—review and editing; O.L.: conceptualization, funding acquisition, investigation, methodology, project administration, supervision, visualization, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

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References

1. Simberloff D *et al*. 2013 Impacts of biological invasions: what's what and the way forward. *Trends Ecol. Evol.* **28**, 58–66. (doi:10.1016/j.tree.2012.07.013)
2. Tershy BR, Shen KW, Newton KM, Holmes ND, Croll DA. 2015 The importance of islands for the protection of biological and linguistic diversity. *Bioscience* **65**, 592–597. (doi:10.1093/biosci/biv031)
3. Bellard C, Cassey P, Blackburn TM. 2016 Alien species as a driver of recent extinctions. *Biol. Lett.* **12**, 20150623. (doi:10.1098/rsbl.2015.0623)
4. Doherty TS, Glen AS, Nimmo DG, Ritchie EG, Dickman CR. 2016 Invasive predators and global biodiversity loss. *Proc. Natl Acad. Sci. USA* **113**, 11261–11265. (doi:10.1073/pnas.1602480113)
5. Spatz DR, Zilliacus KM, Holmes ND, Butchart SHM, Genovesi P, Ceballos G, Tershy BR, Croll DA. 2017 Globally threatened vertebrates on islands with invasive species. *Sci. Adv.* **3**, e1603080. (doi:10.1126/sciadv.1603080)
6. Salo P, Korpimäki E, Banks PB, Nordström M, Dickman CR. 2007 Alien predators are more dangerous than native predators to prey populations. *Proc. R. Soc. B* **274**, 1237–1243. (doi:10.1098/rspb.2006.0444)
7. Sax D *et al*. 2007 Ecological and evolutionary insights from species invasions. *Trends Ecol. Evol.* **22**, 465–471. (doi:10.1016/j.tree.2007.06.009)
8. Medina FM *et al*. 2011 A global review of the impacts of invasive cats on island endangered vertebrates. *Glob. Chang. Biol.* **17**, 3503–3510. (doi:10.1111/j.1365-2486.2011.02464.x)
9. Kumschick S *et al*. 2015 Ecological impacts of alien species: quantification, scope, caveats, and recommendations. *Bioscience* **65**, 55–63. (doi:10.1093/biosci/biu193)
10. Matthews TJ *et al*. 2024 The global loss of avian functional and phylogenetic diversity from anthropogenic extinctions. *Science* **386**, 55–60. (doi:10.1126/science.adk7898)
11. Rogers HS, Buhle ER, HilleRisLambers J, Fricke EC, Miller RH, Tewksbury JJ. 2017 Effects of an invasive predator cascade to plants via mutualism disruption. *Nat. Commun.* **8**, 14557. (doi:10.1038/ncomms14557)
12. Vilà M, Hulme PE (eds). 2017 *Impact of biological invasions on ecosystem services*. Cham, Switzerland: Springer. (doi:10.1007/978-3-319-45121-3)
13. Kamaru DN *et al*. 2024 Disruption of an ant-plant mutualism shapes interactions between lions and their primary prey. *Science* **383**, 433–438. (doi:10.1126/science.adg1464)
14. Epanchin-Niell RS, Hastings A. 2010 Controlling established invaders: integrating economics and spread dynamics to determine optimal management. *Ecol. Lett.* **13**, 528–541. (doi:10.1111/j.1461-0248.2010.01440.x)
15. Baker CM, Bode M. 2016 Placing invasive species management in a spatiotemporal context. *Ecol. Appl.* **26**, 712–725. (doi:10.1890/15-0095)
16. Hulme PE. 2009 Trade, transport and trouble: managing invasive species pathways in an era of globalization. *J. Appl. Ecol.* **46**, 10–18. (doi:10.1111/j.1365-2664.2008.01600.x)
17. Early R *et al*. 2016 Global threats from invasive alien species in the twenty-first century and national response capacities. *Nat. Commun.* **7**, 12485. (doi:10.1038/ncomms12485)
18. Blackburn TM, Pyšek P, Bacher S, Carlton JT, Duncan RP, Jarošík V, Wilson JRU, Richardson DM. 2011 A proposed unified framework for biological invasions. *Trends Ecol. Evol.* **26**, 333–339. (doi:10.1016/j.tree.2011.03.023)
19. Johnston MW, Purkis SJ. 2011 Spatial analysis of the invasion of lionfish in the western Atlantic and Caribbean. *Mar. Pollut. Bull.* **62**, 1218–1226. (doi:10.1016/j.marpolbul.2011.03.028)
20. Kolar CS, Lodge DM. 2001 Progress in invasion biology: predicting invaders. *Trends Ecol. Evol.* **16**, 199–204. (doi:10.1016/S0169-5347(01)02101-2)
21. Pyšek P *et al*. 2020 Scientists' warning on invasive alien species. *Biol. Rev.* **95**, 1511–1534. (doi:10.1111/brv.12627)
22. Christy MT, Yackel Adams AA, Rodda GH, Savidge JA, Tyrrell CL. 2010 Modelling detection probabilities to evaluate management and control tools for an invasive species. *J. Appl. Ecol.* **47**, 106–113. (doi:10.1111/j.1365-2664.2009.01753.x)
23. Savidge JA. 1987 Extinction of an island forest avifauna by an introduced snake. *Ecology* **68**, 660–668. (doi:10.2307/1938471)

24. Dorcas ME *et al*. 2012 Severe mammal declines coincide with proliferation of invasive Burmese pythons in Everglades National Park. *Proc. Natl Acad. Sci. USA* **109**, 2418–2422. (doi:10.1073/pnas.1115226109)
25. Kraus F. 2015 Impacts from invasive reptiles and amphibians. *Annu. Rev. Ecol. Evol. Syst.* **46**, 75–97. (doi:10.1146/annurev-ecolsys-112414-054450)
26. Hinckley A, Montes E, Ayllón E, Pleguezuelos JM. 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*. *Eur. J. Wildl. Res.* **63**, 13. (doi:10.1007/s10344-016-1068-z)
27. Montes E, Pleguezuelos JM, Kraus F. 2021 Rapid endangerment of the lizard Podarcis pityusensis by an invasive snake demands an immediate conservation response. *Amphib. Reptile Conserv* **15**, 238–243. https://www.biodiversitylibrary.org/part/383293
28. Piquet JC, López-Darias M. 2021 Invasive snake causes massive reduction of all endemic herpetofauna on Gran Canaria. *Proc. R. Soc. B* **288**, 1964. (doi:10.1098/rspb.2021.1939)
29. Meyerson LA, Simberloff D, Boardman L, Lockwood JL. 2019 Toward 'rules' for studying biological invasions. *Bull. Ecol. Soc. Am.* **100**, 1–9. (doi:10.1002/bes2.1607)
30. Jeschke JM, Strayer DL. 2008 Usefulness of bioclimatic models for studying climate change and invasive species. *Ann. N. Y. Acad. Sci.* **1134**, 1–24. (doi:10.1196/annals.1439.002)
31. Salvador Milla A. 2015 Lagartija de las Pitiusas—*Podarcis pityusensis* (Boscá, 1883). In *Enciclopedia virtual de los vertebrados españoles*. Museo Nacional de Ciencias Naturales, CSIC. (doi:10.20350/digitalCSIC/8649)
32. Feriche M, Salvador A. 2017 Culebra de herradura—*Hemorrhois hippocrepis* (Linnaeus, 1758). In *Enciclopedia virtual de los vertebrados españoles*. Museo Nacional de Ciencias Naturales, CSIC. (doi:10.20350/DIGITALCSIC/8676)
33. Servei d'Agents de Medi Ambient. 2003 *Aparició de serps en llibertat a l'illa d'Eivissa*. Conselleria de Medi Ambient i Territori, Balearic Government.
34. Dappen N, Losin N, Pérez-Mellado V. 2013 *The symbol: wall lizards of Ibiza and Formentera*. San Diego, CA: Day's Edge Productions. See https://www.natedappen.com/recent-projects-blog/2014/2/5/the-symbol-wall-lizards-of-ibiza-formentera.
35. Pleguezuelos JM, Moreno M. 1990 Alimentación de *Coluber hippocrepis* en el SE de la península Ibérica. *Amphib. Reptilia* **11**, 325–337. (doi:10.1163/156853890X00023)
36. Traveset A. 1995 Seed dispersal of *Cneorum tricocon* L.(Cneoraceae) by lizards and mammals in the Balearic Islands. *Acta Ecol.* **16**, 171–178.
37. Silva-Rocha I, Salvi D, Sillero N, Mateo JA, Carretero MA. 2015 Snakes on the Balearic islands: an invasion tale with implications for native biodiversity conservation. *PLoS One* **10**, e0121026. (doi:10.1371/journal.pone.0121026)
38. Bowles P. 2024 *Podarcis pityusensis*. The IUCN red list of threatened species.
39. Ohman A, Mineka S. 2001 Fears, phobias, and preparedness: toward an evolved module of fear and fear learning. *Psychol. Rev.* **108**, 483–522. (doi:10.1037/0033-295x.108.3.483)
40. Muggeo V. 2008 Segmented: an R package to fit regression models with broken-line relationships. *R News* **8**, 20–25. https://journal.r-project.org/articles/RN-2008-004/RN-2008-004.pdf
41. Mohanty NP, Measey J. 2019 Reconstructing biological invasions using public surveys: a new approach to retrospectively assess spatio-temporal changes in invasive spread. *Biol. Invasions* **21**, 467–480. (doi:10.1007/s10530-018-1839-4)
42. Brooks ME, Kristensen K, Benthem KJ, van Magnusson A, Berg CW, Nielsen A, Skaug HJ, Mächler M, Bolker BM. 2017 glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R J.* **9**, 378. (doi:10.32614/RJ-2017-066)
43. Lüdecke D, Ben-Shachar MS, Patil I, Waggoner P, Makowski D. 2021 performance: an R package for assessment, comparison and testing of statistical models. *JOSS* **6**, 3139. (doi:10.21105/joss.03139)
44. Ministry of Transport, Mobility and Urban Agenda. 2019 Average daily traffic intensity map, 2019 (IMD). Government of Spain. See https://cdn.mitma.gob.es/portal-web-drupal/Mapas_de_trafico/2019/Mapa%20IMD%202019.pdf.
45. Russell JC *et al*. 2016 Importance of lethal control of invasive predators for island conservation. *Conserv. Biol.* **30**, 670–672. (doi:10.1111/cobi.12666)
46. Blackburn TM. 2019 Macroecology and invasion biology. *Global Ecol. Biogeogr.* **28**, 28–32. (doi:10.1111/geb.12838)
47. Andrews KM, Gibbons JW. 2005 How do highways influence snake movement? Behavioral responses to roads and vehicles. *Ichthyol. Herpetol.* **2005**, 772–782. (doi:10.1643/0045-8511(2005)005[0772:HDHISM]2.0.CO;2)
48. Siers SR, Savidge JA, Reed RN. 2014 Invasive brown treesnake movements at road edges indicate road-crossing avoidance. *J. Herpetol.* **48**, 500–505. (doi:10.1670/13-037)
49. Paterson JE *et al*. 2019 Road avoidance and its energetic consequences for reptiles. *Ecol. Evol.* **9**, 9794–9803. (doi:10.1002/ece3.5515)
50. Taylor CM, Hastings A. 2005 Allee effects in biological invasions. *Ecol. Lett.* **8**, 895–908. (doi:10.1111/j.1461-0248.2005.00787.x)
51. Wiles GJ, Bart J, Beck RE JR, Aguon CF. 2003 Impacts of the brown tree snake: patterns of decline and species persistence in Guam's avifauna. *Conserv. Biol.* **17**, 1350–1360. (doi:10.1046/j.1523-1739.2003.01526.x)
52. McCue MD. 2007 Snakes survive starvation by employing supply- and demand-side economic strategies. *Zoology* **110**, 318–327. (doi:10.1016/j.zool.2007.02.004)
53. Kramer AM, Berec L, Drake JM. 2018 Allee effects in ecology and evolution. *J. Anim. Ecol.* **87**, 7–10. (doi:10.1111/1365-2656.12777)
54. Kanarek AR, Webb CT. 2010 Allee effects, adaptive evolution, and invasion success. *Evol. Appl.* **3**, 122–135. (doi:10.1111/j.1752-4571.2009.00112.x)
55. Sherratt JA. 2001 Periodic travelling waves in cyclic predator–prey systems. *Ecol. Lett.* **4**, 30–37. (doi:10.1046/j.1461-0248.2001.00193.x)
56. Crall AW, Jordan R, Holfelder K, Newman GJ, Graham J, Waller DM. 2013 The impacts of an invasive species citizen science training program on participant attitudes, behavior, and science literacy. *Public Underst. Sci.* **22**, 745–764. (doi:10.1177/0963662511434894)
57. Blumstein DT, Daniel JC. 2005 The loss of anti-predator behaviour following isolation on islands. *Proc. R. Soc. B* **272**, 1663–1668. (doi:10.1098/rspb.2005.3147)
58. Helmus MR, Mahler DL, Losos JB. 2014 Island biogeography of the Anthropocene. *Nature* **513**, 543–546. (doi:10.1038/nature13739)
59. Seebens H *et al*. 2017 No saturation in the accumulation of alien species worldwide. *Nat. Commun.* **8**, 14435. (doi:10.1038/ncomms14435)
60. Casbas Pinto G, Vez-Garzón M, Montes E, Colomar V, Lapiedra O. 2026 Data and code for: Real-time invasion dynamics reveal the drivers of predator spread and prey extirpation on an island [Data set]. Zenodo. (doi:10.5281/zenodo.20823410)
61. Casbas Pinto G, Vez-Garzón M, Montes E, Colomar V, Lapiedra O. 2026 Supplementary material from: Real-time invasion dynamics reveal the drivers of predator spread and prey extirpation on an island. Figshare. (doi:10.6084/m9.figshare.c.8570617)