Current distribution of *Phelsuma inexpectata*, a threatened Réunion Island endemic gecko

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Abstract The Manapany day gecko *Phelsuma inexpectata* is a Critically Endangered species endemic to Réunion Island in the Indian Ocean. Studying its geographical distribution and its evolution is important for developing effective biodiversity conservation strategies. We evaluated past and current distributions of *P. inexpectata* using records from 2008–2020 and through recent, intensive field surveys (230 person-days, 2020–2022). We found that its past distribution has declined by more than 28% (5.12 ha), from 19.44 ha to 14.32 ha. In natural habitats, the distribution of *P. inexpectata* has been strongly affected, declining by c. 45%, but we identified new areas of occurrence (10.72 ha) through field surveys. Most of these new areas (79%) were found in anthropogenic habitats where the species had not been documented before. The current distribution of *P. inexpectata* covers c. 24 ha, of which 75% is located in urban areas such as gardens and green urban spaces. Moreover, our field survey showed that at least 10% of its range is now colonized by the invasive gold-dust day gecko *Phelsuma laticauda*. This survey provides an essential baseline for tracking the future distribution of this threatened species and its potential invasive competitor, and for monitoring how changes to its habitat affect the distribution of *P. inexpectata*.

Keywords Critically Endangered, distribution area, invasive species, Manapany day gecko, *Phelsuma inexpectata*, *Phelsuma laticauda*, tropical island, urban herpetology

Introduction

Réunion Island has a long history of habitat and biodiversity loss (Cheke & Hume, 2008). Almost 50% of the island's original landscape has been converted to agricultural and urban use or is now covered by secondary vegetation (Strasberg et al., 2005). Urbanization pressure is particularly intense along the coast (Lagabrielle et al., 2010). The island's herpetofauna has been severely affected by anthropogenic activities, with five of the seven native reptile species extinct or presumed extinct (Arnold & Bour, 2008; Cheke & Hume, 2008). In common with many other oceanic islands, a large part of the native fauna is now extinct (Thébaud et al., 2009).

The Manapany day gecko *Phelsuma inexpectata* is endemic to the south of Réunion Island (Fig. 1; Bour et al., 1995; Austin et al., 2004). It is thought to have inhabited areas of native vegetation such as palm savannah and dry forest but these habitats have been almost completely destroyed (Strasberg et al., 2005; Sanchez et al., 2009). Remnant areas of native vegetation are now extremely scarce in the gecko's range and are mainly localized on coastal cliffs. In these natural environments, *P. inexpectata* mainly inhabits thickets of screwpine *Pandanus utilis* and Mauritius hemp *Furcraea foetida* (Plate 1; Choeur et al., 2023). In anthropogenic environments, it inhabits gardens and green urban spaces, where it occurs on planted screwpine and ornamental, exotic plants (Plate 1; Sanchez et al., 2009).

Between 1995 and 2011, several subpopulations of *P. inexpectata* disappeared or were found to be close to extinction (Bour et al., 1995; Probst & Turpin, 1997; Sanchez et al., 2009; Sanchez & Probst, 2011; Choeur, 2021). Subpopulations have been heavily fragmented by agriculture and dense urban networks, and also by areas of invasive vegetation, for example by degraded woods and thickets. The species faces additional threats including competition from the invasive gold-dust day gecko *Phelsuma laticauda*, which is native to Madagascar and has recently been documented within the range of *P. inexpectata* (Sanchez & Caceres, 2019). *Phelsuma inexpectata* is categorized as Critically Endangered on the IUCN Red List based on criteria B1ab(ii,iii,iv,v); i.e. with extent of occurrence < 100 km² (B1), populations severely fragmented (a), and with a continued decline (b) observed in: area of occupancy (ii), area, extent and quality of habitat (iii), number of subpopulations (iv), and number of mature individuals (v) (Sanchez, 2021).

Habitat modification, fragmentation and biological invasions are acknowledged as major drivers of population decline and extinction of island reptiles (Böhm et al., 2013; Leclerc et al., 2018; Cox et al., 2022; Farooq et al., 2024). In light of this, effective conservation strategies require detailed, up-to-date information about species distributions (Soulé et al., 2005; Böhm et al., 2013) but the most recent distribution assessment for *P. inexpectata* was > 10 years old prior to this study (Sanchez & Probst, 2011). Here we use data from 2008–2020 to estimate trends in *P. inexpectata* range and we update its distribution from field surveys undertaken during 2020–2022. We also describe the distribution of *P. laticauda* in *P. inexpectata* range.

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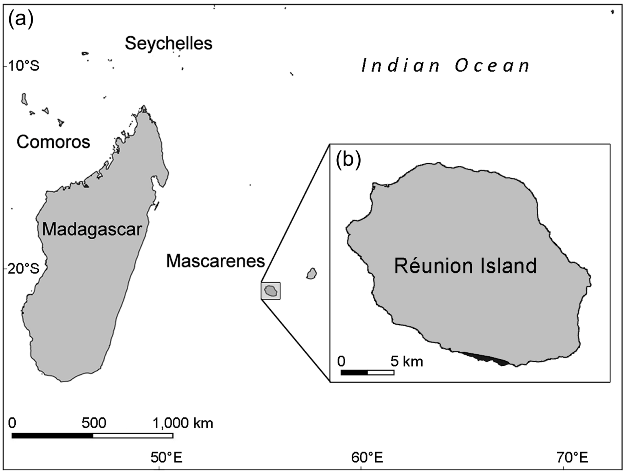

FIG. 1 (a) The location of Réunion Island in the south-western Indian Ocean and (b) the current range of *Phelsuma inexpectata* indicated in black.

Methods

Species distribution

Phelsuma inexpectata is a small (total length < 13 cm), arboreal and diurnal reptile (Plate 1). It is brightly coloured and does not flee from people, so the species is relatively easy to spot during searches. It is active all year round and mainly uses palm or palm-like trees for basking and hiding (e.g. screwpine, coconut tree *Cocos nucifera*, Agavaceae spp.; Sanchez et al., 2009; Sanchez & Probst, 2011; Choeur et al., 2023). It has poor dispersal abilities (< 100 m; Sanchez & Caceres, 2019; Choeur, 2021).

We established the past distribution of *P. inexpectata* from occurrences recorded between January 2008 and August 2020. We reviewed a database of 3,262 presence records registered at the Système d'information de l'inventaire du patrimoine naturel de La Réunion (SINP) and provided by the regional environmental services (Direction de l'Environnement, de l'Aménagement et du Logement). This dataset integrates observations collected through non-standardized methods as well as detections from distribution and capture–mark–recapture studies. We examined these records and sorted them according to their level of validity, geographical consistency and precision of the geolocation. We excluded occurrence records categorized as doubtful, those with geolocation precision > 20 m, and those with aberrant geolocations. We retained and mapped a total of 2,983 data points (91% of the dataset). We represented the distribution of *P. inexpectata* in 20 × 20 m grid cells to allow future updates of the distribution map. Finally, we created a past distribution map based on the 486 cells containing *P. inexpectata* observations (identified as previously occupied cells).

To assess the presence of the species and update its distribution, we visited all previously occupied cells (n = 486, 19.44 ha) between November 2020 and August 2022 (22 months) on 230 person-days, distributed throughout the year. Cells located in publicly accessible habitat were searched for 15 minutes by one observer (session 1). Both the grid cell size (400 m^2) and survey duration (15 minutes per session) were specifically tailored to the species' home range and detectability (derived from previous studies; Choeur, 2021). We searched for geckos visually, with or without binoculars, during their activity period (07.00–17.00) in sunny or partially cloudy weather, and recorded the geolocation for each detection. In some cells, we confirmed presence of the species during the first inspection session. To increase the accuracy of the presence–absence data, we carried out a second visit to those cells in which no gecko was detected during the first search (session 2), and if necessary, we visited a third time to check for species presence (session 3). If no gecko was detected in a cell after a total search effort of 45 minutes (15 minutes on 3 different days), we recorded the species as absent from this cell. Considering the species' relatively high detection probability, the likelihood of false negatives was very low after three 15-minute sessions. We followed an adjusted protocol when visiting cells located on private land (door-to-door protocol) because constraints on access meant that the duration of sampling was not constant (mean 8.8 min/cell). In these cases, one or two observers searched the area for geckos following the same method but visiting up to four times. We also recorded the presence of the species in new cells where no detections had been registered previously (opportunistically recorded detection). In addition, we recorded the presence of the invasive *P. laticauda* during our field surveys. Because of the sensitive nature of the distribution data of *P. inexpectata*, we have not included distribution maps in this article.

Land use

To investigate whether the presence of the species was associated with land use, we specified the habitat type of each previously occupied cell and of each new cell occupied by *P. inexpectata*. Although no habitat data were available from the previously occupied cells, we assumed that there had been no major changes between the previous sampling period (2008–2020) and our recent survey (2020–2022), based on personal observations in the field. We classified cells into three habitat categories: (1) anthropogenic, containing environments modified or degraded by human activities (e.g. housing, agricultural, roads, cultural activity) including private gardens, green spaces, palm and cane cultivation, (2) natural, containing remnants of natural habitat unaffected by human activities including thickets of screwpine and Mauritius hemp, and (3) mixed, containing both anthropogenic and natural habitats (Plate 1).

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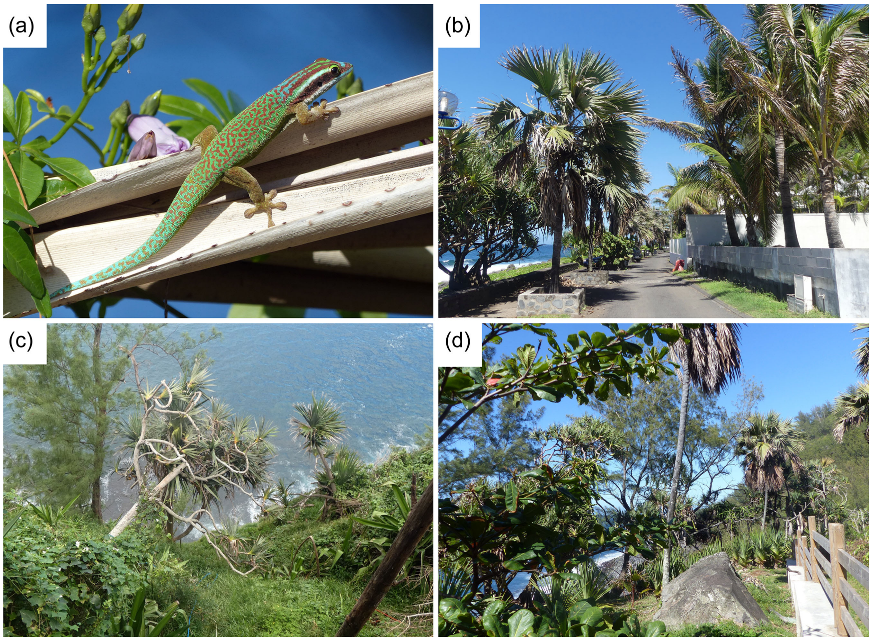

PLATE 1 (a) The Manapany day gecko *Phelsuma inexpectata*, and examples of (b) anthropogenic, (c) natural and (d) mixed habitats inhabited by the species.

We tested whether habitat type determined lack of presence in the previously occupied cells using a χ^2 test. We performed statistical analyses using *R 4.1.0* software (R Core Team, 2021), with a significance level of 0.05.

Results

We estimated that *P. inexpectata* was present in an area of 19.44 ha during 2008–2020 (486 cells, 20 × 20 m), mainly in anthropogenic habitats (n = 320 cells, 66%) with fewer records from natural (n = 97, 20%) and mixed habitats (n = 69, 14%; Table 1, Fig. 2a). We searched the same area during 2020–2022 but were unable to access 27 cells (5.5%, located on private land or on dangerous cliffs), resulting in a sample of 459 cells from which to assess changes in species distribution (Fig. 2b). We found no evidence of *P. inexpectata* in 28% of the cells searched (n = 128, 5.12 ha; Fig. 2b).

We recorded a sharp decline in species presence in natural habitats, detecting no evidence of *P. inexpectata* in 45% of the previously occupied cells (n = 44, −1.76 ha). Species presence also declined in mixed and anthropogenic habitats but to a lesser extent. We found no evidence of *P. inexpectata* in 29% of cells in mixed habitat ($\chi^2 = 5.81$, df = 1, $P < 0.05$; n = 20, −0.8 ha) and in 20% of anthropogenic habitat ($\chi^2 = 25.94$, df = 1, $P < 0.001$; n = 64, −2.56 ha). Of the cells where we did not detect *P. inexpectata,* we had searched 55% (n = 70) for 45 minutes (all three sessions completed), and 45% (n = 58) following the door-to-door protocol (up to four sessions).

We recorded *P. inexpectata* in 268 new cells (10.72 ha) in which its presence had not been documented previously. The majority (79%) of these cells were located in anthropogenic habitat (n = 211, 8.44 ha), with a further 13% in mixed habitat (n = 36, 1.44 ha) and 8% in natural habitat (n = 21, 0.84 ha; Table 1, Fig. 2a).

Overall, we observed *P. inexpectata* in 599 cells (331 previously occupied cells + 268 new cells) in our 22-month survey (2020–2022), equating to 23.96 ha. The species was mainly located in anthropogenic habitat (75%, n = 447, 17.88 ha), but *P. inexpectata* was also recorded in mixed (14%, n = 84, 3.36 ha) and natural (11%, n = 68, 2.72 ha) habitats (Table 1, Fig. 2a). Nearly all occupied cells (99%) were below 150 m elevation.

We detected the invasive *P. laticauda* in 93 cells: in 44 cells where *P. inexpectata* was recorded previously and in the recent survey (13% of the 331 cells occupied previously and recently), 32 cells where *P. inexpectata* was recorded previously but not in the recent survey (25% of the 128 cells occupied previously but not recently), and 17 cells where *P. inexpectata* was recorded only in the recent survey (6% of the 268 newly occupied cells). Within the current range of *P. inexpectata*, we recorded sympatry in 61 cells (2.44 ha), representing at least 10% of the species' distribution. The majority of the sympatric cells were in anthropogenic habitat (87%, n = 53 cells) but sympatry was also observed in mixed habitat (11%, n = 7 cells) and natural habitat (2%, n = 1 cell).

Discussion

Species distribution

In 2022, the Critically Endangered *P. inexpectata* occupied c. 24 ha along the southern coast of Réunion Island. To our

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TABLE 1 Presence of the Manapany day gecko *Phelsuma inexpectata* in anthropogenic, mixed and natural habitats on Réunion Island during two sampling periods, 2008–2020 and 2020–2022. Presence was recorded as the number of cells occupied and converted to area occupied based on the size of the grid cells (20 × 20 m). The % values given for the presence in 2008–2020 and total presence in 2020–2022 indicate the per cent of presence records in a specific habitat type of the total presence records across all habitat types.

	Number of cells	Area (ha)
Anthropogenic habitat		
Presence 2008–2020 (66%)	320	12.80
2020–2022 Surveys		
Total presence (75%)	447	17.88
Presence in previously occupied cells	236	9.44
Presence in new cells	211	8.44
Absence in previously occupied cells	64	2.56
Cells not surveyed	20	0.80
Mixed habitat		
Presence 2008–2020 (14%)	69	2.76
2020–2022 Surveys		
Total presence (14%)	84	3.36
Presence in previously occupied cells	48	1.92
Presence in new cells	36	1.44
Absence in previously occupied cells	20	0.80
Cells not surveyed	1	0.04
Natural habitat		
Presence 2008–2020 (20%)	97	3.88
2020–2022 Surveys		
Total presence (11%)	68	2.72
Presence in previously occupied cells	47	1.88
Presence in new cells	21	0.84
Absence in previously occupied cells	44	1.76
Cells not surveyed	6	0.24
All habitats		
Presence 2008–2020	486	19.44
2020–2022 Surveys		
Total presence	599	23.96
Presence in previously occupied cells	331	13.24
Presence in new cells	268	10.72
Absence in previously occupied cells	128	5.12
Cells not surveyed	27	1.08

knowledge, it is the rarest endemic terrestrial vertebrate on the island in terms of its distribution.

The species' known range was estimated to be c. 19 ha pre-2020, based on records from 2008–2020 registered with SINP by a variety of sources. We collected more information on the species' distribution in systematic surveys during 2020–2022, identifying an additional 10 ha of new range but also noting the species' absence from c. 5 ha where it had been recorded in the past. As a result of differences in search protocols, it was not possible to determine whether the new areas had previously been occupied or were colonized only recently. We found most of the newly described areas (8.4 ha) in anthropogenic habitat, mainly gardens and urban green spaces. The urban distribution of *P. inexpectata* could be even more extensive and future research should focus on this habitat, which is often more difficult to access than natural habitats. The potential for detecting *P. inexpectata* in new areas of natural habitat is low as all remaining natural patches have been carefully searched.

We observed a sharp decline in the area occupied by *P. inexpectata* in the past, recording presence in only 14 ha out of the 19 ha where it was found previously. This range contraction was particularly pronounced in natural habitats, where the species was absent from almost half of the natural areas occupied during 2008–2020. We searched each 20 × 20 m cell intensively for 3 × 15 minutes (over 3 days) and conclude that non-detection in natural areas was almost certainly a result of the species' absence rather than individuals being present but remaining undetected.

In contrast, because of access and search constraints in privately owned, anthropogenic habitats, species occurrence in these cells could have been underestimated in the past and the species may have been more widely distributed. Alternatively, anthropogenic habitats could

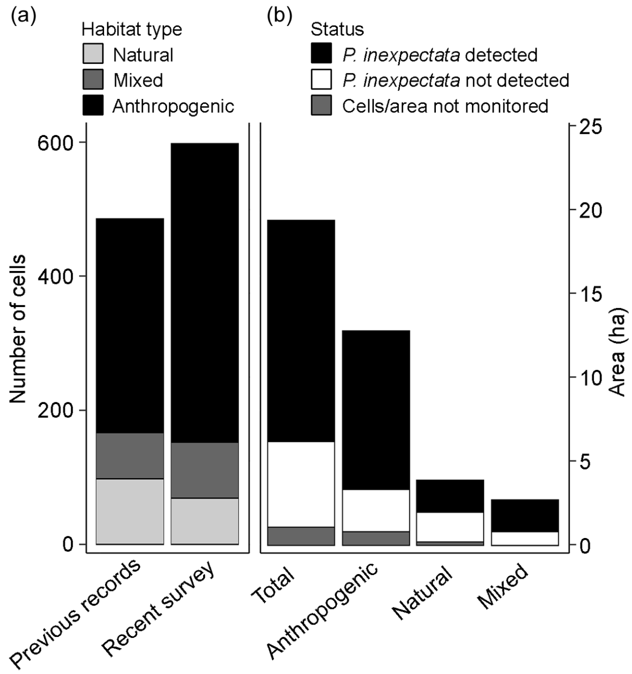

FIG. 2 (a) Number of 20 × 20 m cells and the area occupied by *P. inexpectata* in natural, mixed and anthropogenic habitats, estimated from previous records (2008–2020) and our recent survey (2020–2022). (b) Number of cells and the area previously occupied and included in our recent survey in which *P. inexpectata* was detected, not detected, and those that could not be monitored, by habitat type.

have been poorly documented because earlier records were mainly based on opportunistic data rather than systematic searches. Therefore, it is unclear whether the species was more common but unrecorded in anthropogenic habitats in the past, and consequently we cannot determine whether the 20% contraction of the species' range in anthropogenic habitats calculated from our data is an accurate assessment.

The overall contraction in the range of *P. inexpectata* could have resulted from a number of factors, including changes in habitat (Sanchez & Probst, 2011) or abiotic conditions (Dubos et al., 2021), an increase in predation or competition from other reptiles, mammals, birds or ants (Sanchez & Caceres, 2019; Choeur, 2021; Souchet et al., 2024), or even the use of biocides against mosquitos or geckos (Sanchez et al., 2009; Ineich et al., 2019). Whilst the impact of these various factors has been linked to the decline of other lizard species (Alexander et al., 2002; López-Darias et al., 2024), particularly within the genus *Phelsuma* (Cole & Harris, 2011; Sanchez & Probst, 2016; Pointer et al., 2024), it is difficult to assess their effects on *P. inexpectata*. We do not know how the habitat has evolved at a fine scale, either in natural or anthropogenic habitats, and no data are available to assess the effects of other factors.

Environmental conditions on Réunion Island have changed in the last 50 years. There has been a significant rise in mean temperatures (0.15–0.20 °C per decade) and decrease in rainfall (6–8% per decade) in the south-western region of the island (Météo-France, 2022). Changes in temperature can affect sex ratio (Wapstra et al., 2009; Edmands, 2021) in *Phelsuma* species (Peš et al., 2024), and can impair individual physiological performance (Huey et al., 2009), thereby affecting population dynamics and elevating the risk of extinction. Additionally, the availability of food (insects, floral nectar and fruits) could be negatively affected by lower rainfall and reduced water availability (Numata et al., 2022; Rajkumari et al., 2024). Climate change is expected to intensify in future, with range shifts (including contractions) predicted for related species (Dubos et al., 2022). A recent modelling study predicts a decline in climatic suitability for *P. inexpectata* across its current range (Dubos et al., 2021). However, the relative impact of these different factors is difficult to estimate and may vary considerably depending on the local environment.

Subpopulations in natural habitats have declined dramatically and appear to be more sensitive to range contraction and more liable to local extinction than those in anthropogenic habitats. Natural habitats occur mainly around coastal cliffs, where the landscape has remained unchanged for at least 10 years (M. Sanchez, unpubl. data, 2008–2010; Plate 1). Anthropogenic habitats such as gardens offer a more favourable habitat for *P. inexpectata* because they often comprise a variety of palm species and are frequently watered, providing food resources all year round (floral nectar and fruits that attract potential insect prey). This is in contrast to natural habitats that support few palm species and are more exposed to severe drought and rising temperatures. Moreover, anthropogenic environments provide a variety of artificial micro-habitats such as buildings, pipes, protective cavities and other structures. These offer protection from extreme weather (wind, rain, sun, cyclones), refuge from predators, egg-laying sites and a variety of basking sites. Plant diversity and access to anthropogenic structures are recognized as key factors for the survival of *Phelsuma* populations (Cole, 2005; Buckland et al., 2014a; Bungard et al., 2014; Augros et al., 2017a, Sanchez & Probst, 2017a).

Other species within the order Squamata also benefit from anthropogenic modifications to the landscape such as the addition of suitable artificial structures, although this is not always the case (Ineich, 2010; Augros et al., 2017a; French et al., 2018; Doherty et al., 2020; Graitson et al., 2020). Our study highlights that for *P. inexpectata*, habitats modified by people can be favourable, providing structural and trophic diversity, and could be beneficial in the long term if plant species diversity is maintained. Across the world, several insular gecko species have adapted to anthropogenic environments, including urban areas (Ineich, 2010; Hawlitschek et al., 2011; Augros et al., 2017a,b; Sanchez & Probst, 2017b; Humphrey & Ward, 2018; Woolley et al., 2019; Bauer et al., 2022), highlighting the significance of these habitats for the conservation of threatened geckos.

Invasive species

In 2011 there was no record of *P. laticauda* in the study area despite intensive searches for geckos undertaken to determine the distribution of *P. inexpectata* (Sanchez & Probst, 2011). This means that substantial colonization has taken place over c. 15 years. In 2022, at least 10% of the *P. inexpectata* distribution area was occupied by *P. laticauda*. The actual level of occupancy is probably higher because of the low detection rate of *P. laticauda* at low density. Moreover, *P. laticauda* was detected in all types of habitat inhabited by *P. inexpectata* including isolated remnants of native coastal vegetation (Sanchez & Probst, 2016).

Aspects of the biology and ecology of *P. laticauda* favour its spread into new areas at the expense of the endemic *P. inexpectata*. Unlike the endemic, *P. laticauda* can use highly modified habitats such as dense urban areas, degraded woods and thickets, and cropland (Sanchez & Probst, 2016), allowing it to colonize new areas easily. Moreover, it disperses easily (Caceres et al., 2022; M. Sanchez, unpubl. data, 2025) and probably reproduces year-round (Goldberg & Kraus, 2011), whereas *P. inexpectata* has low dispersal capabilities and a seasonal reproductive strategy (Choeur et al., 2022). *Phelsuma laticauda* is thought to be highly competitive (Hawlitschek et al., 2011) and aggressive towards other species (Henkel & Schmidt, 2000; Lund, 2015), and it also feeds on other geckos (Gehring et al., 2010). It is therefore expected to spread rapidly and have a negative impact on populations of the endemic *P. inexpectata*.

Conservation

We have updated the distribution of *P. inexpectata* and characterized the habitat types it occupied on Réunion Island in our recent survey. This information is important when assessing the conservation status of a threatened species such as *P. inexpectata* that is characterized by a limited distribution and low mobility. These baseline data are essential for tracking changes in the distribution of this Critically Endangered species and its potentially invasive competitors, and for studying the effects of anthropogenic alterations to its habitat. Our fine-scale 20 × 20 m grid allowed us to make a detailed estimate of the area occupied and to record changes to its range. Additionally, our data provide operational information for monitoring and management of a species whose range is under intense anthropogenic pressure (Thorn et al., 2011; Böhm & Popescu, 2016; Sudo & Nakaoka, 2020).

The conservation of *P. inexpectata* will be a significant challenge but we highlight three major action points. Firstly, in 2022 the majority of its range (75%) was in low-elevation, human-modified areas, mainly gardens and urban green spaces, which are subject to high development pressure (Lagabrielle et al., 2010). Gardened environments are heterogeneous ecosystems that have the potential to contribute substantially to the conservation of the species, and should therefore be planned and managed accordingly. Maintaining and improving habitat quality and variability could have a positive effect on populations of *P. inexpectata* by increasing resource availability and microhabitat diversity (Bullock, 1986; North et al., 1994; Croak et al., 2013). Favourable habitats could be created by large-scale planting of gecko host plants in urban areas. We strongly recommend participatory conservation approaches such as Gecko Garden Refuges (Krieg, 2020), which educate local people and should be actively promoted and extended across the entire gecko range and adjacent areas. We also advocate regular monitoring of the Manapany day gecko population to measure the effectiveness of these conservation efforts. Finally, we emphasize that the long-term viability of *P. inexpectata* populations could be threatened by the use of biocides (e.g. for mosquito control; Alexander et al., 2002) and may also be significantly affected by political decisions related to land use, such as granting permission for development (Sanchez & Caceres, 2019).

Secondly, it is essential to preserve the remaining 2.72 ha of natural habitat to safeguard the survival of *P. inexpectata* in its historical range. In the short term, conservation efforts should be focused on habitat restoration and the control of predators to maintain the remnant subpopulations. In addition, it is important to protect this area from any anthropogenic alteration such as destruction, modification or fragmentation caused by encroachment by people or degradation by introduced invasive plant species. The creation of a nature reserve in this area could be an effective tool to improve *P. inexpectata* conservation in its natural habitat, and may also benefit other threatened species, notably seabirds and plants (Sanchez & Caceres, 2019; Choeur, 2021).

Thirdly, a good knowledge of the ecology, biology and population dynamics of *P. inexpectata* is crucial to understanding the causes of the observed decline in numbers, but this can only be acquired through long-term studies in both natural and urban areas. We propose that research priorities should focus on two issues: (1) an investigation of the potential ecological impact of invasive predators or competitors, notably *P. laticauda* (Cole, 2005;

Buckland et al. 2014b; Florence-Bennett, 2020; Norbury et al., 2023), and (2) the influence of habitat structure and composition on population dynamics, including plant species communities and the importance of artificial microhabitats (Ineich, 2010; Zeng et al., 2014; Cosendey et al., 2019).

To conclude, we emphasize the need for effective and immediate conservation actions to halt the decline and avoid the extinction of the Critically Endangered Manapany day gecko *P. inexpectata*, which is endemic to Réunion Island. These interventions must be supported by research programmes to better understand the causes of its decline and to identify the crucial factors affecting its survival.

Author contributions

Study design: JC, MS; fieldwork: MS, A Bonanno, MC, A Bousseyroux; data analysis: MS, A Bonanno, JC; writing: MS, JC, A Bonanno, MC, A Bousseyroux.

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Conflicts of interest None.

Ethical standards This research abided by the *Oryx* guidelines on ethical standards. No specific approval was required for our study.

Data availability The data that support the findings of this study are not publicly available; they are classified as Sensitive under the French Environmental Code (Article L. 124-4 §8), as their disclosure could jeopardize the conservation of a highly threatened species. These data may be made available under certain conditions and upon reasonable request from the Système d'Information de l'Inventaire du Patrimoine Naturel de La Réunion.

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