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A resurvey of threatened endemic tree populations in seasonally dry tropical forests of Reunion Island (Indian Ocean) suggests imminent extinctions

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ABSTRACT

Seasonally dry tropical forests are among the most threatened forest types in the world. For instance, less than 1 % of original seasonally dry tropical forests remains on Reunion Island (South-West Indian Ocean). There, five endemic woody taxa restricted to seasonally dry tropical forests are included in a dedicated national action plan. This study reports on a resurvey conducted as part of this plan, in which 51 historically described subpopulations were revisited and 46 new subpopulations were discovered. Half of the historical individuals were either found dead or not found. The annual survival rate was therefore relatively low and similar between taxa (0.93–0.95). Because of the lack of regeneration observed in the field, the estimated annual recruitment was even more critical, and varied by a factor of 10 from *Abutilon exstipulare* (0.09 juveniles produced per reproductive plant) to *Tabernaemontana persicariifolia* (< 0.01). Based on these data, we performed a series of population viability analyses that led either to extinction within a few decades or to population size at which extinction becomes very likely over the long term. This situation urges local conservation stakeholders to make every possible effort both on site and ex situ to save this unique flora.

1. Introduction

Tropical forests are often considered as a uniform entity of evergreen rainforests, but there are significant differences between tropical forests in important biophysical variables such as precipitation, temperature or solar radiation. For instance, more than 40 % of tropical and subtropical forest areas receive less than 1,500 mm of annual precipitation and experience a pronounced dry season lasting several months (Murphy & Lugo, 1986), making the so-called seasonally dry tropical forests the second most common forest type in the world (Hasnat & Hossain, 2020).

These forests often host a remarkably high biodiversity and are an important source of livelihood for rural populations (Neudert et al., 2018). Historically, human settlements have favoured seasonally dry conditions, which were characterised by lower disease incidence, easy-to-clear vegetation, and more productive soils compared to wet conditions, which could support shifting agriculture and land conversion to pasture for grazing (Griscom & Ashton, 2011). Tropical dry regions are therefore historically characterized by a higher human population density than humid regions, resulting in higher pressure on such forests and greater deforestation rates than in wet forests (Schröder et al., 2021).

As a result, seasonally dry tropical forests are also among the most endangered terrestrial ecosystems in the world (Janzen, 1988; Miles et al., 2006), and they continue to experience some of the highest rates of deforestation (Hansen et al., 2013). Seasonally dry tropical forests have shrunk to a tiny proportion (sometimes < 1 %) of the original global forested area, and about 97 % of the remaining seasonally dry tropical forest areas are considered at risk (Miles et al., 2006). Anthropogenic changes in land-cover, forest fires, resource extraction, climate change and biological invasions are among the most important causes of

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change in seasonally dry tropical forests (Hansen et al., 2013; Miles et al., 2006; Sánchez-Azofeifa et al., 2005). The coincidence of high human population densities and the last dry forest remnants challenges their conservation, which is sometimes seen as competing with other land use needs of the society (Rodríguez-Echeverry, 2024).

As seasonally dry tropical forests are an important reservoir of biodiversity, their loss contributes significantly to the erosion of the Earth's biodiversity and a decline in associated ecosystem services (Balvanera et al., 2011; Cabin et al., 2000). This is particularly true for tropical islands with high proportion of endemic taxa (found nowhere else in the world). For instance, the seasonally dry tropical forests on the Pacific islands have shrunk to less than 10 % of their original area, and almost all remaining fragments are smaller than 100 ha (Gillespie et al., 2013). In the Caribbean, two thirds of the original seasonally dry tropical forests have also been lost, with over 80 % of their remnants in the region considered as highly fragmented (Portillo-Quintero & Sánchez-Azofeifa, 2010). In Madagascar, seasonally dry tropical forests have declined by 30–40 % since the 1970 s (Vieilledent et al., 2018), and they are twice as poorly protected as wet forests (Waeber et al., 2015).

Despite their global importance and high vulnerability, seasonally dry tropical forests remain one of the least studied tropical habitats (Mooney, 2011; Prieto-Torres et al., 2021; Stoner & Sánchez-Azofeifa, 2009). A few modelling approaches, including population viability analyses (a technique that uses demographic data in analytical models to assess extinction risk), have been developed to evaluate the threats faced by populations of a small number of flagship vertebrate species such as primates (Barreto et al., 2022; Volampeno et al., 2015). However, as far as we know, there is no equivalent analysis for plants in seasonally dry tropical forests. Yet, a better understanding of how the loss and degradation of seasonally dry tropical forests affect their flora would undoubtedly help to implement more efficient management strategies.

Recently, revisitation studies, i.e. resurveys to examine whether a species is still present in places where it was observed in the past, have proven to be a valuable source information on population dynamics and extinction risk, especially for long-lived plants such as trees and shrubs (Holderegger & Spillmann, 2022). In this study, we provide a quantitative assessment of the extinction risk of five critically endangered (CR) woody taxa on the island of Reunion (Mascarene Islands, South-West Indian Ocean), where less than 1 % of original seasonally dry tropical forests remain (Sarrailh et al., 2008; Strasberg et al., 2005). We show that resurveys can help to estimate demographic parameters that can subsequently be used to assess species' chances of recovery or risk of extinction.

2. Materials and methods

2.1. Study site

This study was conducted on Reunion, the largest (2,512 km^2) and youngest island (2–3 million years old) of the Mascarene archipelago, which also comprises the islands of Mauritius and Rodrigues. The climate of Reunion is tropical and characterised by two seasons: a warm and rainy austral summer followed by a relatively cool and dry winter (Réchou et al., 2019). Annual rainfall ranges from 500 mm on the leeward side of the island to $>$ 8,000 mm on its windward side. Reunion harbours a remarkable diversity of ecosystems zonated along an elevational gradient ranging from sea level to 3,070 m a.s.l. (Piton des Neiges). Due to the high degree of endemism of its native vascular flora (24 % of single-island endemism and 40 % of archipelago-endemism) (IUCN French Committee et al., 2023) and dramatic loss in primary vegetation (over two thirds of the island) (Strasberg et al., 2005), Reunion has been included in the biodiversity hotspot 'Madagascar and the Indian Ocean Islands' (Myers et al., 2000). In the last few years, the number of native vascular plant species threatened with extinction has grown at a rapid rate, from 30 % in 2010 to 41 % in 2023 (although this change is also attributable to non-genuine reasons such as a different assessment method between both dates and an increasing amount of data available; IUCN French Committee et al., 2023).

Seasonally dry tropical forests now only exist in the form of profoundly altered remnants on Mauritius and Rodrigues, but the leeward coast of Reunion supports better preserved patches up to 1,000 m a.s.l., covering several dozens of km^2 (Fig. 1) (Strasberg et al., 2005). The seasonally dry forests have been severely destroyed for coffee cultivation and timber harvesting after the colonization of the island in the 17th century and, more recently, transformed for urban development (Sarrailh et al., 2008). The leeward coast of Reunion has a high and increasing population density, which generates escalating anthropogenic pressures on tropical dry forests, especially on private lands. The remaining patches are highly fragmented and degraded by invasive alien plants such as *Furcraea foetidia* (L.) Haw. (Asparagaceae), *Hiptage benghalensis* (L.) Kurz (Malpighiaceae), *Lantana strigocamara* R.W. Sanders (Verbenaceae), *Leucaena leucocephala* (Lam.) de Wit (Fabaceae), *Litsea glutinosa* (Lour.) C.B.Rob. (Lauraceae), *Searsia longipes* (Engl.) Moffett (Anacardiaceae), *Schinus terebinthifolia* Raddi (Anacardiaceae) and *Tecoma stans* (L.) Juss. ex Kunth (Bignoniaceae), as well as by forest fires, seed predation and bark stripping by rats, grazing by goats and cattle, the expansion of sugar cane fields and road construction projects (Barbé et al., 2015).

2.2. Model species

In the late 1980s, the alarm was first sounded that the seasonally dry forest flora on Reunion was highly threatened, which led to numerous surveys and a few initial protection measures (Dupont et al., 1989). In 2021, a national action plan (NAP) 'woody species of lowland dry forest remnants' (*espèces ligneuses des reliques de la bande adlittorale xérophile*) was established for six tree and shrub taxa for a period of five years (Mallet et al., 2024). NAPs aim to organise coherent monitoring of the populations of the species concerned, to implement coordinated measures to restore viable populations or their habitats, to inform the stakeholders concerned and the public, and to promote the integration of species conservation into human activities and public policies. Here, we focused on five of the six taxa (Table 1, see Appendix A for pictures of the taxa). Two species are exclusively endemic to Reunion, *Abutilon exstipulare* (Cav.) G.Don (Malvaceae) and *Latania lontaroides* (Gaertn.) H. E.Moore (Arecaceae), two others are also found on Mauritius, *Tabernaemontana persicariifolia* Jacq. (Apocynaceae) and *Volkameria heterophylla* Vent. (Lamiaceae), and one species is distributed on all three Mascarene Islands (archipelago endemic) with one subspecies endemic to Reunion and Mauritius, *Terminalia bentzoe* (L.) L. f. subsp. *bentzoe* (Combretaceae) and another subspecies endemic to Rodrigues, *T. bentzoe* subsp. *rodriguesensis*. The sixth taxon included in the NAP, *Ruizia cordata* Cav. (Malvaceae), was excluded from the study as only four old individuals are known to occur in the wild, which is most likely below the minimum viable population (making this endemic species one the most threatened at global scale). All taxa were categorised as CR (IUCN French Committee et al., 2023). They are hereafter referred to by their genus name only.

2.3. Resurvey

As part of the NAP, several actions have been carried out since 2022, including the resurvey of 51 historical localities where the taxa occurred in the past, and additional prospections around known historical locations and in poorly botanised areas (Appendix B). Historical localities were relevés (with data on numbers of individuals) recorded in the local information system for biodiversity Borbonica (which gathers observations from almost all active botanists on the island; https://www.borbonica.re/) from 1998 to 2021. At each site, the number of individuals found alive or dead, or not found was counted. Based on the botanical knowledge of the people involved and time spent on site (a missing tree was sought for 30 min to one hour), we estimate the probability that

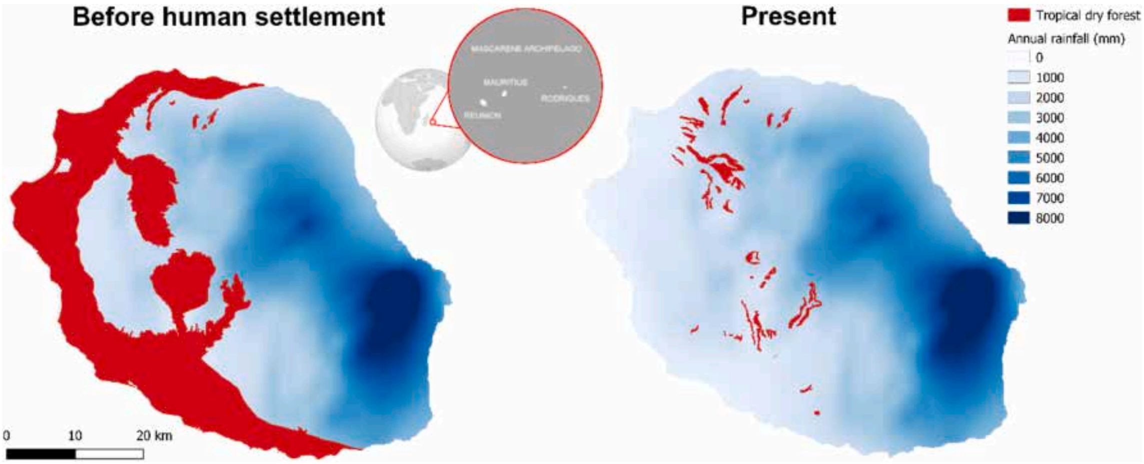

Fig. 1. Original (left) and current (right) extent and geographical distribution of seasonally dry tropical forests in the island of Reunion (adapted from Strasberg et al., 2015).

Table 1
Summary of the five seasonally dry forest woody plant taxa endemic to the Mascarene archipelago considered in this study. Endemism: R = Reunion, M = Mauritius. "?" denotes uncertainty of the observation and requires further investigation for confirmation. Age at maturity (estimated in years) was derived from the monitoring and evaluation of the LIFE + project 'COREXERUN' (Prolhac, 2020) and from personal observations of the Mascarin Botanical Garden for *Latania lontaroides*. Pollinators and seed dispersers are unpublished data from CBN-CPIE Mascarin.

Taxon	Family	Endemism	Habit	Age at maturity	Pollinators	Current seed disperser(s)	Desiccation tolerance	Traditional use
Abutilon exstipulare	Malvaceae	R	Shrub	3	Insects	Gravity	Orthodox	None
Latania lontaroides	Arecaceae	R	Palm	12	Insects	Gravity	Recalcitrant	Wood, fruits
Tabernaemontana persicariifolia	Apocynaceae	R + M	Small tree	5	Insects?	Birds + gravity?	Unknown	None (toxic)
Terminalia bentzoe	Combretaceae	R + M	Large tree	5	Insects	Gravity	Orthodox	Pharmacopoeia, wood
Volkameria heterophylla	Lamiaceae	R + M	Small tree	5	Insects?	Birds + gravity?	Orthodox	Pharmacopoeia

living individuals were overlooked as very unlikely (< 5 %). In addition, many other sites were explored where new individuals (not included in Borbonica) were discovered (Appendix C). At each locality (both historical and new) the current number of juvenile and adult plants was recorded. Afterwards, we used the term 'juveniles' to collectively describe the life stages prior to reproductive maturity so that saplings and seedlings are also encapsulated (Arasa-Gisbert et al., 2024).

For each resurveyed locality, we estimated a survival rate S as the proportion of historically recorded individuals that are still alive, and calculated an annual survival rate $S_a = S/t$, where t is the number of years between a historical record and its resurvey. The weighted mean, which considers the number of individuals in each locality and the standard deviation of the annual survival rate, was then calculated from all resurveyed localities. We also calculated the mean recruitment R as the average number of juveniles produced per reproductive plant across all localities (including updated historical records and new records). We finally estimated an annual recruitment rate $R_a = R/m$, where m is the age at maturity of the species so as to account for the fact that current juveniles have been produced over the last m years (Table 1). The resurvey was completed in 87 man-days.

2.4. Population viability analysis

We conducted a series of population viability analyses (PVA) to predict how current survival and recruitment rates would translate in terms of population viability in the future. As we do not know the exact population size of the five taxa, we created two scenarios. In scenario 1 (pessimistic), the current population size corresponds to the number of mature individuals observed during the resurvey (historical individuals still alive and newly discovered individuals). We therefore assume that the individuals not resurveyed are all dead. In scenario 2 (optimistic), the current population size is set to 250, i.e. the maximum number of mature individuals for a taxon to be considered CR according to the IUCN-red-list criterion C. To account for uncertainty in parameter estimation, we performed a sensitivity analysis with observed values, observed values + 10 % and observed values – 10 % for mortality ($1 - S_a$) and recruitment rates (R_a). Age at sexual maturity was also included as a parameter in the PVA (Table 1). No assumptions were made about environmental stochasticity and density dependence, as we ignore their effects on vital rates in the absence of a dedicated research. For each taxon, we ran 1000 simulations between 2025 and 2100 on an annual basis. All PVA models were created using the package 'nepva' (Searle et al., 2022) developed with the software R (R Core Team, 2018).

3. Results

Among the 172 individuals resurveyed in the seasonally dry tropical forests of Reunion, only 85 (49 %) were found alive, 18 (11 %) were found dead and 69 (40 %) were not found despite our effort. Almost a third (30 %) of the dead and missing individuals belonged to the species *Tabernaemontana* and a quarter to the species *Volkameria* (28 %) and *Abutilon* (25 %), while the two other taxa together accounted for only 17 % of dead or missing individuals (Fig. 2A). *Abutilon* has been extirpated from 44 % of localities where it was previously recorded, *Tabernaemontana*, *Terminalia* and *Volkameria* disappeared from more than 20 % (21–29 %) of their historical localities, while *Latania* persisted in all localities (Fig. 2B).

Many individuals and localities were also discovered during the new

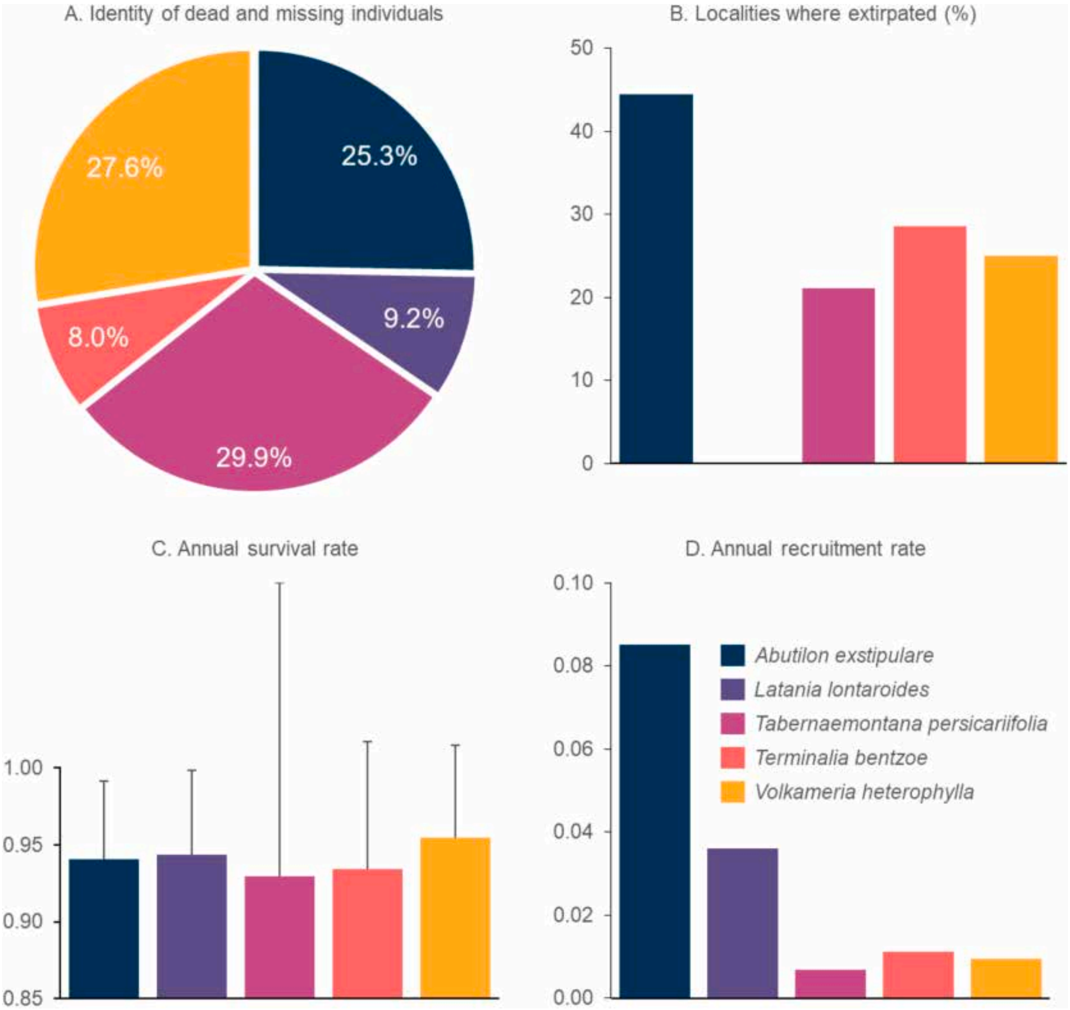

Fig. 2. Results of a resurvey of 172 historical individuals of five seasonally dry forest woody plant taxa endemic to the Mascarene archipelago over 51 localities on Reunion. A: Taxa to which the 87 individuals found dead or not found during the resurvey belong. B: Percentage of the localities where the taxa were historically recorded with no living individuals anymore. C: Annual survival rate, i.e. proportion of individuals surviving from year to year averaged over all localities with vertical bars representing standard deviation. D: Annual recruitment rate, i.e. number of juveniles produced per adult and per year across all localities.

census (Fig. 3). The numbers of newly discovered individuals were five times as high as survivors in resurveyed historical subpopulations for *Abutilon*, three times as high for *Terminalia*, twice as high for *Latania* and equally high for *Tabernaemontana* and *Volkameria* (Table 2). On Reunion, the minimum size of wild populations (scenario 1) of our five seasonally dry forest woody plant taxa thus ranged between 35 individuals for *Tabernaemontana* and 62 individuals for *Terminalia*.

The annual survival rate estimated from resurveyed individuals S_a did not vary much (0.93–0.95) among taxa (Fig. 2C). The annual recruitment rate estimated from resurveyed and newly discovered individuals R_a was extremely low, varying by a factor of 10 between the small tree species *Volkameria* and *Tabernaemontana*, which produce on average less than 0.01 juveniles per adult per year, and the shrub species *Abutilon*, which produces 0.09 juveniles per adult per year (Fig. 2D).

The population viability analyses show a sharp decline over the century for the five taxa if nothing more is done to save them (Fig. 4). *Tabernaemontana* and *Terminalia*, both of which exhibited low S_a and R_a values, are expected to become extinct in the wild on Reunion before the end of the century. The former will even fall below 10 individuals from 2040 and the latter shortly after 2050. For the three other species, the projections are somewhat more optimistic, but they still reach numbers of individuals that will certainly be below the quasi-extinction (or population collapse) threshold by the end of the century ($<$ 10 individuals under the 'pessimistic' scenario 1, $<$ 50 under the 'optimistic' scenario 2). These projections showed little variation with a 10 % change in vital rates, which demonstrates little sensitivity to uncertainties in vital rate estimation (Appendix D).

4. Discussion

A revisitation of 51 historical subpopulations of five endemic woody taxa in the seasonally dry tropical forests of Reunion revealed rapid declines that are likely to lead either to extinctions in the wild or to population sizes at which extinctions become very probable within a few more decades. The sharp decline of the taxa appears to be due primarily to regeneration failure, reflected as the absence or extremely low number of juveniles at the inventoried sites. Predicted extinction risks remained high in all simulated conditions and were not highly sensitive to a 10 % variation in vital rates, which demonstrates that a more significant change in vital rates is required to save these taxa from extinction in the wild.

On Reunion, numerous fleshy-fruited tree species show a worrying lack of regeneration due to the extinction of large-bodied frugivores (e.g. giant tortoises, flying foxes, parrots, fruit pigeons, skinks) by the first half of the 18th century (Albert et al., 2020). However, as some of the study species are dispersed by wind (*Abutilon* and *Terminalia*; Table 1), the dramatic loss of the dispersal role played by frugivores may not be the unique reason behind the observed near absence of regeneration.

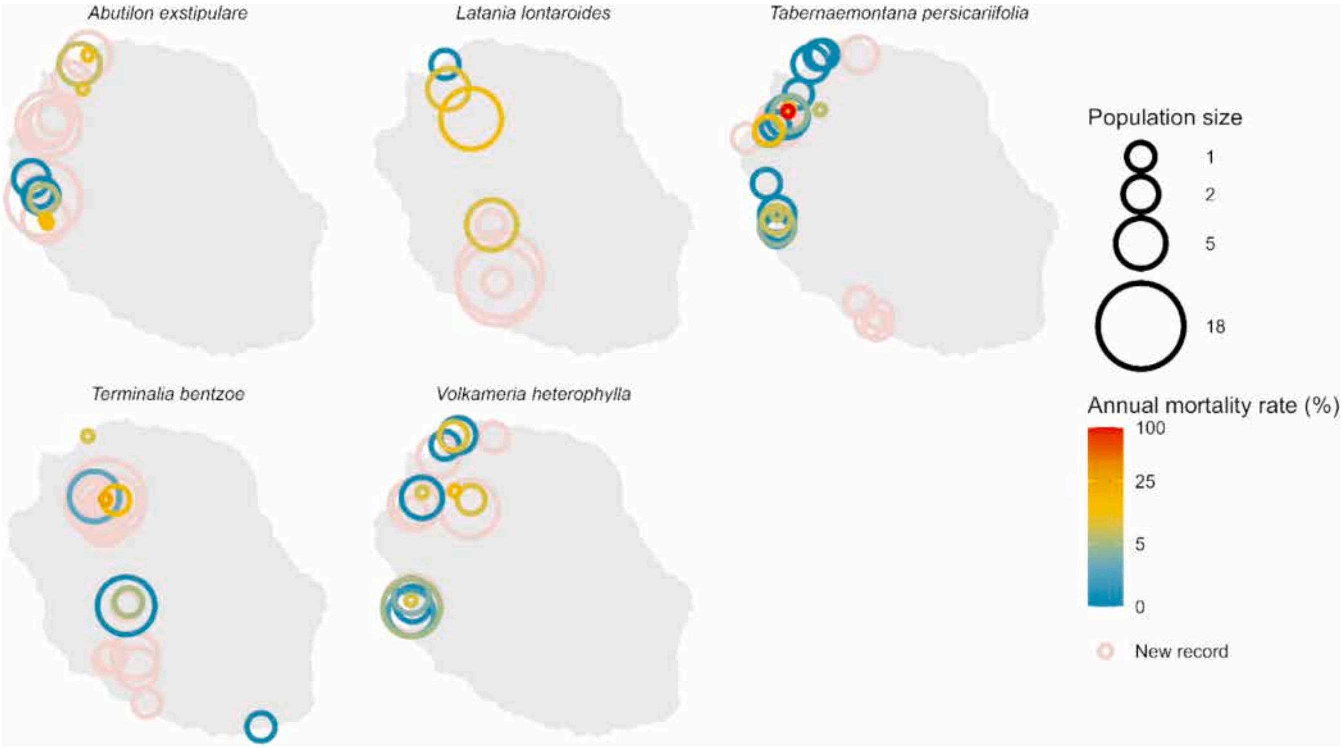

Fig. 3. Current distribution and size of the subpopulations of the five seasonally dry forest woody plant taxa endemic to the Mascarene archipelago resurveyed in this study.

Table 2
Current state of the population of the five seasonally dry forest woody plant taxa based on this resurvey.

Taxon	Historical # of individuals resurveyed	# of resurveyed individuals still alive	# of newly discovered individuals	Estimated total # of individuals	Mean recruitment per reproductive plant
Abutilon exstipulare	31	9	43	52	0.25
Latania lontaroides	25	17	35	52	0.43
Tabernaemontana persicariifolia	47	21	14	35	0.04
Terminalia bentzoe	22	15	47	62	0.06
Volkameria heterophylla	47	23	29	52	0.05

Interestingly, the five species are pollinated by insects or at least exhibit a typical insect-pollination syndrome (e.g. sweet-smelling odour, bilabiate flowers; Table 1). The possibility that a lack or low number of pollinators contributes to a lack of regeneration can therefore not be excluded in absence of specifically dedicated studies. Invasive alien plants that thrive in dry tropical forests could also interfere with native pollination networks (Traveset & Richardson, 2014). Moreover, considerable evidence has indicated that biological invasions could alter soil physicochemical properties and native microbial communities (Steinlein, 2013), which is likely to affect native plant regeneration in invaded forests (Mascaro et al., 2008). Thus, further research on mutualistic interactions should be urgently implemented in order to better understand what limits regeneration of threatened endemic trees in seasonally dry tropical forests of Reunion. A study on another CR tree species emblematic of the seasonally dry forests of Reunion, *Foetidia mauritiana* Lam. (Lecythidaceae), corroborates our data by revealing that, despite a relatively preserved genetic diversity, the disrupted gene flow between fragmented subpopulations leads to a high selfing rate associated with a very low rate of viable seed production (high proportion of empty seeds) and thus seedling recruitment (Cuénin et al., 2019). This likely reflects what is happening to at least some of our studied taxa. They also experience significant mortality rates in response to the steady deterioration of their habitat. This is evidenced by a study of floristic changes over a 16 year period (1995–2011) in six seasonally dry forest remnants that found a + 400 % increase in alien species abundance (Barbé et al., 2015). This most likely reflects a lack of protection: only 26 % of individuals and 45 % of populations are located in protected areas and this proportion reaches 0 % for *Abutilon*, and 4 and 3 %, respectively for *Tabernaemontana* (Table 3). This is also probably a consequence of a severe lack of active management of threatened endemic plant populations in the western lowlands, even within protected areas.

The approach used in this research, based on a resurvey of threatened populations of long-lived plants in conjunction with PVA, appears rather convincing, especially for under-studied taxonomic groups and regions. Revisitation studies using historical information can sometimes overestimate extinction probabilities due to the imperfect detectability of plants in resurveys (Martínez-Villegas et al., 2024) and because newly colonized sites are rarely considered (Holderegger & Spillmann, 2022). As we focused on large woody plants and given their almost arrested regeneration, our results might however be less significantly affected than other similar studies. The outcomes are of course perfectible (e.g. key parameters such as genetic erosion and environmental stochasticity have not been considered), but the approach has the advantage of generating consistent forecasts that can serve, for example, as a basis for a sensitivity analysis of persistence probability under different

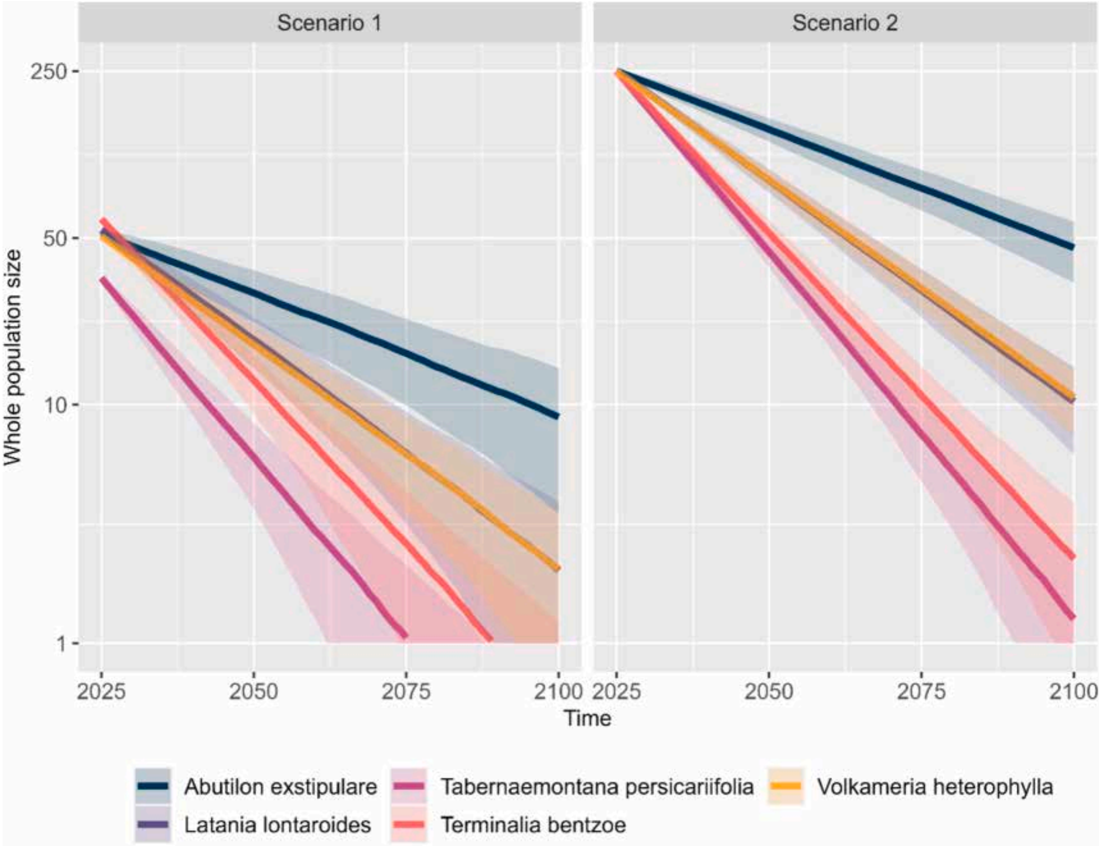

Fig. 4. Mean predicted population projection of five seasonally dry forest woody plant taxa endemic to the Mascarene archipelago over 75 years obtained from a population viability analysis. In scenario 1 (pessimistic), the current population size is the number of mature individuals observed during our resurvey while in scenario 2 (optimistic), the current population size is set to 250. The actual population size is probably in between. Solid lines are the mean of 1,000 simulations and shaded areas denote 95 % confidence intervals.

Table 3
Proportion of resurveyed and newly discovered individuals and subpopulations located in the core zone of the Reunion National Park and located in unprotected areas. No individuals occur in other types of protected area established outside the National Park including natural or biological reserves, prefectural biotope protection orders, and sensitive natural areas.

Taxon	Individuals within National Park (%)	Individuals without legal protection (%)	Populations within National Park (%)	Populations without legal protection (%)
Abutilon exstipulare	0	100	0	100
Latania lontaroides	38	63	33	67
Tabernaemontana persicariifolia	4	96	3	97
Terminalia bentzoe	67	33	81	19
Volkameria heterophylla	18	82	19	81
All	26	74	45	55

management scenarios. The approach is also a pragmatic solution if the species have a chance to disappear in the short term, i.e. possibly before we have all the data required to develop more advanced models. In our case, we suggest as a first step to resurvey more historical subpopulations in order to reduce the uncertainties about total population sizes, which highly influenced simulated extinction risk. The question then arises as to what can be done to minimize this extinction risk.

Based on our findings and consistency with other data from the NAP, we recommend a range of conservation measures for the last wild subpopulations of our five woody taxa including: i) prioritizing subpopulations according to land tenure security; ii) in accessible localities (e.g. on reasonable slope, near a trail) where tenure is secured, controlling invasive alien plants and restoring habitats so as to facilitate recovery of native species and prevent reinvasion; iii) reinforcing subpopulations (i.e. reintroducing juveniles produced ex situ) in priority localities to improve population viability; iv) installing exclosure fences or removing herds and developing an active fire suppression program; v) strengthening private landowners' efforts to preserve threatened species through increased awareness and possibly through the development of incentive programs; vi) reintroducing individuals in areas of high protection status where the taxa occurred historically but disappeared, so as to establish new subpopulations; vii) reconnecting fragments into an integrated network of seasonally dry forests on the west coast of Reunion. At the same time, ex situ conservation measures should be taken such as building collections of living plants (arboreta) and a bank of seeds (if orthodox, see Table 1) representative of the genetic diversity of the taxa over their remaining range, first on private lands.

Some of these actions have already been initiated or are beginning to be developed. For example, a massive tree plantation program (e.g. > 6000 individuals of *Terminalia*) has been implemented in massif La

Montagne, north-west of Reunion (LIFE + projects 'COREXERUN' in 2009–2014 and 'Forêt sèche' in 2014–2020). Nevertheless, our study demonstrates that additional measures to protect the last wild populations are required. Formal policy objectives should be accompanied by explicitly considering avenues for effective local engagement, governance and monitoring mechanisms and resources. Furthermore, closer partnerships between local conservation stakeholders including local authorities, funders, researchers, practitioners and landowners, can certainly contribute to prevent the collapse of this fascinating ecosystem and its unique flora. We hope that the data presented in this paper will convince them that seasonally dry tropical forests should be given higher conservation priority.

The seasonally dry tropical forests on Reunion Island also need to be placed in a more general context. Conservation actions to protect the Mascarene flora have so far been carried out in an unplanned and uncoordinated manner between Reunion and the Republic of Mauritius (e.g. both territories have their own Red List of threatened species for vascular plants). Although most conservation programs are currently implemented at national and subnational levels, regional and global coordination appears particularly important for solving complex environmental challenges, such as protecting and restoring the last seasonally dry tropical forests (Kark et al., 2009).

CRediT authorship contribution statement

Cassandra Hoarau: Writing – original draft, Methodology, Investigation, Formal analysis. **Arnaud Rhumeur:** Writing – review & editing, Supervision, Data curation. **Léa Marie:** Writing – review & editing, Data curation. **Bertrand Mallet:** Writing – review & editing, Data curation. **Julien Triolo:** Writing – review & editing, Data curation. **Olivier Flores:** Writing – review & editing. **Dominique Strasberg:** Writing – review & editing. **Robin Pouteau:** Writing – original draft, Supervision, Methodology, Investigation, Formal analysis, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendices. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jnc.2025.126899.

Data availability

All the data on which this article is based are contained in the manuscript and supplemental materials

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