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Extinction risk and invasion success are associated with different functional traits in a tropical island flora

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Islands host a disproportionately high richness of threatened native and invasive alien species. Despite intense research efforts, mechanisms underpinning extinction risk or invasion success are still not fully understood, which hinders the development of effective conservation strategies. The two-sides-of-the-same-coin (2sotsc) hypothesis, which states that traits involved in extinction risk and invasion success are identical, but with opposite values, remains largely untested at local scales where management occurs. Using five functional traits (specific leaf area, leaf dry matter content, maximum height, seed mass and dispersal syndrome) for 187 plant species from Reunion Island (Indian Ocean), we compared (i) threatened and non-threatened native woody species and (ii) invasive and non-invasive alien species. Seed mass was greater in threatened than in non-threatened woody natives. We found no trait difference among woody aliens, while specific leaf area was lower in invasive than in non-invasive aliens (woody and non-woody). Since different traits capture species differences in terms of extinction risk and invasion success, the underlying mechanisms are likely to differ. The species-centred perspective of the 2sotsc hypothesis appears too simplistic, which calls for better integrating community- and ecosystem-level impacts to resolve the complexity of extinction and invasion dynamics on islands and support informed conservation decision-making.

1. Introduction

The current global extinction rate is 10 to 100 times higher than the average rate observed over the past million years and shows no signs of slowing down [1]. Among the major factors leading to biodiversity loss and increased extinction risks, biological invasions are considered a significant threat contributing to animal and plant extinctions worldwide [2,3]. Importantly, 90% of extinctions attributed to biological invasions occurred on islands, which are home to a large share of threatened species, many of which are endemic [2]. The specificities of islands, including their geographical and historical isolation [4,5], depauperate and taxonomically disharmonic biota compared with continents [4,6], could explain this high vulnerability to invasive alien species [7]. However, while the mechanisms leading a species to become threatened or invasive are fairly well understood for some animal

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organisms (e.g. prey–predator relationships), they remain rather unclear for plant species [8]. In the light of the growing threat posed by plant invasions to island native plants, it is essential to foster our understanding of these mechanisms to inform effective conservation efforts of the unique island floras.

As measurable characteristics related to individual performance and its response to biotic and abiotic environmental conditions [9], functional traits represent a promising route to unravel the mechanisms leading a plant species to be threatened or invasive [10]. Invasive species generally exhibit acquisitive strategies such as short-lived leaves with high specific leaf area (SLA), high relative growth rate and small seeds [11–17]. However, results diverge within the literature regarding the significance of these traits as predictors of invasion success. This lack of consensus can in part be explained by the use of different control groups (e.g. non-invasive alien species or native species), definitions of invasion success itself, environments, growth forms or spatial scales [10].

In contrast, few studies have compared the functional characteristics of threatened and non-threatened native species, with inconsistent results. Traits associated with reproduction (e.g. short flowering time, selfing, biotic pollination), dispersal (e.g. low seed number, low dispersal distance, zoochory) and competitive capacity (e.g. small size in low-productivity environments, large size in productive environments) have been reported to partly explain extinction risk [18–20]. However, extrinsic factors appear to play a greater role in determining threat status than intrinsic factors [19]. According to Fréville *et al.* [18], vulnerability to extinction becomes apparent only when the population or species is exposed to a risk, and traits alone would only weakly explain the vulnerability of a species. As a result, addressing the impact of invasion on threatened species requires consideration of the characteristics of the invasive species by which threatened species are affected [10,14].

The two-sides-of-the-same-coin (2sotsc) hypothesis offers a conceptual framework to jointly consider the traits conferring extinction risk and invasion success, associated with threatened and invasive species, respectively. This hypothesis predicts that functional traits that characterize threatened species would be the same as those that characterize invasive species, but with opposite trends, while non-threatened native species and non-invasive alien species would display intermediate values of these traits [21,22]. Currently, only two studies have addressed this hypothesis for plants, which they tested at continental and global scales [23,24]. Bradshaw *et al.* [23] compared invasive Fabaceae species to all other Fabaceae species on the one hand, and threatened Fabaceae species to all other Fabaceae species on the other hand, without differentiating alien and native species. Schmidt *et al.* [24] focused on angiosperm species native to North America to test first whether the best trait predictors of extinction risk and invasion success were identical, and then whether the effects of the potential common predictors were opposite. Overall, both studies found support for the 2sotsc hypothesis at large scales.

Competition between plant species, however, happens at local scales, so for the 2sotsc hypothesis to be valid and useful to inform mechanisms leading to the exclusion of threatened species by invasive ones, tests on threatened and invasive species that coexist locally in the same habitats are needed. If validated, the hypothesis could help local biodiversity managers prioritize native species that are the most likely to become threatened and alien species that are the most likely to threaten native species on the basis of their traits, and conceive appropriate conservation actions. In this study, we tested this hypothesis for the first time in a highly invaded and endemic-rich tropical island system (Reunion Island, southwest Indian Ocean).

2. Material and methods

(a) Study site

Reunion Island belongs to the Mascarene Islands, along with Mauritius and Rodrigues (figure 1). It is the youngest (2–3 million years old) and largest island (approx. 2500 km^2) of the archipelago. Due to their high richness in endemic vascular plant species and the high level of degradation of their primary vegetation, the islands are included in the biodiversity hotspot 'Madagascar and the Indian Ocean Islands' [25]. Reunion Island is characterized by a wide elevational gradient (culminating at 3070 m.a.s.l.), complex topography and precipitation asymmetry (ranging from 500 mm yr^{-1} on the leeward side to up to 8000 mm yr^{-1} on the windward side), which creates a remarkable diversity of habitats. However, although human colonization of the island is relatively recent (seventeenth century), the vegetation has been strongly shaped by anthropogenic activities, notably through the introduction of alien species [26,27]. Today, no less than 41% of native vascular plant taxa are considered threatened (395 threatened taxa out of 962 assessed; [28]), while a total of 2170 alien plant taxa were recorded on the island, i.e. more than twice the number of native taxa. Among these alien taxa, 472 are considered invasive [29].

(b) Species sampling

We focused our sampling on threatened species due to their narrow distributional range, and inventoried co-occurring non-threatened native, non-invasive alien and invasive alien species. A total of 36 threatened species were selected based on their archipelago endemism, the number of known subpopulations and their clear taxonomic delineation. The Mascarine database (https://mascarine.cbnm.org/) was used to prioritize the subpopulations to be sampled on the basis of the reliability of species occurrences (e.g. collected by a recognized organism or amateur botanist, consistent with the known ecology of the species) and their accessibility. Five subpopulations per threatened species were selected, favouring sites where several threatened species co-occurred. A total of 132 sites were inventoried between February 2023 and July 2024 (figure 1).

In each site, all individual woody plants with a diameter at breast height (DBH) ≥ 1 cm were inventoried in a 10 × 10 m plot. Non-woody alien species with DBH < 1 cm were identified in five 1 × 1 m quadrats located at each corner of the plot and at its centre. Non-woody native species were not considered, as terrestrial herbaceous species are largely underrepresented

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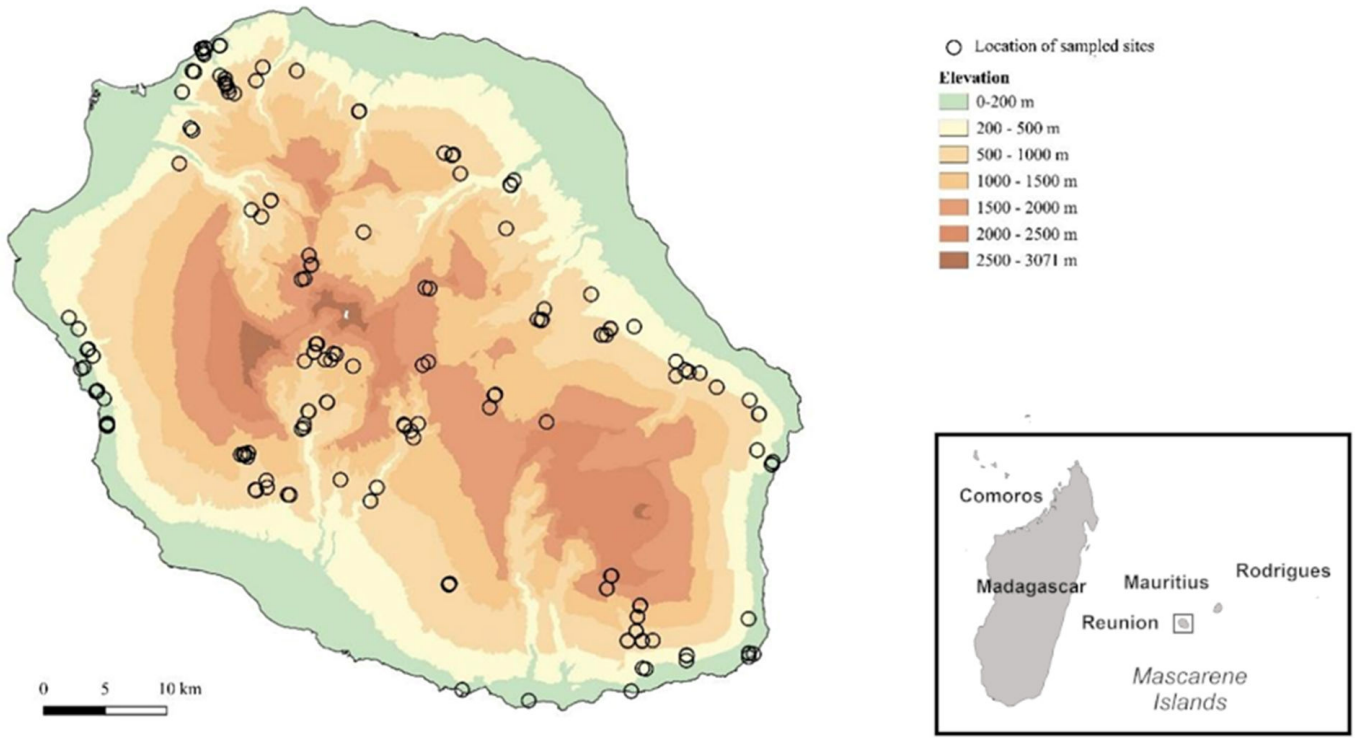


Figure 1. Location of Reunion Island in the southwest Indian Ocean (inset) and of sampled sites on a digital elevation model.

in the native flora of Réunion Island, which was completely forested before the arrival of humans [27]. This protocol allowed the identification of 124 woody native species and 63 alien species, including 39 woody and 24 non-woody. Native species were separated into two categories: threatened species on the one hand, with an IUCN Red List category 'near threatened' (NT), 'vulnerable' (VU), 'endangered' (EN) or 'critically endangered' (CR) and non-threatened species on the other hand, with a category 'least concern' (LC) [28]. Alien species were also divided into two categories: invasive alien species with a maximum invasiveness score (5) in the Index of the Vascular Flora of Réunion Island [30], and non-invasive alien species with lower invasiveness scores (1–4). The invasive status thus corresponds to highly invasive taxa in the natural environment, with proven or suspected impact.

To examine the 2sotsc hypothesis among species that co-occur within the same habitats, each species was assigned to two habitat preference categories. Regarding temperature, species were classified as eurythermal (tolerating a wide range of temperatures), megathermal (requiring warm temperatures) or mesothermal (requiring intermediate temperatures). Our sampling did not cover the oligothermal vegetation (characterized by low temperatures), such as summit shrublands, which are much less invaded. Regarding humidity, species were identified as indifferent, hygrophilous (associated with moist to wet conditions) or semi-xerophilous (associated with dry to moist conditions). These habitat typologies were taken from [31].

(c) Functional traits

Five functional traits were selected based on their relevance to plant ecological strategies, link to extinction risk or invasion success, ease of measurement, non-destructive nature and availability in floras or databases (table 1). SLA, the ratio of leaf area to leaf dry mass (in $cm^2\,g^{-1}$) and leaf dry matter content (LDMC), the ratio of leaf dry mass to fresh mass (in $g\,g^{-1}$), were measured from leaves collected in the field (see electronic supplementary material, Methods for details). SLA and LDMC were first averaged per individual and then per species. We included in our analyses all species for which at least one individual was collected as, according to Baraloto *et al.* [32], sampling at least one individual per species is a reasonable trade-off in tropical forests between a robust assessment of interspecific trait variation and mobilization of financial and human resources for sampling.

Seed mass, maximum height and dispersal syndrome were preferentially taken from local bibliographic sources and datasets [33–37]. However, when no local data were available, which was frequent for alien species, global databases were also used [38,39], despite potential limitations [40]. When values were available as intervals, the average value was retained. Some missing data were completed from the scientific literature. For these three traits, the final database included 93 and 15% of local data for native and alien species, respectively. Because not all traits were available for all species, the number of species varied between analyses (electronic supplementary material, table S1).

(d) Statistical analyses

In a first analysis, we only retained dicotyledon woody species (i.e. excluding palms, *Cordyline*, *Dracaena* and *Pandanus* spp., and tree ferns) as no monocotyledon tree-like plants, which develop different ecological strategies [41], were sampled among

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Table 1. Summary of the functional traits used in this study. SLA = specific leaf area, LDMC = leaf dry matter content.

trait	unit	transformation	definition
SLA	$cm^2\ g^{-1}$	none	ratio between leaf area and dry leaf mass
LDMC	$g\ g^{-1}$	none	ratio between dry and fresh leaf masses
maximum height	m	none or log (with non-woody aliens)	maximum canopy height at maturity
seed mass	g	log	mean seed mass
dispersal syndrome	—	binary encoding	biotic (animal-mediated): yes = 1, no = 0
			abiotic (wind-, water- or gravity-mediated, or explosive): yes = 1, no = 0

aliens. Woody plants with a maximum height below 1.30 m (which corresponds to the DBH measurement height) were not considered. Selected woody species represented 163 species, including 124 native (46 threatened and 78 non-threatened) and 39 alien species (15 invasive and 24 non-invasive). In a second analysis, the dataset was extended to also include non-woody alien species, giving a total of 63 alien species (19 invasive and 44 non-invasive), so as to highlight possible traits specific to invasive alien plants regardless of their habit.

To identify trait differences between (i) threatened and non-threatened native species and (ii) invasive and non-invasive alien species, generalized linear mixed models (GLMM) were built for each paired combination of the four quantitative traits (SLA, LDMC, maximum height, seed mass) as predictors and the two statuses as dependent variables (n = 8 models). When necessary, trait values were transformed to approach a normal distribution (table 1). The threat and invasion statuses were encoded as a binary variable. To account for the likely differences in mean trait value between the different habitats, species habitat preference was set as a random effect, which allowed for a different intercept in the trait–status relationship for each habitat. To determine whether phylogeny should also be included as a random effect in the GLMM to account for the potential non-independence in trait values due to phylogenetic relatedness between species [15], we performed a phylogenetic signal analysis (Blomberg's K and Pagel's λ). A non-zero signal was detected for some traits (electronic supplementary material, table S2), but the GLMM accounting and not accounting for phylogeny resulted in the same significance levels (data not shown). Type II analyses of variance (ANOVA) were performed on each model to examine whether the trait had a significant influence on the status. Following the same method, we compared in a second step the trait values of threatened woody native species with those of invasive woody alien species, and the trait values of threatened woody native species with those of all invasive alien species (woody and non-woody).

Dispersal syndromes were encoded as a binary variable (biotic or abiotic). To determine whether the dispersal syndrome was associated with the threat or invasion status, we tested for each status whether the proportion of dispersal syndrome was significantly different from that expected by chance. To do so, for each status (e.g. invasive alien species) represented by n species in our sampling, we performed 9999 random draws of n species within the total pool of species (e.g. alien species), and calculated a p-value to examine whether the observed proportion significantly differs from the distribution of proportions obtained randomly. All statistical analyses were conducted using R software [42].

3. Results

As temperature preference has an insignificant or only small influence on traits, we only include humidity preference as a random effect in the GLMM, so as to keep the number of predictors low in regard to the size of our dataset (electronic supplementary material, figures S1,S2). Seed mass was the only trait that differentiated threatened native species from non-threatened ones (figure 2A). The four other tested traits (SLA, LDMC, maximum height and dispersal syndromes) showed no influence on the threat status of native species. In woody alien species, no traits differentiated invasive alien species from non-invasive ones (figure 2B), but when incorporating non-woody alien plants, we found that invasive species had lower SLA values than non-invasive ones (figure 2C). Furthermore, our analyses revealed no significant effect of trait values on species status, neither when threatened woody natives were compared with invasive woody aliens (figure 2D) nor when threatened woody natives were compared with all invasive aliens (figure 2E).

4. Discussion

We compared key functional traits among threatened native and invasive alien plant species within a highly invaded and endemic-rich tropical island system to test the 2sotsc hypothesis at the local scale for the first time. Overall, our results did not support this hypothesis. This contrasts with the two previous studies that tested it at larger scales and found that threatened and invasive species showed specific and distinct growth forms and habitat preferences on the one hand [23], and chromosome number, ploidy and seed mass on the other hand [24]. While factors related to climate and introduction history could be stronger drivers at a global scale, species interactions might play a more prominent role in structuring plant assemblages at a local scale [43–45].

We showed that seed mass was the only trait differentiating between threatened and non-threatened species. In island environments, such as on Reunion Island, this could result from the loss of dispersers of large-seeded woody species due to the

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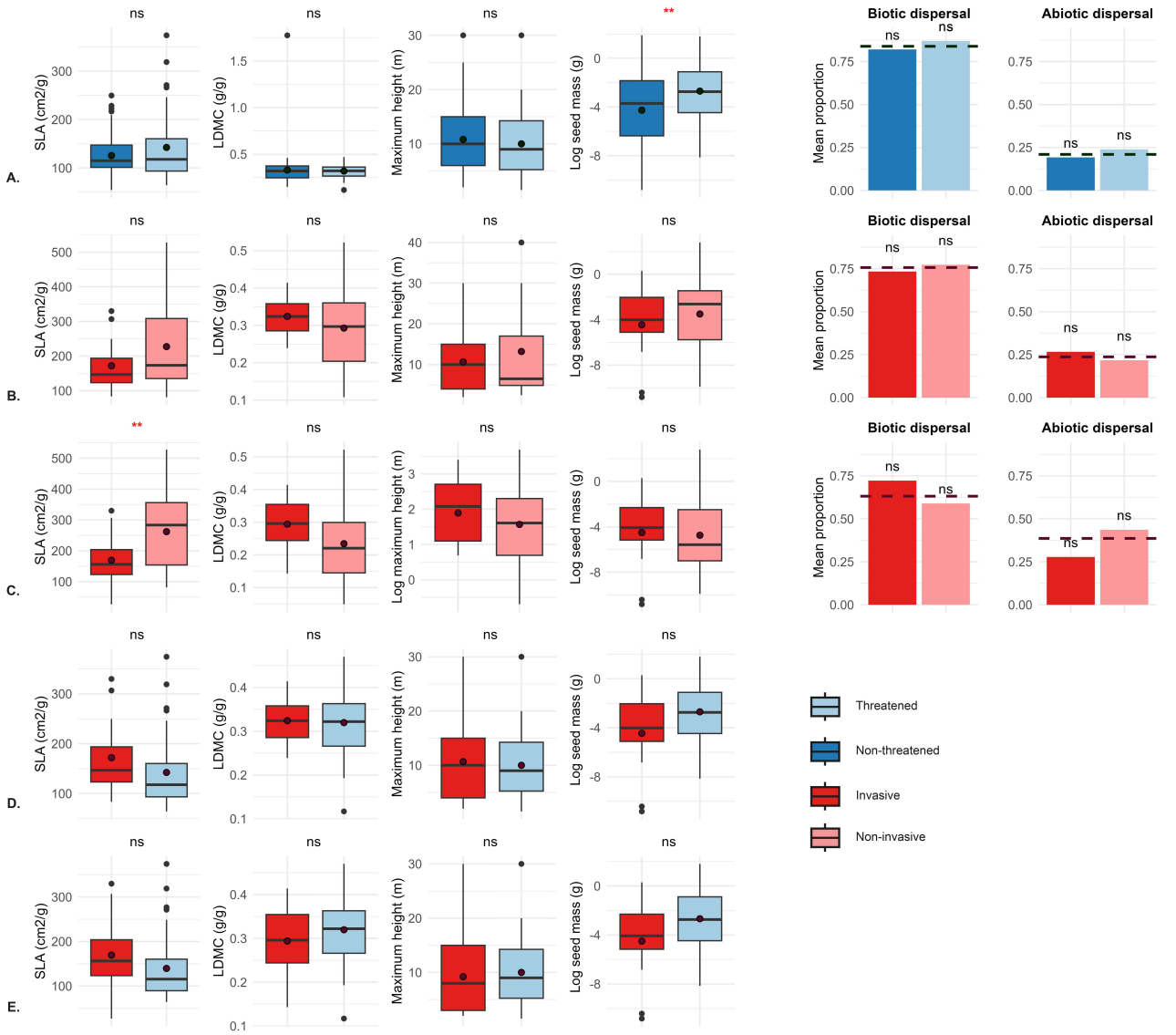


Figure 2. (A) Comparison of woody natives according to their threat status, (B) woody aliens according to their invasion status, (C) all aliens according to their invasion status, (D) woody threatened natives and woody invasive aliens, (E) woody threatened natives and all invasive aliens. Numerical traits: mean values are indicated by a large black dot and outliers by small black dots outside the boxplots. *p*-Values were derived from an analysis of variance of species status in generalized linear mixed models with habitat humidity as a random effect. Significant values are represented in red. The significance level is represented by asterisks: ** For 0.01 > *p*-value > 0.001 and ns denotes *p*-values > 0.05. SLA = specific leaf area, LDMC = leaf dry matter content. Dispersal syndromes: *p*-values were derived from randomization tests comparing the observed mean proportion by status to random mean expectations (dotted black line).

extinction of vertebrate frugivores (giant tortoises, fruit bats, pigeons, parrots) following human settlement [36,46,47]. Without dispersers, seeds accumulate under the canopy of the parent plants, which tend to attract predators, pathogens and increase intraspecific competition with adults [48–50]. Moreover, large-seeded fleshy-fruited trees are particularly impacted by the loss of large-bodied animals, as seed ingestion can influence, or even be necessary for, germination success, particularly through the degradation of the seed coat or the removal of the pulp [51–54]. Thus, defaunation often impairs the recruitment of new individuals, contributing to population decline. Furthermore, approximately two-thirds of the most invasive woody species have fleshy fruits or other dispersal structures that are attractive to dispersers [45]. If the fruits of invasive alien species are more attractive or more conspicuous than the fruits of native species, this may result in direct competition for limited dispersal services [55].

We found no differences between threatened and non-threatened native species for the other four traits. SLA, LDMC and dispersal syndrome were not tested by Bradshaw *et al.* and Schmidt *et al.* [23,24]. However, Bradshaw *et al.* [23] identified maximum height as positively associated with the probability of being threatened with extinction and as an explanatory factor for invasion success. However, for invasive species, trends were complex and varied across growth forms and botanical families. Schmidt *et al.* [24] concluded, as we did, that height is not a significant predictor of extinction risk or invasion success.

Few studies compared invasive alien species with non-invasive alien species, but among those that did, no clear difference was identified [56,57]. In contrast, we found that invasive alien species had a significantly lower SLA than non-invasive alien species when non-woody plants were included in the analysis. This finding is corroborated by studies reporting that so-called acquisitive traits are not necessarily associated with higher growth and competitively superior species, depending on other

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trait variation (e.g. leaf tissue density can influence carbon dioxide diffusion and light penetration, and thus photosynthetic capacity, independently of SLA [58]) or local resource availability [59]. The different results that we obtained without including non-woody alien plants suggest that leaf traits involved in invasion success vary across growth forms, possibly because they influence resource use efficiency in coordination with plant height and woody traits [59,60].

Providing robust tests of the 2sotsc hypothesis may actually be difficult for several reasons. First, the definition of an invasive species has long remained variable among studies. The IUCN's EICAT (Environmental Impact Classification of Alien Taxa) methodology is currently being developed to harmonize such definitions but its use has so far remained limited. Second, some critically endangered species only have a few, potentially non-representative, individuals available for sampling and this could bias estimated species trait values. In our case, this is particularly likely for SLA, whose value is strongly influenced by the amount of light received [15]. More generally, intraspecific trait variability may blur interspecific comparisons when the sampling or data source differs across species. In our study, while the data for native species came from measurements carried out within the Mascarenes, those for seed mass and maximum height of alien species were, for the most part, from other regions. This could lead to misestimations of the values actually observed on Reunion Island, as in an island environment, alien species are likely to have different attributes from their continental counterparts because of the founder effect, i.e. a loss of genetic variation that occurs when a small number of individuals establish from a larger population [12]. As a result, we cannot exclude that the different data origins might mask a difference in seed mass or plant height between threatened native and invasive alien species and lead to a false negative.

As key dimensions of plant ecological strategies, the traits that we selected are theoretically well-suited to express species sensitivity to disturbance [11]. Because co-occurring threatened native and invasive alien species were found to exhibit similar values of these traits, our study might suggest that both groups do not differ in their response to disturbance. A possible explanation could be that our sampling design, based on forest plots, filtered invasive alien species with the ability to establish in areas with no or limited disturbance, which is relatively common on islands [61]. This tendency may, however, differ in more disturbed insular habitats or in continental regions where invasive plants more often appear to benefit from human transformation of the environment [62]. There, extinction risk and invasion success may represent two sides of the same coin.

The fact that extinction risk and invasion success are linked to different traits on Reunion Island could be explained by the stronger role of interactions in shaping plant communities, and thus potentially invasion success, in tropical environments in comparison with temperate environments [45]. In particular, threatened native species might be those most affected by changes in interaction networks when invasive species arrive [63], e.g. those most specialized in their interactions, or those whose survival, growth or reproduction depend most on them [64]. Moreover, on islands, the small population size, the asymmetry of interactions with 'super-generalist' species and the unpredictable nature of resource production are likely to amplify the negative effects that invasive alien species can cause by altering the structure of interaction networks [45]. To better understand the threat posed by invasive alien species, it appears essential to study the role of dispersal as well as pollination, allelopathy and mycorrhizal and soil microorganism interactions, which are particularly underexplored despite their high potential in explaining extinction and invasion processes. Overall, both extinction and invasion processes cannot be reduced to differences in functional traits and comparisons of species taken in isolation from their local biotic and abiotic environments. A practical implication of our results not supporting the 2sotsc hypothesis at the local scale might therefore be that species-level conservation should be supplemented by preserving or restoring interaction networks.

Additionally, while native island floras are threatened by invasive alien species [65], they are also subject to other pressures that can interact synergistically. On Reunion Island, *Sideroxylon majus* has, for instance, suffered from overexploitation for its hardwood for construction [66]. *Ochrosia borbonica* is also used in pharmacopoeia for its anti-pyretic properties, and *Terminalia bentzoe* for its anti-microbial and anti-inflammatory properties [67,68]. For species associated with traditional medicine practices, harvesting and bark stripping constitute a significant pressure that can hardly be detected based on functional traits. Functional ecology, therefore, makes it difficult to account for the 'socio-economic' characteristics of species, which can lead to their overexploitation [69].

Overall, further work is needed to expand trait measurements across species range, while considering harvesting practices and traits that capture functions more closely associated with plant performance and biotic interactions to fully resolve the complex and multidimensional nature of extinctions and invasions on islands, and support informed conservation planning.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. The data supporting the findings of this study are available at [70].

Supplementary material is available online [71].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. E.A.: conceptualization, data curation, formal analysis, investigation, methodology, writing—original draft; C.A.-P.: data curation, writing—review and editing; O.G.F.: data curation, writing—review and editing; R.-P.G.: data curation, writing—review and editing; C.F.: conceptualization, methodology, writing—review and editing; I.M.: conceptualization, methodology, writing—review and editing; D.S.: data curation, writing—review and editing; R.P.: conceptualization, data curation, funding acquisition, investigation, methodology, project administration, supervision, writing—original draft.

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

Conflict of interest declaration. We declare we have no competing interests.

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facilities at the Mare Longue Research Field Station during the field campaign. Plant functional traits were measured in the Plant Protection Platform (3P, IBiSA). We appreciate the insightful comments from the Handling Editor and two anonymous referees.

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