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High evolutionary and functional distinctiveness of endemic monocots in world islands

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Abstract

Functionally and evolutionarily distinct species have traits or an evolutionary history that are shared by few others in a given set, which make them priority species for biodiversity conservation. On islands, life in isolation has led to the evolution of many distinct forms and functions as well as to a high level of endemism. The aim of this study is to assess the evolutionary and functional distinctiveness of insular monocotyledons and their distribution across 126 islands worldwide. We show that evolutionary and functional distinctiveness are decoupled but that both are higher on islands than on continental areas. Anagenesis on islands followed by extinctions and/or diversification on the mainland may have led to highly evolutionarily distinct species while functionally distinct species may have arisen from ecological niche shift or niche expansion. Insular endemic species with high evolutionary distinctiveness but not with high functional distinctiveness are significantly range-restricted compared to less distinct species, possibly indicating differences in dispersal potential. By showing that distinctiveness is high on islands and that the most distinct species are range-restricted, our study has important conservation implications. Indeed, islands are among the most threatened systems of the world, and extinctions of the most distinct species could lead to significant loss of phylogenetic and functional diversity.

Keywords: functional distinctiveness, island biogeography, monocotyledons, evolutionary distinctiveness, range restriction.

65

66 **Introduction**

67 The distinctiveness of a species is defined as the rarity of some of its characteristics compared to
68 all other species in a given set (Pavoine et al. 2005). When those characteristics are related to
69 ecological functions, distinctiveness is referred to as functional distinctiveness. Distinctiveness
70 can also be related to species' evolutionary history, i.e. its isolated position on the tree of life.
71 This is referred to as evolutionary distinctiveness (e.g; Pavoine et al. 2005; Redding et al. 2014 ;
72 Kondratyeva et al. 2019). Distinctiveness has been poorly studied in community ecology or
73 biogeography (see Grenié et al. 2018) even though it is used in conservation biology (Isaac et al.
74 2007; Gumbs et al. 2020; Robuchon et al. 2021). By harbouring significant amounts of
75 functional diversity, functionally distinct species may ensure key ecosystem processes and
76 services to humanity (Mouillot et al. 2008; Kondratyeva et al. 2019). For example, Petchey,
77 Hector, & Gaston (2004) studied 12 plant traits and showed that functionally distinct species
78 may contribute to ecosystem functions by increasing plant biomass production. Loss of
79 functionally distinct species may therefore directly impact ecosystem stability, resilience and
80 multi-functionality (Fonseca and Ganade 2001; Oliver et al. 2015). On the other hand,
81 phylogenetic isolation may lead to distinct ecological functions so that species with high
82 evolutionary distinctiveness could contribute significantly to ecosystem functioning (Cadotte et
83 al. 2008; Redding et al. 2008; Cadotte and Davies 2010). Most importantly, evolutionarily
84 distinct species contribute greatly to the phylogenetic diversity of a set of species (Cadotte et al.
85 2008; Redding et al. 2008). Phylogenetic diversity represents a reservoir of yet-to-be-discovered
86 resources for humanity, also called option-values, and the most evolutionarily distinct species
87 may capture a large proportion of these resources (Faith 1992; Faith 2018). Although debated,

evolutionarily distinct species may also contribute greatly to the evolutionary potential of a set of species (Faith 1992) and, beyond utilitarian values of biodiversity, preserving evolutionarily distinct species should preserve the evolutionary heritage of our planet (Faith 2016; Gumbs et al. 2021). Based on this rationale, evolutionary distinctiveness is a well-recognised measure for biodiversity conservation (Redding and Mooers 2006; Isaac et al. 2007; Stein et al. 2018).

Insular systems are important biodiversity hotspots, as they harbour a very high proportion of species that are found nowhere else on Earth and that represent a unique evolutionary history as well as a multitude of forms and functions (Warren et al. 2015; Ottaviani et al. 2020). The island biota could thus be composed of many evolutionarily and functionally distinct species, but their role in shaping insular diversity has been only recently investigated (Veron et al. 2019a). In addition, very little is known about the rise and distribution of species distinctiveness. Examining patterns of species distinctiveness on islands may provide new insights of processes underlying species evolution and strengthen conservation strategies. Here, we focused on monocotyledon plant species (monocots), a morphologically and functionally diverse clade comprising a quarter of all flowering plants including orchids, palms and cereals.

In order to study both functional and evolutionary distinctiveness, it is necessary to assess how these aspects of biodiversity are related. However, functional and evolutionary distinctiveness have rarely been studied in conjunction (but see Cooke et al. 2020), particularly in insular communities. On islands, the relationship between evolutionary and functional distinctiveness may be weak, as early diversification and simultaneous cladogenesis may result in a lack of phylogenetic signals for some traits of insular species (Losos 2008). The radiation of *Bidens* (Asteraceae) on Hawaii is a classic example, where closely-related species display a greater diversity of traits (e.g. growth form, floral morphology) than all other representatives of this

genus worldwide (Knope et al. 2012). This is probably due to the diversity of habitat types found on the archipelago and to the loss of these species' dispersal potential (Knope et al. 2012). In addition, phenotypic changes in insular species do not necessarily involve speciation or a cladogenetic pattern, thus variation in evolutionary history does not necessarily reflect trait variation (Whittaker and Fernández-Palacios 2007). Moreover, the number of traits considered, convergences and/or models of trait evolution among other reasons can lead to the decoupling of functional and evolutionary distinctiveness (Veron et al. 2019b). Therefore, we first investigated to what extent functional and evolutionary distinctiveness of monocots are related.

Another unresolved question is whether species distinctiveness differs between insular and continental communities. On islands with long history in isolation, the availability of unfilled niches and the oceanic climate, along with extinctions that would have isolated species in both the Tree of Life and the functional trait space, may have given rise to many evolutionarily and functionally distinct species (Gillespie and Roderick 2002; Grandcolas et al. 2014). However, there have been few studies assessing whether insular species are more distinct than continental ones, and results may be taxon-specific (Jetz et al. 2014). We investigated this question in a large and important plant group and provided an additional line of evidence for preserving insular biodiversity.

Some distinct species are at high risk of extinction because they are range-restricted (Cadotte and Davies 2010; Harnik 2011). Range-restriction is a key factor associated with extinction risk, and is one of the main criteria used to assess the threat status of species by the International Union for Conservation of Nature (IUCN) (Rodrigues et al. 2006). As with distinct species, range-restricted species have been reported to provide unique functions within ecosystems as well as unique services to humanity (Mouillot et al. 2013; Leitão et al. 2016). Species that are both

range-restricted and distinct may therefore support highly vulnerable and unique functions and option-values (Rosauer et al. 2009; Violle et al. 2017). We expect that many of such species may be found on islands. Indeed, islands have a remarkably high level of endemism, which is around 9 times higher than on continents (Kier et al. 2009). More specifically, many insular species are spatially range-restricted, occurring only on a few islands, and/or in very restricted areas (e.g., Caesar et al. 2017). Beyond the practical implications for conservation, assessing the correlation between distinctiveness and range restriction may shed light on the mechanisms shaping both species distinctiveness and distribution in islands. For example, factors that have led to past extinctions may have led to the isolation of species on the phylogenetic tree and/or in functional space and shrunk their distribution range. However, the association between range-restriction and distinctiveness in insular species is unclear. Specifically, to the best of our knowledge, the relationship between range-size and functional distinctiveness has never been tested in plants (see Cooke et al. 2020 for birds and mammals). In an attempt to fill this gap, we explored the relationship between species distinctiveness and range restriction of monocots in world islands. As plant distribution patterns are driven by factors influencing colonization (e.g. Negoita et al. 2016), such as the proximity of the island to a pool source during its geological history, we also studied how the characteristics of the islands where highly distinct monocots occur can account for their range restriction.

Overall, there is a growing consensus for a better representation of multiple dimensions of biodiversity in biogeography (Davies and Buckley 2011; Violle et al. 2014) especially on islands (Patiño et al. 2017). As far as we know, functional and evolutionary species distinctiveness on islands had never been studied before and our study brings a fresh contribution to this need. Through our analyses, we addressed four main questions that may lay the foundations for future

research on this topic and highlight the importance of islands to preserve evolutionary and functional distinctiveness: 1) To what extent are evolutionary and functional distinctiveness related?; 2) Are insular species more evolutionarily and functionally distinct than mainland endemics?; 3) Are evolutionarily and functionally distinct insular species range-restricted?; 4) Is the range restriction of distinct species associated with the geographical characteristics of the islands they occur on?

Materials and methods

Geographical and occurrence data

Occurrence data was obtained from the e-monocot database that is now part of the World Checklist of Selected Plant Families (WCSPF; wcsp.science.kew.org), and is regularly updated. It records presences and absences of monocot species across the world within geographic units as defined by the Biodiversity Information Standards (BIS; Vocabulary Maintenance Specification Task Group 2017). BIS help to “establish international collaboration among the creators, managers and users of biodiversity information and to promote the wider and more effective dissemination and sharing of knowledge about the world's heritage of biological organisms” (<https://www.tdwg.org/>). We extracted spatial distribution data for all native terrestrial monocot species in 126 island regions as delimited by the level 3 of the BIS. The number of species we used vary between 6,682 and 2,581 depending on the analysis performed and data availability (see ” see section Relationship between evolutionary and functional distinctiveness”). We used level 3 of BIS as it was the most appropriate to study islands at a global scale. This level of spatial resolution considers factors such as the distance of the disjunction of an island or group of islands with the mainland, its size, and its phytogeographical significance. Therefore, one main advantage of the spatial scale we used is to define regions based on their ecological boundaries

and associated communities, which can comprise a single island or a group of islands. In addition, analyses undertaken at broader scale, representing natural boundaries are key to advance our understanding of ecological and evolutionary processes in island biogeography (Triantis et al. 2015).

Species characteristics

To estimate evolutionary distinctiveness (ED), a monocot phylogeny was extracted and pruned from an updated version of the megaphylogeny of land plants (Qian and Jin 2016). In total, 6,682 species with occurrence data were also present in the phylogeny and were attributed an ED score. Regarding functional distinctiveness (FD), we used six quantitative traits: adult plant height, stem specific density, leaf size expressed as leaf area, leaf mass per area, leaf nitrogen content per unit mass, and diaspore mass (see Díaz et al. 2015 for details). These traits have been widely used and recognized as fundamental representatives of the ecological strategies of plants (Díaz et al. 2015). Our dataset comprised 2,581 species with at least one trait value and present in our phylogeny. Yet, not all these species had values for the 6 traits. Missing trait values were therefore imputed by running a Random Forest algorithm 1,000 times and then estimating the mean value of the 1,000 imputations. The Random Forest method imputes missing values for a species according to the non-missing values of other traits and of other species having similar functional features, therefore species without any trait values could not be considered. Although priority should be given to trait data collection, the random forest algorithm was shown to perform well to impute missing trait data (Penone et al. 2014). We performed a sensitivity analysis to 1) assess to what extent missing values may have influenced our results; 2) estimate the correlation between traits; 3) assess the contribution of each trait to FD scores 4) compare the obtained distinctiveness scores with other indices (Appendix 1). This sensitivity analysis showed

that trait imputation performs well to estimate functional distinctiveness values (e.g. high correlations between functional distinctiveness scores computed on a complete dataset and those obtained after artificial deletion and imputation of trait values; little influence of the number of missing data per species on scores of functional distinctiveness [see Appendix 1]). Furthermore, Díaz et al. (2015) already performed several tests and treatments on this dataset, e.g. “detecting erroneous entries (due to errors in sampling, measurement, unit conversion, etc.)”; “ensuring that extreme values that correspond to truly extreme values of traits in nature are not mistakenly identified as outliers”; test for robustness when missing values occur.

Estimating evolutionary and functional distinctiveness

As recommended by Pavoine et al. (2017), the distinctiveness of each monocot species was calculated with the distance-based metric *AV* (“average”) representing the average dissimilarity between a focal species and all others. It is thus sensitive to deep divergences but there is also a contribution of recent divergences (Pavoine et al. 2017). The *AV* metric works with a matrix of dissimilarity between species. Regarding ED, we computed phylogenetic pairwise distances (Paradis and Schliep 2019). Regarding FD, we computed pairwise functional distances with Gower’s metric (Gower 1971). Using phylogenetic and functional distances between species, we calculated species distinctiveness scores with the *distinctDis* function from the *adiv* package (Pavoine 2020b) in R (R Core Team 2020). ED is estimated in million years (Myr) of evolution. FD is a unitless index ranging from 0 (lowest distinctiveness possible) to 1 (highest distinctiveness possible). Distinctiveness scores per species are given in Appendix 2.

Are species more distinct on continents or on islands?

We sorted species into three non-overlapping categories a) insular endemics, i.e. present only on islands or group of islands; b) continental endemics, i.e. present only on continents; c) non-endemics, i.e. those found on at least one island or group of islands and in one location on the continent. We then estimated the distribution and average distinctiveness score for the three categories. We tested whether the average distinctiveness was significantly different between the three categories: we randomized species among categories without replacement 1,000 times, estimated the new average distinctiveness per category in the randomized sets, and compared the results to the observed distinctiveness in each category. Correcting the average ED scores under phylogenetic constraint did not affect the results and allowed us to perform pairwise correlations between categories (Appendix 3).

Relationship between evolutionary and functional distinctiveness

For each endemism category, we tested the correlation between evolutionary and functional distinctiveness of monocot species. Because species distinctiveness scores depend on the reference set of species, we re-calculated a new ED score only for the 2,581 monocot species for which we previously calculated FD. Thus, the correlation between both ED and FD was assessed between similar sets of species. In addition, ED scores from this subset did not modify the relative ED rank of species compared to their rank within the larger set (significant Pearson correlation equals to 0.96). As a complementary analysis helping to understand the relationship between evolutionary and functional distinctiveness, we measured phylogenetic signal of each of the six traits individually (Appendix 1). We used the K^* test based on the core statistics of Blomberg et al. (2003), as suggested by Pavoine (2020).

Are the most distinct insular species also the most geographically range restricted?

Focusing on endemic monocotyledons present on islands we tested the correlation (Pearson's test) between distinctiveness and geographical range restriction as measured by the number of islands or group of islands where each species occurs. The fewer the islands, the more range-restricted the species is. We also used linear regressions corrected for phylogenetic signal in model residuals to perform pairwise tests between categories and correct models by adding a phylogenetic constraint (Appendix 3). Other factors related to range-restriction such as distance to other landmasses will be considered in the next section analysis. We focused on endemic insular species because the number of islands where each species occurs can be considered as a measure of their full range-size but analyses for non-endemic insular species are presented in Appendix 4.

In line with conservation projects that gave priority to the most distinct species (e.g. Isaac et al. 2007), we tested whether the species with the highest ED and FD occurred on fewer islands compared to species with lower distinctiveness values. We divided species into five classes according to their distinctiveness score: "top distinctiveness", "high distinctiveness", "moderate distinctiveness", "low distinctiveness", "very low distinctiveness" (ranked in the 5%, 25%, 50%, 75% and >75% of the distribution, respectively). For each class, we calculated the mean number of islands or group of islands where each monocot species occurred. We randomized species among classes 1,000 times and estimated whether the observed mean number of islands where species occurred per distinctiveness class was lower than in the randomized set (see also Appendix 3). The main reason to bin species by distinctiveness class is to mainstream our results into actual biodiversity conservation. Generally, the aim to use distinctiveness for biodiversity conservation is to identify the most distinct species in order to protect them. Therefore, many papers studying distinctiveness identified "top distinct species" (Isaac et al. 2007, Huang 2012,

Forest et al. 2018, Robuchon et al. 2021). In particular, the EDGE of existence program funds conservation projects to preserve some of the most evolutionarily distinct and threatened species of the planet (<https://www.edgeofexistence.org/>). In our study, binning species by distinctiveness class allowed us to identify the most distinct species and to make a preliminary assessment of their extinction risks by investigating their range restriction.

Geographical characteristics of islands and species distinctiveness

In this section, we aimed to understand how factors influencing species dispersal could explain the number of islands or group of islands in which distinct species are found. We first investigated the relationship between certain island features and the distribution of distinct species. We focused on geographical characteristics related to past, present and future dispersal events (Table 1). When information was not available at the BIS-level 3 scale, it was measured from single-island values (Table 1). However, we acknowledge that the relationship between these features and species dispersal involves a high level of complexity that we could not account for. For example, not only current distance to other landmasses and current area may explain the presence of a species on an island: long lasting environmental changes that may have modified archipelago configurations through time may also have a role in shaping island biodiversity (Norder et al. 2019). Other factors to consider are therefore plate tectonics, climate change, sea level change but also species dispersal vectors or modes and their interactions (Fajardo et al. 2019).

Insert Table 1

Our aim was to assess the characteristics of the islands where distinct monocot species occur, potentially revealing the factors that enabled or impeded colonization by dispersal (Table 1).

This approach is species-centred and not area-centred. It addresses the general features of the islands where each highly distinct species occurs, rather than investigating the features of islands with the highest average distinctiveness. We made this choice because distinctiveness characterizes each species in a set and not just the species set. Moreover, counting the number of distinct species or averaging distinctiveness scores in an area-centred approach may be inadequate as it will not consider phylogenetic and/or functional complementarity (Veron et al. 2019b). For each species, we estimated the average value of each of the nine geographical characteristics of the islands or groups of islands where it occurred (Table 1). For qualitative variables, i.e. past connection to the mainland and glaciations, we attributed a quantitative value to each of their attributes (glaciated=1; non-glaciated=0; connected to the mainland=1; non-connected to the mainland=0). We then performed generalized linear models and multi-model selection with species distinctiveness as the response variable and island average features as the explanatory variables (see also Appendix 3). Multi-model selection was based on the generation of “best model sets” relying on Akaike's Information Criteria (AIC). The best models were those which had a cumulative AICc weight (a measure of relative statistical support) that reached 95% of the total AICc weights. Parameter estimates were then averaged across the selected models using the model averaging function (full average; Barton and Barton (2019)). We identified the strongest interactions using Boosted Regression Trees, which were added to the multi-model selection process.

Results

Functional and evolutionary distinctiveness are not correlated

Functional and evolutionary distinctiveness were weakly correlated, although the correlation coefficient was higher for insular endemic species (Pearson's correlation coefficients: $r=0.16$,

0.13, 0.018 and 0.093, for insular endemics, insular non-endemics, continental endemics and all monocot species, respectively, with $p\text{-value} \leq 0.05$). This result was congruent with the low phylogenetic signal of traits and was robust to our sensitivity tests (see Appendix 1).

Insular endemics are more distinct

The mean ED and FD per endemism category was respectively 236.7 Myr and 0.061 for insular endemics, 234.9 Myr and 0.043 for continental endemics, and finally 224.5 Myr and 0.047 for non-endemics (Fig. 1). Distribution maps of the most evolutionary and functionally distinct species are presented in Appendix 5. Average ED was significantly higher than expected by chance for insular endemics and continental endemics. Average FD was significantly higher than expected by chance for insular endemics, and for species occurring on both islands and continents. Using phylogenetic analysis of variance, we found that ED and FD were higher for insular endemic species compared to other categories (Appendix 3).

Insert figure 1

Evolutionarily but not functionally distinct species have a restricted geographical range

Geographical range was found to decrease slightly but not significantly with ED in insular non-endemic monocot species (Pearson's coefficient $r=-0.043$, $p=0.26$), but increased significantly with FD in insular endemic species ($r=0.43$, $p<0.001$).

Insular endemic monocot species in the top 5% for either ED or FD were present on average on 1.7 and 3.2 islands, respectively (Table 2). The top 5% ED endemic species were found on fewer islands than expected by chance while the top 5% FD species occurred on more islands than expected by chance (Table 2, Appendix 3).

Insert table 2

Spatial distribution of distinctiveness and its relationship with geographical features of islands

Both functionally and evolutionarily distinct monocot species were located at low latitudes, indicating that there may be a possible latitudinal gradient for distinctiveness (Table 3). As for the longitudinal effect, it was generally greater for FD than ED. We observed a high number of differences between the effects of island features on FD and ED. Concerning evolutionary distinctiveness, we found a significant positive effect of age and of the continental origin of islands and a significant negative effect of glaciation, elevation and distance to the mainland (a similar result was found for non-endemic species, Appendix 4). The effect of the proportion of the surrounding landmass and area on evolutionary distinctiveness was weak to non-significant (Table 3, Appendix 4). Regarding high functional distinctiveness of endemic monocots, it was related to small area, high elevation, large distance from the mainland but not from other landmasses, the oceanic nature of island and the occurrence of past glaciations (Table 3).

Insert table 3

Discussion

Decoupling functional and evolutionary distinctiveness

The primary goal of our study was to perform the very first assessment of monocots distinctiveness on islands and to highlight its possible origins, contributions for conservation and research prospects. Distinct species contribute greatly to the diversity of island biota, to beta-diversity patterns with mainland communities, and to centres of endemism (Veron et al. 2019a).

356 Island regions that harbour both functionally and evolutionarily distinct monocots include the
357 Indonesian islands, the Philippines, Taiwan, Hainan, New Guinea, Japan, Sumatra, and
358 Madagascar. However, the most functionally and evolutionarily distinct species were not the
359 same (appendices 2 and 5). One of the main reasons for lack of association between ED and FD
360 is the evolutionary lability of species traits. This is supported here by the weak phylogenetic
361 signal of traits representing the ecological strategies of monocots (Appendix 1). On islands,
362 evolutionary lability of traits may occur in the case of an adaptive radiation, where
363 representatives may have very similar ED but very distinct FD scores accentuated by vacant
364 niche space and/or by competition (Gavrillets and Losos 2009). Another reason for trait lability is
365 convergent evolution, which has been reported in multiple lineages on multiple islands
366 (Whittaker et al. 2017). This is the process whereby evolutionarily unrelated organisms show
367 similar features as a result of natural selection and adaptation under similar environmental
368 constraints. Yet, there are many possible reasons why FD and ED of plants are not coupled and
369 we also observed that ED and FD of species found on the mainland were not correlated. A recent
370 debate about the extent to which phylogenetics captures trait diversity has put in evidence that
371 the traits considered as well as their number, along with the model of evolution and the spatial
372 and phylogenetic scale strongly influence the way one can infer the other (see discussions in
373 Mazel et al. 2017 and Owen et al. 2019). Further eco-evolutionary studies and additional data
374 would be necessary to better understand why traits fundamental to plant ecological strategies are
375 not conserved in the phylogeny (Cássia-Silva et al. 2020). In particular, Cornwell et al. (2019)
376 elucidated the genetic, trait and distribution data that are missing for plants. Their study defines
377 targets for data collection and compilation, which could help increase the robustness of our
378 findings.

Species distinctiveness is higher on islands than on continents

Our second important finding was that insular endemic monocots were, on average, more functionally and evolutionarily distinct than species occurring on continental areas. Highly evolutionarily distinct species endemic to islands may have arisen from deep divergences. Some endemic taxa belong to species poor families and are therefore distantly related to other species, such as *Japonolirion osense* (Petrosaviaceae) (Cameron et al. 2003). However, higher evolutionary distinctiveness on islands compared to the mainland was unexpected. Indeed, the initial insular species pool is generally a subset of the continental pool, and, therefore, one would expect that insular species would not be more ancient and more evolutionarily isolated than continental species (see Nattier et al. 2017 for an analysis of the age of island biota). Moreover, high speciation rates on islands may result in the diversification of many closely related species, which is expected to decrease the distinctiveness of insular species. Historical events on continents could explain this contradictory finding. One main process could be extinction of species populations on the continent and survival on islands leading to evolutionary isolation (Gillespie and Roderick 2002; Grandcolas et al. 2008). High climatic fluctuations and extreme events on the mainland, concomitant with a relatively stable climate on islands, promoted extinctions on the continent and allowed persistence on islands, especially for plants (Cronk 1997; Whittaker and Fernández-Palacios 2007; Jetz et al. 2014). Climate change on the continents may not only have led to extinctions but also to diversification. Diversification on the mainland could result in the split of unique phylogenetic branches on the continent while species on islands remained evolutionarily isolated. For example, orchids and grasses represent large continental radiations contributing to relatively low average ED values of monocots on the mainland (e.g. Bouchenak-Khelladi et al. 2014; Pérez- Escobar et al. 2017). Furthermore, the

current high evolutionary distinctiveness on islands could be due to anagenetic speciation followed by extinctions or diversification on the mainland. Anagenesis refers to the sequential evolution of a branch over time (Rensch 1959) and leads to spatial segregation of a given insular endemic species and its sister species. It is a main model of evolution in islands that are flat, continental and located at intermediate distances from the mainland, which are also the characteristics of the islands where we observed the occurrence of highly distinct species (Stuessy et al. 2006; Rosindell and Phillimore 2011). We therefore suggest that, anagenesis, extinctions and recent radiations of continental populations may partly explain the evolutionary isolation of insular endemics at the global scale (Gillespie and Roderick 2002; Grandcolas et al. 2014). It is worth noting that biogeographic considerations only give primary insights on the rise of evolutionarily distinct monocots and the story is sometimes very complex (Grandcolas et al. 2014). Further research is therefore necessary on this topic: potential biases in phylogenetic tree topology and branch lengths due to missing data could be tested by building a larger phylogenetic tree, effects of extinctions could be better understood by investigating fossil records, and distinguishing clearly between models of evolution would require genetic studies focused on each highly distinct species.

We showed that the functional distinctiveness of monocots was higher on islands than on the mainland as well. This finding was reported in other taxonomic groups and particular traits, such as body size in mammals (Faurby and Svenning 2016), morphology, attack strategy and development in Hymenoptera and Braconidae (Santos et al. 2016). Here, we showed that it was also true in the monocots we studied regarding the multiple traits fundamental to their ecological strategies. Two main mechanisms may account for a higher functional distinctiveness of monocots on islands: niche expansion and niche shift. Niche expansion occurs when species

richness is low and disharmony is high, i.e. an imbalance in the taxonomic composition of species assemblages between islands and the mainland, thereby resulting in a diversity of vacant niches to be colonized (Whittaker et al. 2017). For example, Diamond (1970) reported that following the colonization of species-poor islands in the Pacific Ocean, insular birds occupied a wider altitudinal range and a greater diversity of habitats, and had a wider vertical foraging range than their continental counterparts. Supporting the niche expansion hypothesis, we found that functionally distinct species occurred on islands where species richness is assumed to be low, i.e. islands that were oceanic, small, far from the mainland, and which have been glaciated during the Last Glacial Maximum, possibly leading to the loss of its distinct biota. Niche shift relates to changes in the biological and ecological characteristics of insular species compared to their continental counterparts (MacArthur and Wilson 1967; Simberloff 1974). The persistence of insular species and especially plants may have been conditioned by adaptations to the oceanic climate of islands resulting in the evolution of specific ecological strategies.

Range-restriction of distinct species

The few studies exploring the relationship between evolutionary distinctiveness and geographical range restriction showed that the most distinct species were not more range-restricted than other species (Jetz et al. 2014; Thuiller et al. 2015; Stein et al. 2018). Here, although the correlation between the range-restriction of a species (i.e. the number of islands or group of islands where it occurs) and its ED was generally low, we found that the most evolutionarily distinct monocot species were spatially range-restricted. Some factors that generate high distinctiveness within insular systems also generate endemism, such as the adaptation to particular environmental conditions and the fact that many islands act as a refuge. As stated above, extinctions could have isolated insular species in the Tree of life, but they could have also restricted species to very few

or to a single island and driven endemism through the loss of continental populations (Whittaker and Fernández-Palacios 2007). Extinctions may therefore be responsible for both higher distinctiveness and higher range-restriction on islands. On the opposite, we also found that species with very low distinctiveness had relatively small range sizes (although they tend to be larger than for the most evolutionarily distinct species). This possibly reflect in-situ speciation events leading to closely-related species restricted to few islands. Investigating rates of extinction, speciation and range evolution across the phylogeny of monocots could give further insights on the origin and distribution of ED on islands (Goldberg et al. 2011). Another potential mechanism explaining range-restriction of very distinct species is dispersal. While island features can provide insights on how high species distinctiveness arose, they are also related to colonization rates and could help understand how dispersal influenced the distribution of these highly distinct species. The most evolutionarily distinct monocots are often single-island endemics and rarely occur on islands where recent and/or long-distance dispersal would be needed to settle new populations. They are uncommon on remote, glaciated, young and oceanic islands. Future research is needed to understand whether this spatial distribution could be due, or not, to the dispersal potential of evolutionarily distinct species (Gillespie et al. 2012).

The patterns we found regarding the range-restriction of the most functionally distinct monocots are opposite to the patterns of the most evolutionarily distinct species. On average, highly functionally distinct monocots were found only on a small number of islands, which is congruent with studies showing that rare functions are usually supported by rare species (Mouillot et al. 2013). Yet, using null models, we found that insular endemic monocots with the highest FD scores are not significantly more range-restricted than less distinct species. Violle et al. (2017) recently proposed a multifaceted framework for defining “functional rarity” by combining

characters pertaining to functional distinctiveness and range restriction. Within their framework, 12 forms of functional rarity are possible, such as widespread species with distinct traits, as we found here. By contrast to the most evolutionarily distinct endemic monocots, functionally distinct endemic species occur on oceanic, remote and glaciated islands, which are patterns suggesting that functionally distinct species experience long-distance dispersal. The relationships between island features, plant distinctiveness and spatial range provide some insights into the role of species dispersal in range restrictions of the most evolutionarily and functionally distinct species. However, reconstructing dispersal events is complex and further research would be needed. In particular, investigating dispersal vectors and modes of distinct species as well as the influence of environmental and dispersal filtering could provide further insights on the distribution of species distinctiveness on islands (e.g. Heleno and Vargas 2015; Fajardo et al. 2019).

Implications for conservation

Highly evolutionarily distinct species capture large amounts of evolutionary history (or phylogenetic diversity [PD]) and highly functionally distinct species represent some rare functional trait values shared with few others. From a conservation perspective, this implies that the loss of highly distinct species will directly lead to the loss of some irreplaceable ecosystem functions and evolutionary branches (e.g. Leclerc et al. 2020). Preserving phylogenetic diversity is considered as a proxy for the conservation of the variety of species features (Faith 2018), and is associated with option values from benefits provided by biodiversity to people and nature (Faith 2016). The Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services adopted Phylogenetic Diversity as the indicator of the “maintenance of options” provided by feature diversity for future generations ("Nature's Contributions to People" category

number 18; Díaz (2019)). This PD indicator was further developed by the IUCN Species Survival Commission Phylogenetic Diversity Task Force, now focusing on the conservation of evolutionary distinct species, in a formulation destined to be easily disaggregated into regional and national scales (Gumbs et al. 2021). It is presently being considered to be integrated as a Headline or Component Indicator in the Post-2020 biodiversity framework (sbstta-24-03-add1). However, feature diversity captured by evolutionary diversity should be distinguished from functional trait diversity, as phylogenetics does not “magically make inferences about every favourite character” (see above and the discussion in Faith (2018) and Owen et al. (2019)). In this study, we considered only six plant traits so that the functional distinctiveness scores estimated here are not fully representative of the plant feature diversity that is captured by evolutionary diversity and which is linked to the maintenance of option-values. However, these six traits are fundamental features pertaining to the ecological strategies of plants and it is expected that the loss of species with distinct ecological strategies may have very different consequences from the loss of species with common ecological strategies (Cooke et al. 2020). From a conservation perspective, the FD and ED scores we measured are therefore complementary.

An important consideration for conservation is that, among insular endemics, those with high distinctiveness could be threatened with extinction. Especially because the most evolutionarily distinct endemic species are found on a very low number of islands and their range-restriction may be the sign of a higher extinction probability (e.g. Harnik et al. 2012). Species occurring on islands are among the most vulnerable on Earth due to the combined effects of human-induced threats, species naiveté, short distribution ranges, unique species interactions, low functional redundancy and/or low population sizes (Caesar et al. 2017; Leclerc et al. 2018). In addition,

according to the age-dependent extinction hypothesis, whereby long-branches on the Tree of Life are more likely to be lost (Warren et al. 2018), the most evolutionarily distinct species may be at a higher risk of extinction depending on how ancient they are. The most functionally distinct monocots were not more geographically range-restricted than other species, although they were distributed across a small number of islands. A recent study showed that insular mammals and birds threatened by cultivation and wildlife exploitation support unique and extreme functions and are therefore functionally irreplaceable (Leclerc et al. 2020). In plants, although some studies investigated the impact of several threats on functional diversity (e.g. Flynn et al. 2009), we do not know studies that directly investigated the risks of loss of the most functionally distinct species (but see Grenié et al. (2018) for an example with corals and Loiseau et al. (2020) for birds and mammals). Further assessment of extinction risks, such as the ones performed by IUCN, would therefore be needed to understand the extent to which the most functionally distinct species are threatened. This would allow to explore the consequences on functional diversity in the event of their extinction.

Based on the IUCN threat status, conservation programs for the most evolutionarily distinct and threatened species do exist (the EDGE program of the Zoological Society of London; Isaac et al. 2007), but not for functionally distinct species. Concerning plants, the EDGE program has recently added gymnosperms to their list, but not angiosperms as of yet (Forest et al. 2018). We would argue that insular endemic species with high ED and FD could contribute to a global list for the conservation of the evolutionary heritage and functional diversity of monocots.

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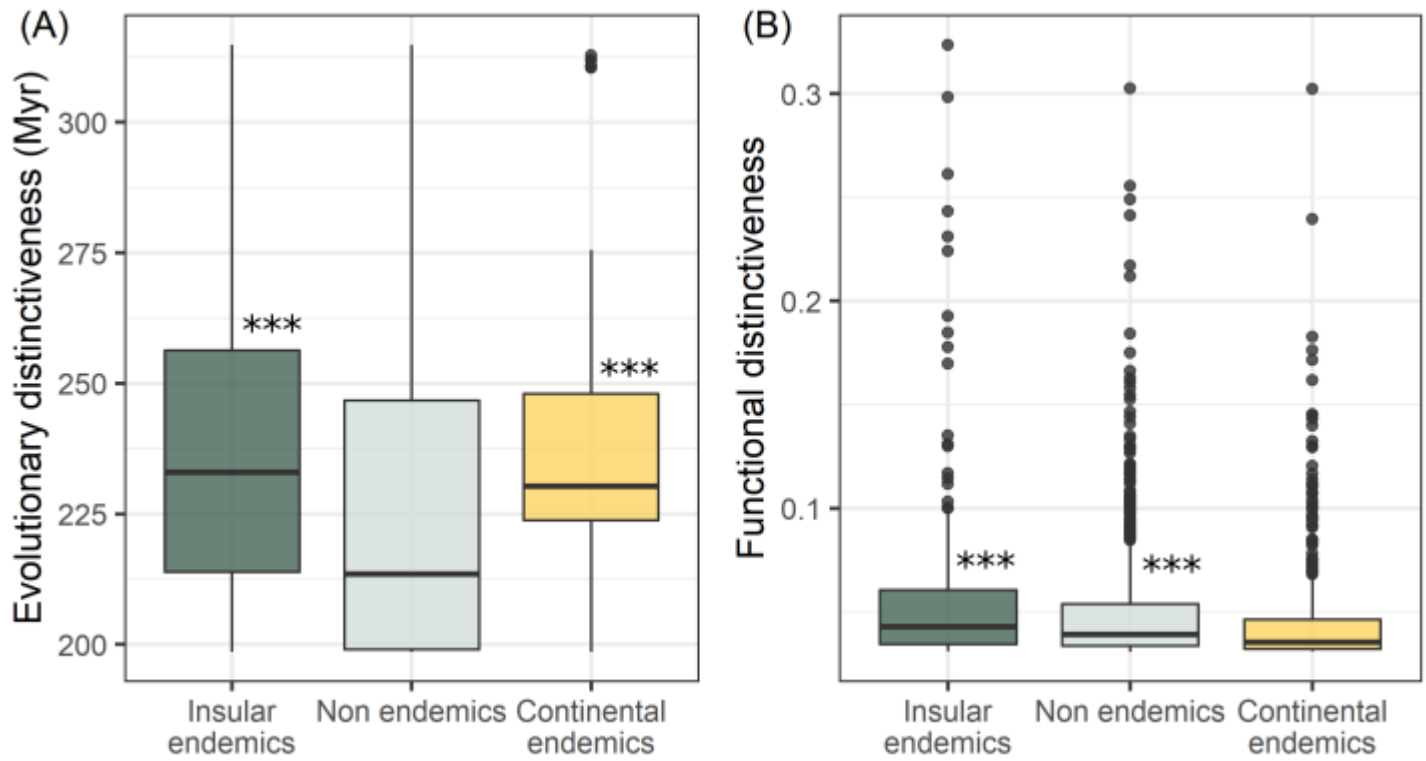
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Fig. captions

Fig. 1: Box plots for (A) evolutionary and (B) functional distinctiveness of monocotyledons including insular endemic, non-endemic and continental species. Species evolutionary distinctiveness scores were calculated for each of 6,682 species from the phylogenetic tree (in millions of years) and functional distinctiveness scores were calculated for a subset comprising 2,581 species for which trait data was available (unitless). Average evolutionary distinctiveness was significantly higher than expected by chance for insular endemics and continental endemics; average functional distinctiveness was significantly higher than expected by chance for insular endemics and for species occurring on both islands and continents ($P < 0.001$, ***)

Fig.1



Tables

Table 1: Main assumptions regarding the influence of nine islands features on dispersal potential and geographical range restriction.

<i>Island characteristics</i>	<i>Assumption regarding its relation to dispersal</i>	<i>Data references</i>	<i>Measurement when a polygon is composed of several islands*</i>
<i>Distance from the continent (km)</i>	Colonization events may be less frequent toward/from distant islands (MacArthur and Wilson 1967)	Global Island Database (GID; UNEP-WCM 2013)	Minimum distance to the continent over all islands
<i>Proportion of surrounding landmass (SLMP)</i>	Colonization events may be less frequent toward/from isolated islands (MacArthur and Wilson 1967)	Weigelt et al. (2013)	Average SLMP
<i>Elevation (m)</i>	Elevation may provide a climatic refuge for ancient lineages that may presently rarely disperse (Steinbauer et al. 2016)	Weigelt et al. (2013)	Average elevation

<i>Area (m²)</i>	Successful colonization events may be more likely toward/from large islands (MacArthur and Wilson 1967)	GID (UNEP-WCM 2013)	Mean of areas over all islands
<i>Oceanic or Continental</i>	Oceanic islands were initially void of life and species settled through colonization whereas continental islands already harboured species assemblages when they fragmented.	Weigelt et al. (2013)	The most frequent type of island is retained
<i>Glaciated or non-Glaciated</i>	If glaciation led to local extinctions of most plant species on an island, then dispersal after glaciation may account for the current presence of ancient species on an island that underwent glaciation (e.g. Alsos et al. 2005)	Gillespie and Clague (2009); Will Iles pers. Comm (12/2018).	The most frequent feature is retained
<i>Age (millions of years)</i>	On young islands the occurrence of ancient endemics may be due to dispersal events (from continents, or inter- or intra-archipelago) (Emerson and Gillespie 2008) but see (Heads 2018))	Gillespie and Clague (2009); Will Iles pers. com.(12/2018)	Minimum age over all islands
<i>Latitude (decimal degrees)</i>	A variable used to account for a potential spatial effect	GID (UNEP-WCM 2013)	Latitude of the centroid
<i>Longitude (decimal degrees)</i>	A variable used to account for a potential spatial effect	GID (UNEP-WCM 2013)	Longitude of the centroid

*Maximum elevation, average area and minimum age were not accounted for due to correlations with other variables

Table 2: Average number of islands per type (functional or evolutionary) and class (from very low to top distinct species) of distinctiveness for insular endemic species. In some cases, the average number of islands is significantly lower (red cells) or higher (blue cells) than expected by chance. Randomization procedure consisted in randomizing species among classes 1,000 times and estimated whether the observed mean number of islands where species occurred per distinctiveness class was lower than in the randomized set. Distinctiveness subsets “top distinctiveness”, “high distinctiveness”, “moderate distinctiveness”, “low distinctiveness”, “very low distinctiveness” correspond to the 5%, 25%, 50%, 75% and >75% of the distinctiveness score distribution, respectively. These scores were estimated over 6,682 monocot species for ED and 2,581 monocot species for FD.

	Top distinct- iveness	High dis- tinctiveness	Moderate distinctive- ness	Low distinct- iveness	Very Low distinctive- ness
Evolutionary Distinctive- ness	1.7	1.7	2.1	2.0	1.8
Functional Distinctive- ness	3.2	2.4	1.7	1.8	1.8

Table 3: The effect and relative importance of selected island features estimated from multi-model selection on evolutionary and functional distinctiveness of endemic species. ***: $P < 0.001$; **: $P < 0.01$; *: $P < 0.05$; •: $P < 0.1$. Summed AICc weights (Σw_i) indicate the relative importance of each variable. SLMP= Surrounding Landmass Proportion; GMMC= connection to the mainland during the last glacial maximum.

Evolutionary distinctiveness			Functional distinctiveness		
<i>Estimate</i>	<i>Pr(>z)</i>	Σw_i	<i>Estimate</i>	<i>Pr(>z)</i>	Σw_i

SLMP	-4.2	.	0.62	0.33	***	1
Distance	-2.6	*	0.89	0.049	**	0.98
Area	0.62		0.28	-0.083	***	1
Elevation	-6.3	***	1	0.029		0.42
Age	5.1	**	0.98	NA		
GMMC	7.07	***	1	-0.22	***	1
Glaciated	-5.9	***	1	0.081	***	1
Latitude	-6.79	***	1	-0.26	***	1
Longitude	-4.25	**	0.79	0.084	***	1
Latitude:SLMP	7.21	***	1	0.01		0.25
Latitude:Age	1.53		0.29	-0.14	***	1

Electronic supplementary material

Appendix 1: Sensitivity analysis

Appendix 2: ED and FD scores of each species

Appendix 3: Phylogenetic analyses of variance

Appendix 4: Range restriction and distinctiveness of non-endemic insular species.

Appendix 5: Spatial patterns of distinctiveness in islands

Declarations

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The authors’ interest is the multiple facets of biodiversity on islands. All authors work on projects investigating phylogenetic and functional diversity on a global scale. RP, TH, MM and SV conceived the project, and obtained the research funds. All authors contributed to the manuscript

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The datasets used and/or analysed during the current study are available from the corresponding author on reasonable request