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Demystifying the convergent ecological specialization of desiccation-tolerant vascular plants for water deficit

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• **Background and Aims** Desiccation-tolerant vascular plants (DT plants) are able to tolerate the desiccation of their vegetative tissues; as a result, two untested paradigms can be found in the literature, despite contradictions to theoretical premises and empirical findings. First, it is widely accepted that DT plants form a convergent group of specialist plants to water deficit conditions. A derived paradigm is that DT plants are placed at the extreme end of stress tolerance. Here, we tested the hypotheses that DT plants (1) are in fact convergent specialists for water deficit conditions and (2) exhibit ecological strategies related to stress tolerance, conservative resource-use and survival.
• **Methods** We used biogeographical and functional-traits approaches to address the mentioned paradigms and assess the species' ecological strategies. For this, 27 DT plants were used and compared to 27 phylogenetically related desiccation-sensitive vascular plants (DS plants).
• **Key Results** We could not confirm either of the two hypotheses. We found that despite converging in desiccation tolerance, DT plants differ in relation to the conditions in which they occur and the ecological strategies they use to deal with water deficit. We found that some DT plants exhibit advantageous responses for higher growth and resource acquisition, which are suitable responses to cope with more productive conditions or with higher disturbance. We discuss that the ability to tolerate desiccation could compensate for a drought vulnerability promoted by higher investment in growth and bring advantages to deal with quick and pronounced variation of water, rather than to drought solely.
• **Conclusions** DT plants are not only selected by drought as an environmental constraint. The alternative functional designs could promote the diversity of ecological strategies, which preclude their convergence to the same resources and conditions. Thus, DT plants are a heterogeneous group of plants in how they deal with drought, despite their desiccation tolerance ability.

Key words: Biogeography, desiccation tolerance, desiccation-tolerant vascular plants, ecological strategies, drought, functional traits, resource-use, resurrection plants, species–environment relationship, stress tolerance, water deficit.

INTRODUCTION

The differential performance of organisms across resources and conditions promotes patterns correlating species and the environment (Chase and Leibold, 2003). Based on this idea, biologists have historically attempted to understand ecological processes by approaching the species' responses to the environment (Lavorel and Garnier, 2002; Funk *et al.*, 2017). However, oversimplifying our understanding of species–environment relationships based on single responses can entail misleading assumptions. For instance, species classifications based on one trait hinders the importance of multiple trade-offs that arise from an array of traits that influence the performance of organisms (Dias *et al.*, 2020; Shipley *et al.*, 2016; Funk *et al.*, 2017). This is because traits can interact and produce alternative functional designs in which species exhibit equivalent fitness for similar resources and conditions, loosening an individualized trait selection (Marks and Lechowicz, 2006; Pistón

et al., 2019; Dias *et al.*, 2020). In other words, a trait alone may not necessarily indicate the action of a selective force for species occurrence in a given habitat. Thus, inferences must be carefully drawn when correlating the species' response to the ecological processes shaping the distribution of species across environments.

Desiccation-tolerant vascular plants (DT plants) comprise a polyphyletic group of plants able to tolerate desiccation (i.e. <13–20 % of protoplasmic water). Because of that, they are reported to be convergent specialists for water deficit conditions (e.g. Gaff, 1977; Alpert, 2000, 2005; Porembski and Barthlott, 2000; Marks *et al.*, 2021). This paradigm is reinforced by the notion that most DT plants, from different phylogenetic lineages (i.e. convergence when less related entities seem more related than they phylogenetically are; Doolittle, 1994), have their occurrence strongly linked to ecosystems distinguished by periods of water deficit (i.e. many of those species are considered rock outcrop specialists; Porembski and Barthlott, 2000; Marks *et*

al., 2021). Because desiccation tolerance is understood as such (Volaire, 2018), a second and derived paradigm suggests that all DT plants are placed at the extreme end of stress tolerance, with the most conservative resource-use to guarantee survival at the cost of faster growth (e.g. Alpert and Oliver, 2002; Bartels, 2005; Teodoro *et al.*, 2021). This implies that DT plants lack advantageous traits for rapid growth in productive conditions or compensate for biomass loss. That is, DT plants would fail to compete for resources or fail to occur when drought exceeds leaves' capacity to tolerate desiccation. These paradigms have never been tested and lead to the assumption that all DT plants are exclusively selected by water deficit playing a selective role as a stressful factor (*sensu* Grime, 1977). Consequently, the impact of competition and disturbance on DT plants might be overestimated (e.g. Gaff and Bole, 1986; Porembski, 2000; Alpert and Oliver, 2002).

However, specialist plants are expected to exhibit responses in which costs and benefits are supposedly more advantageous in a narrower range of resources and conditions. In other words, specialists have traits only suitable to specific ecological conditions. This ecological specialization can reflect limited plasticity or low intraspecific variability (Levins, 1962; MacArthur and Levins, 1964; Devictor *et al.*, 2010). However, DT plants respond to the water variability with morpho-anatomical and physiological plasticity (e.g. leaf folding and accumulation of sugars during drying; Oliver *et al.*, 2000; Porembski and Barthlott, 2000; do Nascimento *et al.*, 2020; Marks *et al.*, 2021; Porembski *et al.*, 2021). They are also likely to exhibit high genetic diversity due to their occurrence in terrestrial island ecosystems (de Paula *et al.*, 2017; Rexroth *et al.*, 2019; Porembski *et al.*, 2021).

Furthermore, it has been widely reported that DT plants differ in their traits, how they cope with desiccation, and the drought conditions in which they occur (e.g. Gaff and Latz, 1978; Gaff, 1986; Gaff and Bole, 1986; Meirelles *et al.*, 1997; Marks *et al.*, 2021). This could mean DT plants do not necessarily overlap in their ecological niche when water deficit is considered, despite their convergent desiccation tolerance response. De Paula *et al.* (2015) reported that some DT plants show competitive capacities in productive conditions, similar to coexisting species that cannot tolerate desiccation (i.e. desiccation-sensitive vascular plants; DS plants). Similarly, Alcantara *et al.* (2015) showed that DT plants are as productive as phylogenetically related DS plants when moisture conditions are favourable for their growth. These two findings agree with theoretical expectations that DT plants grow and reproduce before coexisting species do so when water is available (Scott, 2000; Bartels, 2005). Still, this might not necessarily be true for all DT plants. For example, Teodoro *et al.* (2021) found that a DT plant exhibited lower growth when compared to a phylogenetically related DS plant, even under high moisture conditions.

The contradictions and lack of agreement across theoretical and empirical studies highlight the need for a deeper understanding of the ecological aspects that shape the diversity and distribution of DT plants. Here, erroneous assumptions could negatively affect efforts for their conservation and potential use for biotechnological purposes. In this study, we aimed to evaluate paradigms of DT plants' convergent ecological specialization for water deficit conditions and their placement at the extreme end of stress tolerance, attempting to test the hypotheses that

(1) DT plants are convergent regarding their ecological specialization to water deficit conditions when compared to DS plants, and that (2) DT plants exhibit ecological strategies more related to stress tolerance, conservative resource-use and survival when compared to DS plants. We combined biogeographical and functional approaches to address the questions raised.

MATERIALS AND METHODS

Study species

DT plants can be found in all continents, except Antarctica, although the phylogenetic lineages are unevenly distributed across the globe (Marks *et al.*, 2021). This is because desiccation tolerance of vegetative tissues re-evolved multiple times within tracheophytes due to independent evolutionary events. Desiccation tolerance is found in pteridophytes (e.g. Pteridaceae), monocots (e.g. Velloziaceae) and eudicots (e.g. Gesneriaceae; Oliver *et al.*, 2000; Marks *et al.*, 2021). Plants can overcome desiccation by keeping chlorophyll when desiccating (i.e. homoiochlorophyllous plants) or dismantling the photosynthetic apparatus (i.e. poikilochlorophyllous plants; Marks *et al.*, 2021; Porembski *et al.*, 2021). Losing chlorophyll would allow poikilochlorophyllous plants to cope with desiccation under drought conditions that homoiochlorophyllous plants are not expected to tolerate (Tuba, 2008; Oliver *et al.*, 2020; Marks *et al.*, 2021). Such mechanisms are considered to promote differences in the conditions and resources under which they grow (Gaff, 1977; Gaff and Latz, 1978; Meirelles *et al.*, 1997; Oliver *et al.*, 2020; Marks *et al.*, 2021). Still, exceptions are found. For instance, Selaginellaceae species are homoiochlorophyllous and inhabit exposed locations where poikilochlorophyllous plants are expected to be recorded. Overall, all DT plants occur in habitats with a marked lack of soil, that are prone to quick water depletion and have high solar radiation (e.g. rock outcrops and the canopy; Marks *et al.*, 2021).

Species selection

Assuming a higher variability between species than within them, we selected DT and DS plants based on information on functional traits available for the analyses. First, we selected 27 DT plants whose desiccation tolerance was identified by previous studies (Supplementary Data Table S1). For the DT plants, we used individuals cultivated in the glasshouses from the Botanical Garden of the University of Rostock (Germany) and the Plant Ecology Lab of the University of the State of Rio de Janeiro (Brazil). Complementarily, we included DT plants whose leaf trait information was available in de Paula *et al.* (2015) or in the TRY database (Kattge *et al.*, 2020).

To promote a balanced contrast, we selected 27 DS plants considering their maximum phylogenetic relatedness with the selected DT plants, whenever possible. We also took into account the availability of leaf trait information in the above-mentioned sources (i.e. de Paula *et al.*, 2015 and TRY database) for selection of DS plants. We selected species with the highest geographical and ecological variability possible to bring together a very heterogeneous group of DS plants with regard to water deficit conditions (i.e. generalist and specialist plants in relation to

this constraint). For example, species with different distribution ranges (e.g. the widespread *Juncus inflexus* and the Southeastern Brazil endemic *Pitcairnia azouryi*; POWO, 2022), divergent habitat distributions (e.g. *Pseudolaelia vellozicola*, an epiphyte on Velloziaceae, and *Echinochloa crus-galli*, occurrence of which is extended from forests to wetlands; Porembski, 2003; POWO, 2022), and displaying different strategies to cope with drought (e.g. the succulent *Prescottia montana* and the annual *Melinis repens*; POWO, 2022).

The paradigm of DT plants' convergent ecological specialization for water deficit

For the biogeographical approach, we performed Outlying Mean Index analysis (Dolédec *et al.*, 2000) to identify the habitat affinities of DT and DS plants across drought-related climatic variables. This method uses the climatic information from where species occur to construct an ordination which describes species' climatic niches. This analysis gives a marginality index (MI) and niche breadth value (NB) as descriptors of species ecological specialization. Additionally, we obtained the species' mean niche position along the environmental gradients (NP), which describes the species' affinity for water deficit.

We obtained species occurrence records from the databases 'Tropicos' (http://tropicos.org), Global Biodiversity Information Facility (GBIF; https://www.gbif.org/) and 'Species Link' (http://splink.cria.org.br/). We excluded duplicated, erroneous and uncertain data according to the database Plants of the World Online (POWO, 2022). Then, a presence–absence matrix for all used species was generated, identifying geographical locations, referred to as sampling units, which could contain one or more species. For every sampling unit, we assessed the environmental information regarding the following five climatic variables related to water deficit: (1) Thornthwaite's aridity index, (2) climatic water deficit, (3) drought intensity, (4) drought frequency and (5) drought length. Higher values of Thornthwaite's aridity index and climatic water deficit describe higher water deficit for a given location. Higher values of drought intensity, frequency and length describe more intense, frequent and extensive drought events, respectively.

To obtain Thornthwaite's aridity index, we divided the cumulative monthly difference between precipitation and Thornthwaite's potential evapotranspiration during the year by the modulus of the cumulative potential evapotranspiration over the same period (Thornthwaite, 1948). We calculated the climatic water deficit using absolute values of the cumulative monthly difference between precipitation and Thornthwaite's potential evapotranspiration throughout the year (Esquivel-Muelbert *et al.*, 2017). For drought intensity, frequency and length, a drought event was defined by a given set of consecutive dry months according to the Standardized Precipitation Evapotranspiration Index on a time scale of 1 month and within the period from January 1901 to December 2018. We estimated drought intensity as the whole-period average of cumulative Standardized Precipitation Evapotranspiration Index scores within the drought events. We assessed drought frequency by counting drought events within the period. Finally, we calculated drought length as the whole-period average of the number of months within a drought event. We derived all the climatic

variables from climatic datasets obtained from the Worldclim (https://worldclim.org/) and Standardized Precipitation Evapotranspiration Index (https://spei.csic.es) databases.

For the functional approach, we applied the method proposed by Shipley *et al.* (2017) to predict species Ellenberg Indicator values for moisture (EIV_M) throughout functional traits. We assessed the species' EIV_M by calculating their habitat affinities for the nine first ordinal Ellenberg classes for soil moisture (aquatic habitats were excluded from moisture-level gradient). We described habitat affinities based on the probability of a species being classified in a given EIV_M, in which higher probabilities would describe higher affinities. Then, we generated EIV_M habitat affinity curves for each species. To calculate species' EIV_M, specific leaf area (SLA), leaf dry matter content (LDMC), leaf area (LA) and seed mass (SM) were either (1) measured for DT and DS plants following the methods proposed by Pérez-Harguindeguy *et al.* (2013), (2) obtained from the TRY database (i.e. trait numbers 3109, 3115, 47 and 26, respectively) or (3) collected from de Paula *et al.* (2015). We used at least two leaf replicates from five different individuals for the trait measurements whenever possible. We assessed the functional traits using an oven (T12, Heraeus Instruments, Hanau, Germany), analytical scale (SBC33, Scaltec, Heilingenstadt, Germany), and image scanner (CanoScan LiDE 220, Canon, Amstelveen, The Netherlands). Then, we processed leaf areas in ImageJ software (Schneider *et al.*, 2012). We considered species with trait values from at least three individuals for the species from the TRY database. Pteridophytes were not used in this analysis because they do not produce seed for SM assessment.

Ecological convergence

We used the overlapping index (OV) as a proxy for species convergence to similar ecological conditions in relation to the Outlying Mean Index analysis ordination axes and EIV_M. A higher ecological overlap (i.e. higher OV values) indicates higher convergence between species. We performed multiple pairwise comparisons to estimate the OV, as described by Pastore and Calcagnì (2019). For the Outlying Mean Index analysis ordination axes, we performed kernel density estimations using species' individuals, while for EIV_M, we used the habitat affinity curves. Considering that the desiccation tolerance response can describe ecological convergence for species, DT plants were expected to exhibit higher ecological overlap with each other than when compared to DS plants.

Ecological specialization

For the Outlying Mean Index analysis results, we used MI, NB and Pearson's measure of kurtosis (PK) over kernel density estimations for species individuals' distribution along the two first axes of the ordination. Complementarily, we calculated PK for the species' EIV_M curves (Supplementary Data Table S2). Species ecologically more distant from the average conditions (i.e. higher MI) or with narrower niche breadth along the environmental gradients (i.e. lower NB) are expected to display higher ecological specialization. PK describes the sharpness of the peak for species' optimal conditions. Thus, species whose optimal conditions are more restricted to certain scores of the

ordination axes or EIV_M (i.e. higher PK values) were regarded as more specialist in relation to moisture conditions. In this framework, it was expected that DT plants exhibit a higher MI, lower NB and higher PK when compared to DS plants.

Affinity for water deficit conditions

We used NP along the two first axes of the Outlying Mean Index analysis ordination and from the EIV_M in which species exhibited the highest score (HS_{EIVM}) to describe species' affinity for water deficit conditions. The positive correlation between NP and the environmental variables related to water deficit indicates a higher affinity of species for such conditions, as the HS_{EIVM} for lower EIV_M reflects a higher affinity for lower soil moisture levels. Therefore, DT plants were expected to differ from DS plants by exhibiting a stronger positive correlation with the water deficit variables and higher scores for lower EIV_M.

The paradigm of DT plants in the extreme end of stress tolerance

First, we conducted the globally calibrated method presented by Pierce *et al.* (2017) to estimate species ecological strategies according to Grime's CSR scheme (C-selection – competitiveness, R-selection – ruderalism, S-selection – stress tolerance). In this scheme, C-selection refers to the ability of plants to compete for resources in productive habitats, R-selection denotes plants' capacity to cope with external constraints that lead individuals to a biomass loss, and S-selection describes plants' ability to deal with external constraints that restrict individuals' growth. For this, we assessed the functional traits LA, SLA and LDMC as described above and used the stratefy tool to calculate species affinities for C-selection, S-selection and R-selection of the CSR scheme (Supplementary Data Table S3).

Then, we applied the procedure proposed by Westoby (1998) for estimation of the species ecological strategies within the LHS scheme (L – leaf; H – height; S – seed). SLA, plant height at maturity and SM describe the L, H and S components, respectively. We measured both SLA and SM as discussed previously. In addition, we estimated the canopy height at maturity (1) by measuring the plant height according to the procedure proposed by Pérez-Harguindeguy *et al.* (2013), (2) obtained from the TRY database, (3) collected from de Paula *et al.* (2015) or (4) using species' voucher information. We log-transformed all the three functional traits obtained for the LHS scheme estimation. We did not use pteridophytes in the LHS estimations due to their lack of seeds for SM assessments.

Trade-offs between resource acquisition enhancing growth and resource conservation ensuring survival reflect the species' ability to cope with environmental factors and their position within the CSR and LHS schemes (Westoby, 1998; Reich, 2014; Pierce *et al.*, 2017). A higher score for S-selection strategy corresponds to stress tolerance, conservative resource-use and survival. For the LHS scheme, plans with low SLA, low H and higher SM can be related to stress tolerance, conservative resource-use and survival strategies (Westoby, 1998; Niinemets, 2001; Lavergne *et al.*, 2003; Koch *et al.*, 2004; Moles *et al.*, 2005; Poorter and Rozendaal, 2008; Bolmgren and Eriksson, 2010). While the CSR scheme assumes that the

trade-offs at the leaf level scale to whole-plant and reproductive trade-offs (Pierce *et al.*, 2017), the LHS scheme includes direct measurement of plant reproductive strategies (Westoby, 1998). All functional traits were measured as described above.

Data analyses

First, we split the DT and DS plants into three main phylogenetic groups: pteridophytes, monocots and eudicots (Marks *et al.*, 2021). Then, we performed analyses of covariance (ANCOVAs) to evaluate the differences between DT and DS plants. For the ANOVA's first covariate regarding species' ecological convergence (i.e. OV), we grouped pairwise comparisons between two DT plants as 'desiccation-tolerance × desiccation-tolerance' and comparisons between a DT and a DS plant as 'desiccation-tolerance × desiccation-sensitive'. For the second covariate, we grouped pairwise comparisons within one of the three main phylogenetic groups as 'same phylogenetic groups' (e.g. pteridophytes × pteridophytes) and across phylogenetic groups as 'different phylogenetic groups' (e.g. pteridophytes × monocots). To find significant differences in PK, MI, NB, NP, C-selection, S-selection, R-selection, L, H and S between DT and DS plants, we used the species' response to desiccation as a first covariate (i.e. desiccation-tolerant and desiccation-sensitive), and the phylogenetic groups as the second covariate (i.e. pteridophytes, monocots and eudicots). We chose this analysis to evaluate the differences between DT and DS plants while controlling for the effect of phylogenetic inertia on species scores (Blomberg and Garland, 2002). Whenever the assumptions for parametric analysis were not fulfilled, we performed Box–Cox transformations (Box and Cox, 1964) before conducting the ANCOVAs. To minimize the chance of inflating the type I error rate (Jafari and Ansari-Pour, 2019), the Bonferroni correction method was applied to the ANCOVA *P*-values. The Bonferroni correction was applied always comparisons were performed using different response variable as alternative proxies to investigate the same ecological question.

To analyse HS_{EIVM} for DT and DS plants, we conducted a χ^2 test to verify if the species' highest probability of being classified to a given EIV_M is independent of its response to desiccation. We chose the χ^2 test because it indicates if the distribution of species along EIV_M is statistically related to desiccation tolerance or does not differ from what is expected by chance.

Assessment of species' geographical distribution and to obtaing climate data, besides calculations of indices, probabilities and analyses, were performed with R software (R Core Team, 2021).

RESULTS

The paradigm of DT plants' convergent ecological specialization for water deficit

In general, we did not observe differences between DT and DS plants in the conducted analyses. The Outlying Mean Index analysis PCA1 axis was positively correlated with more extensive and intensive, although less frequent, drought events while the Outlying Mean Index analysis PCA2 axis was negatively

correlated with higher water deficit (Fig. 1). Regarding species EIV_M, it was not possible to delimit between DT and DS plants. Species from both functional groups were more closely related to soil moisture between the Ellenberg ordinal classes 3 and 5.

In relation to the occurrence of species' individuals along the first axis of the Outlying Mean Index analysis ordination, we found a significantly higher ecological overlapping (OV_{PCA1}: $F = 14.9631$, adjusted $P = 0.0003$; Fig. 2; Supplementary Data Table S4) in desiccation-tolerance × desiccation-sensitive comparisons (OV_{PCA1} μ = 0.4124) than in desiccation-tolerance × desiccation-tolerance comparisons (OV_{PCA1} μ = 0.3616). However, no significant difference was found when the axis PCA2 was considered (OV_{PCA2}: $F = 5.5153$, adjusted $P = 0.057$). Similarly, the ecological overlap between DT plants was not significantly different from the ecological overlap between DT and DS plants regarding their EIV_M (OV_{EIVM}: $F = 0.5014$, adjusted $P = 1$).

We did not find a significant effect of species response to desiccation on the overall variability in species distribution shape along the two first Outlying Mean Index analysis axes (PK_{PCA1}: $F = 0.1516$, adjusted $P = 1$; PK_{PCA2}: $F = 0.9352$, adjusted $P = 1$), species ecological distance from the average conditions (MI: $F = 1.4029$, adjusted $P = 1$) and species niche breadth along the environmental gradients (NB: $F = 0.0093$, adjusted $P = 1$; Fig. 3; Supplementary Data Table S5). In addition, we did not find a significant difference in the habitat affinities between DT and DS plants along a soil moisture gradient (PK_{EIVM}: $F = 0.0513$, d.f. = 31, adjusted $P = 1$).

The niche position along the two first Outlying Mean Index analysis axes between DT and DS plants was not significantly

different (NP_{PCA1}: $F = 1.4899$, adjusted P-value $= 0.4560$; NP_{PCA2}: $F = 2.7050$, adjusted $P = 0.2126$; Fig. 4). Besides, the species' HS_{EIVM} was independent of the species strategies to cope with desiccation (HS_{EIVM}: $\chi^2 = 0.7485$, $P = 0.7866$).

The paradigm of DT plants in the extreme end of stress tolerance

It was not possible to observe a distinction between DT and DS plants either in the CSR scheme or in the LHS scheme (Fig. 5; Supplementary Data Table S6). No significant effect of species response to desiccation was found on the variability of their relative proportion of C-selection ($F = 0.3771$, adjusted $P = 1$), S-selection ($F = 2.31$, adjusted $P = 0.4044$) and R-selection ($F = 1.3553$, adjusted $P = 0.7497$). The species' SLA did not differ between DT and DS plants (L: $F = 0.9837$, adjusted $P = 0.9783$), as well as plants' H (H: $F = 0.018$, adjusted $P = 1$) and SM (S: $F = 0.156$, adjusted $P = 1$).

DISCUSSION

We did not find a convergent ecological specialization to water deficit conditions for the DT plants. They also did not exhibit ecological strategies more related to stress tolerance, conservative resource-use and survival than DS plants. We suggest that species are far more complex than having their ecological niches defined only by one response to the environment, as ecosystems do not have just one prominent process exclusively explaining species occupancy.
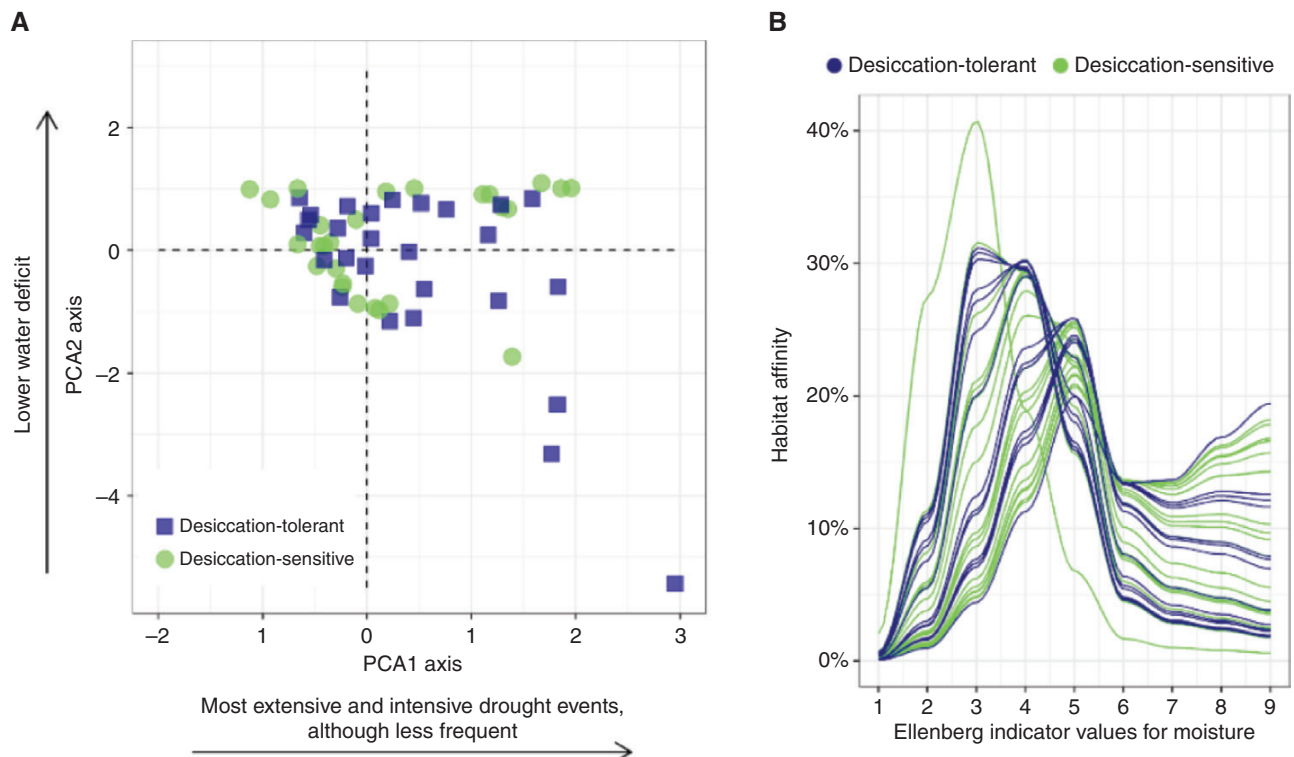
FIG. 1. Species' correlation to water deficit, by their response to desiccation. (A) Species distribution in relation to the two first axes of the outlying mean index analysis. (B) Species' habitat affinities in relation to Ellenberg indicator values for moisture.
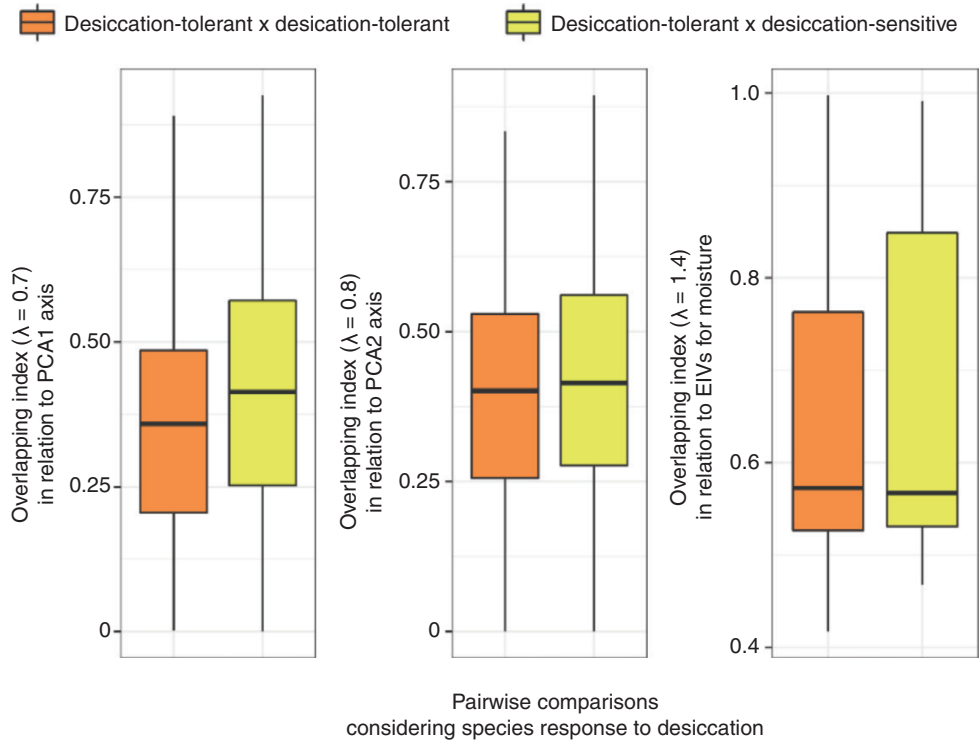
FIG. 2. Species' convergence in relation to water deficit, according to the outlying mean index analysis and Ellenberg indicator values for moisture (EIV$_M$), in which the pairwise overlapping index between desiccation-tolerant and desiccation-sensitive vascular plants is compared to the pairwise overlapping index between desiccation-tolerant species.
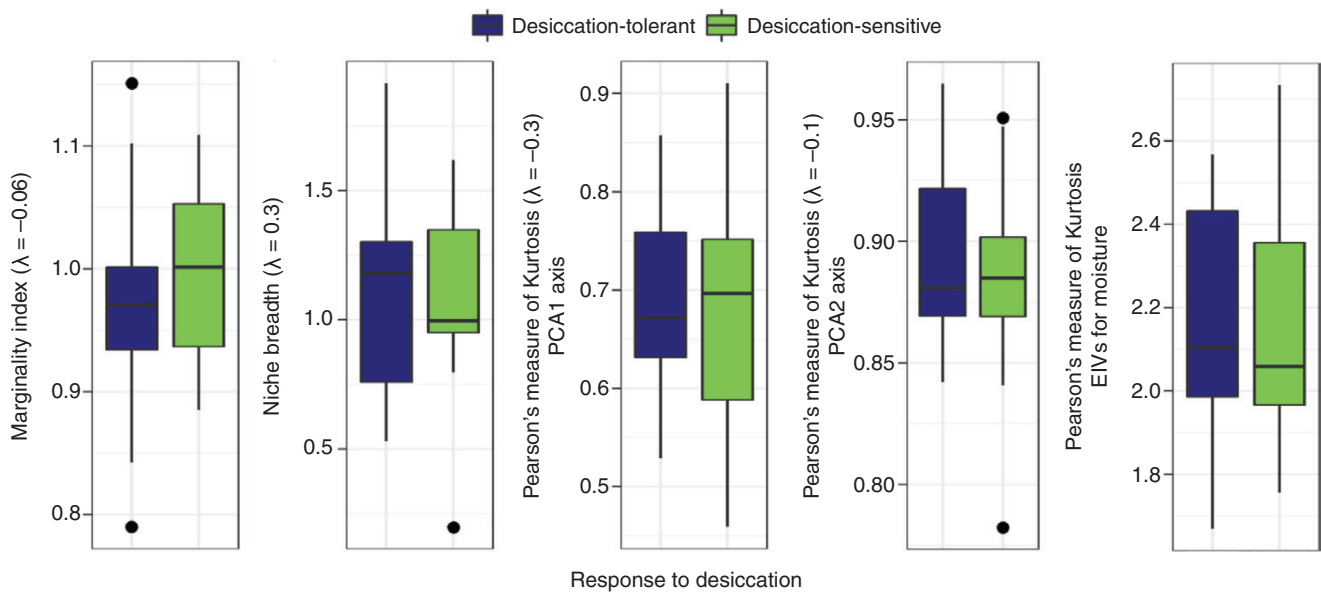

FIG. 3. Comparisons of species ecological specialization along water deficit gradients according to outlying mean index analysis and Ellenberg indicator values for moisture (EIV$_M$), in relation to their response to desiccation.

DT plants were not a homogeneous group in any of the aspects covered by this study. The DT plants' convergence in their response to desiccation should be carefully used to underpin assumptions of species convergence in other regards (Fig. 6). Convergence depends on the specific response or aspect of the environment in question (Winemiller *et al.*, 2015; Funk *et al.*, 2017; Pistón *et al.*, 2019). For example, because of their ability to tolerate desiccation, all desiccation-tolerant plants can cope with drought (i.e. water deficit restricting growth of DP plants). However, it does not mean that all DT plants have the same
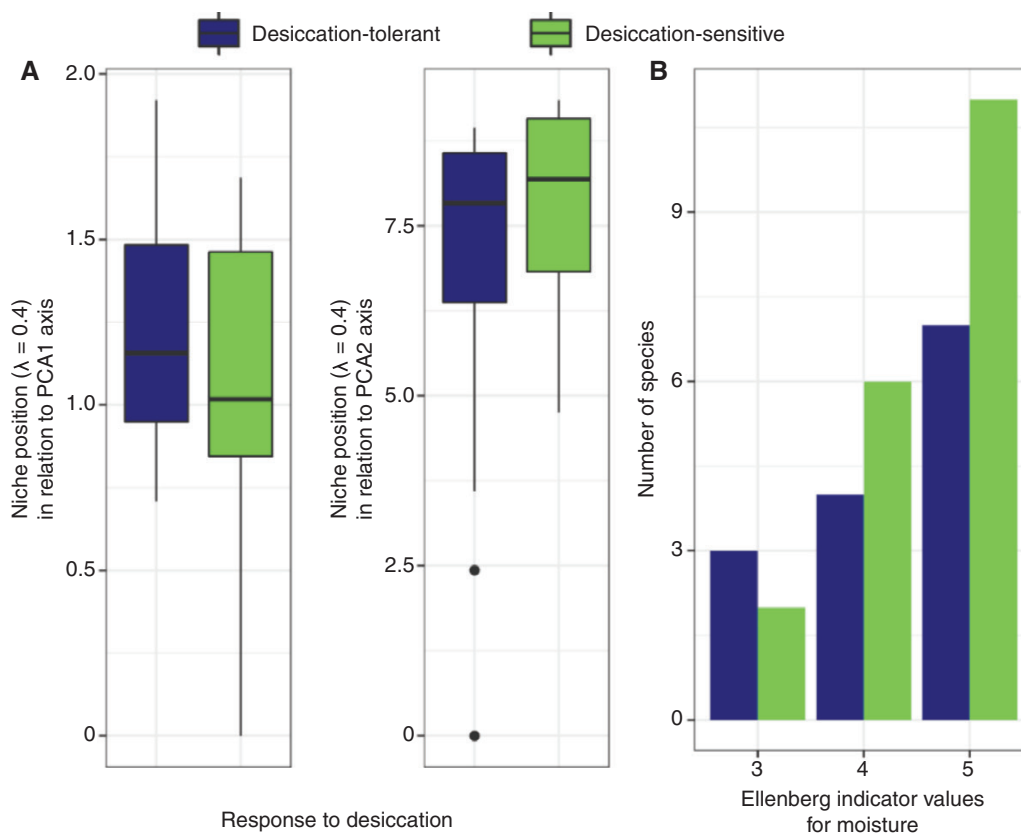
FIG. 4. Comparisons of species affinity for water deficit according to outlying mean index analysis and Ellenberg indicator values for moisture, in relation to their response to desiccation. (A) Species' niche position in relation to the outlying mean index analysis two first axes. (B) Number of species by the Ellenberg indicator value in which their higher habitat affinity was registered.

fitness when facing drought (i.e. water deficit promoting biomass loss, such as when leaves cannot rehydrate or completely re-green).

We should not neglect the statistical improbability of different evolutionary events generating the same complex genetic outcome (Gould, 1970). Some DT plants construct small, expensive and long-lived leaves with slow returns on biomass investment (e.g. the higher S-selection in most monocots). Others invest in long-lived leaves with a higher light interception, which is advantageous in productive conditions (e.g. higher C-selection in many pteridophytes and eudicots). Adding more heterogeneity, it is also possible to find DT plants with cheap photosynthetic tissues in which the carbon returns on biomass investment are higher, favouring short productive opportunities (e.g. the higher R-selection in some Poaceae lineages).

The different ways that DT plant use to perceive and cope with drought can be reflected in the environmental conditions in which they occur. For instance, the poikilochlorophyllous *Afrotrilepis pilosa* and *Vellozia plicata* grow in fully exposed habitats on granite outcrops (Porembski *et al.*, 2021), while the homoiochlorophyllous *Doryopteris collina* and *Ramonda myconi* inhabit more shaded and sheltered habitats on the same type of outcrops (Meirelles *et al.*, 1997; Fernández-Marín *et al.*, 2020). Our results showed that *A. pilosa* and *V. plicata* have a higher relative proportion of stress tolerance (66 and 65 %, respectively) than *D. collina* and *R. myconi* (24 and 21 %,

respectively). Thus, despite converging in their desiccation tolerance, these species do not converge in water deficit conditions in which they are found and in how they deal with water availability. Such differences can also be observed within the same phylogenetic lineages in which species share the same mechanism to tolerate desiccation. For example, in contrast to *V. plicata*, *Barbacenia gounelleana* exhibited an acquisitive resource-use, a CS/CSR strategy (C : S : R = 34 : 41 : 24 %), and had its occurrence related to the most humid sites among all DT plants. Similarly, five DT pteridophytes registered a higher relative proportion for C-selection (*Adiantum latifolium*, *D. collina*, *D. varians*, *Polypodium interjectum*, *Po. vulgare*), while three showed higher scores for S-selection (*Anemia ferruginea*, *Asplenium ceterach*, *As. trichomanes*).

We observed that the moisture conditions in which the DT plants had their HS_{EIVM} varied from fresh soils of average dampness (e.g. *Microchloa kunthii* and *Trilepis lhotzkiana*) to dry rather than moist ground (e.g. *Oropetium aristatum* and *V. plicata*). These findings can be linked to the fact that some DT plants exhibit advantageous responses for higher growth and resource acquisition (e.g. higher LA and SLA; Reich *et al.*, 1998; Niinemets, 2001; Poorter and Rozendaal, 2008). Such responses would reflect suitable ecological strategies to also cope with more productive conditions or with higher disturbance (e.g. higher relative percentage of C and R strategies, higher H, and smaller SM; Westoby, 1998; Pierce *et al.*, 2017). Therefore, our results displace DT plants from the extreme end
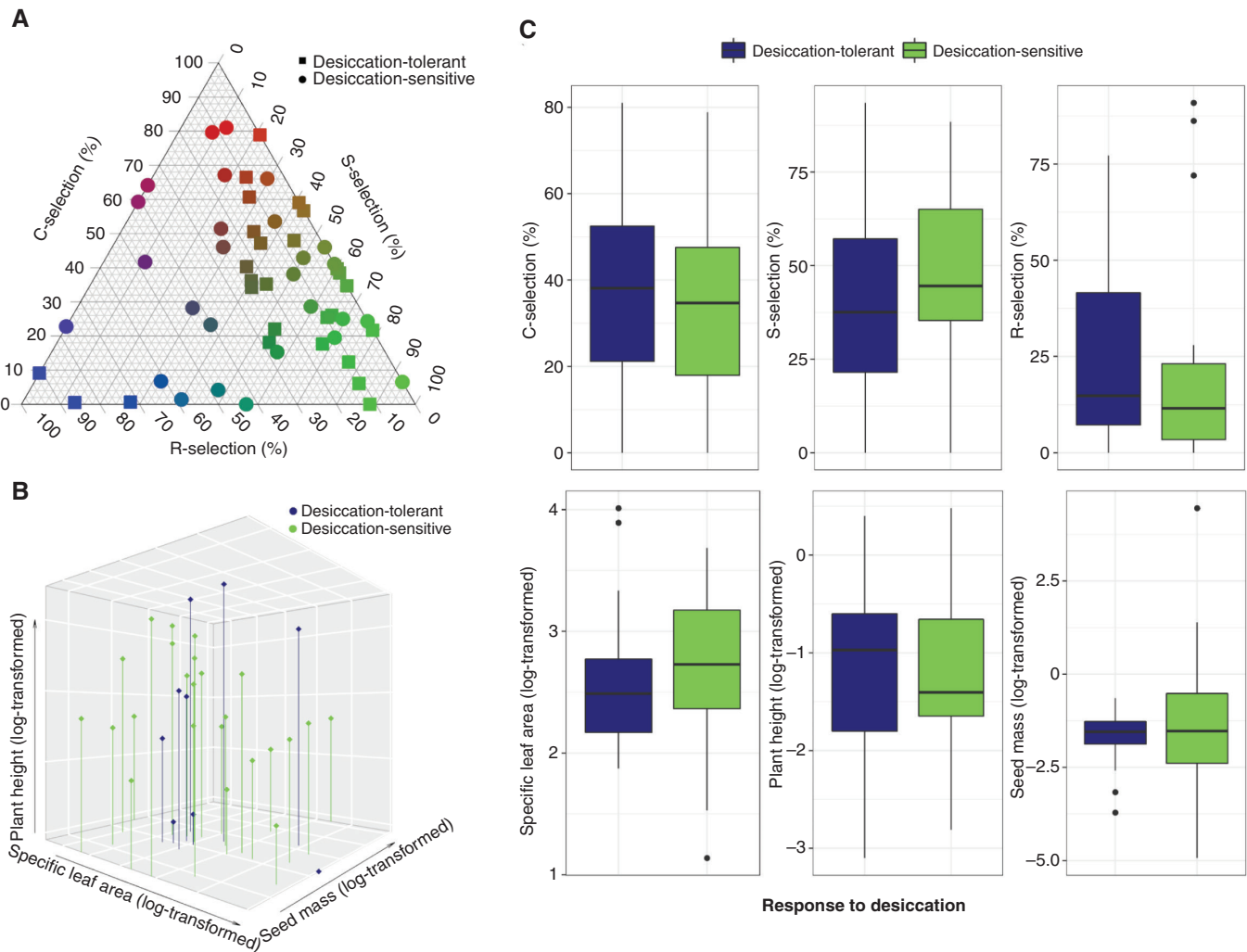
FIG. 5. Ecological strategies of desiccation-tolerant and desiccation-sensitive vascular plants according to Grime's CSR and Westoby's LHS schemes. (A) Species mean position in the CSR scheme. (B) Species mean position in the LHS scheme. (C) Comparisons of the species' relative proportion of C-selection, S-selection, R-selection, specific leaf area, plant height and seed mass in relation to species response to desiccation.

of stress tolerance and reveals the relevance of other ecological processes shaping the distribution of DT plants.

The higher capacity to deal with productive and disturbance conditions can increase DT plants' vulnerability to the negative effects of drought (Reich, 2014). However, their ability to tolerate desiccation could compensate for the drought vulnerability promoted by higher investment in growth. The idea of a trait interaction to mitigate the negative effects of drought can be found in previous studies. For instance, DT plants display folded leaves while drying, reducing photooxidative damage promoted by light incidence over desiccated tissues (Porembski and Barthlott, 2000; Porembski *et al.*, 2021). This means that DT plants exhibit a greater leaf area for light capture when water is available, giving them higher competitive abilities for resources. However, they decrease their exposed surface area when water is unavailable, increasing stress tolerance capacity. Other traits support this response. For example, leaf folding correlates with a venation structure that avoids irreversible damage in their hydraulic system during

leaf folding (i.e. parallel nervature in monocots or net-like venation pattern in Gesneriaceae; Kampowski *et al.*, 2018; Porembski *et al.*, 2021). Besides leaf folding during desiccation and its appropriate venation structure, many DT monocot species also develop a velamen radicum (e.g. in Velloziaceae species). The velamen radicum increases water capture and storage (Porembski and Barthlott, 2000; Oliveira *et al.*, 2005; Zotz *et al.*, 2017; Porembski *et al.*, 2021), reducing DT plants' exposure to water deficit conditions and improving their competitive abilities (Oliveira *et al.*, 2005).

Alternatively, some DT plants might not have their occurrence restricted to the existence of drought as an external constraint that limits productivity. For those species, drought leads to a disturbance, where individuals lose biomass caused by irreversible damage, or being perceived by species as a secondary selective agent (Grime, 1977; Wilson and Lee, 2000; Pierce *et al.*, 2017). This may be the case for the two annual plants *O. aristatum* and *O. thomaeum* (Porembski *et al.*, 2021), which had high relative proportions of ruderalism (72 and
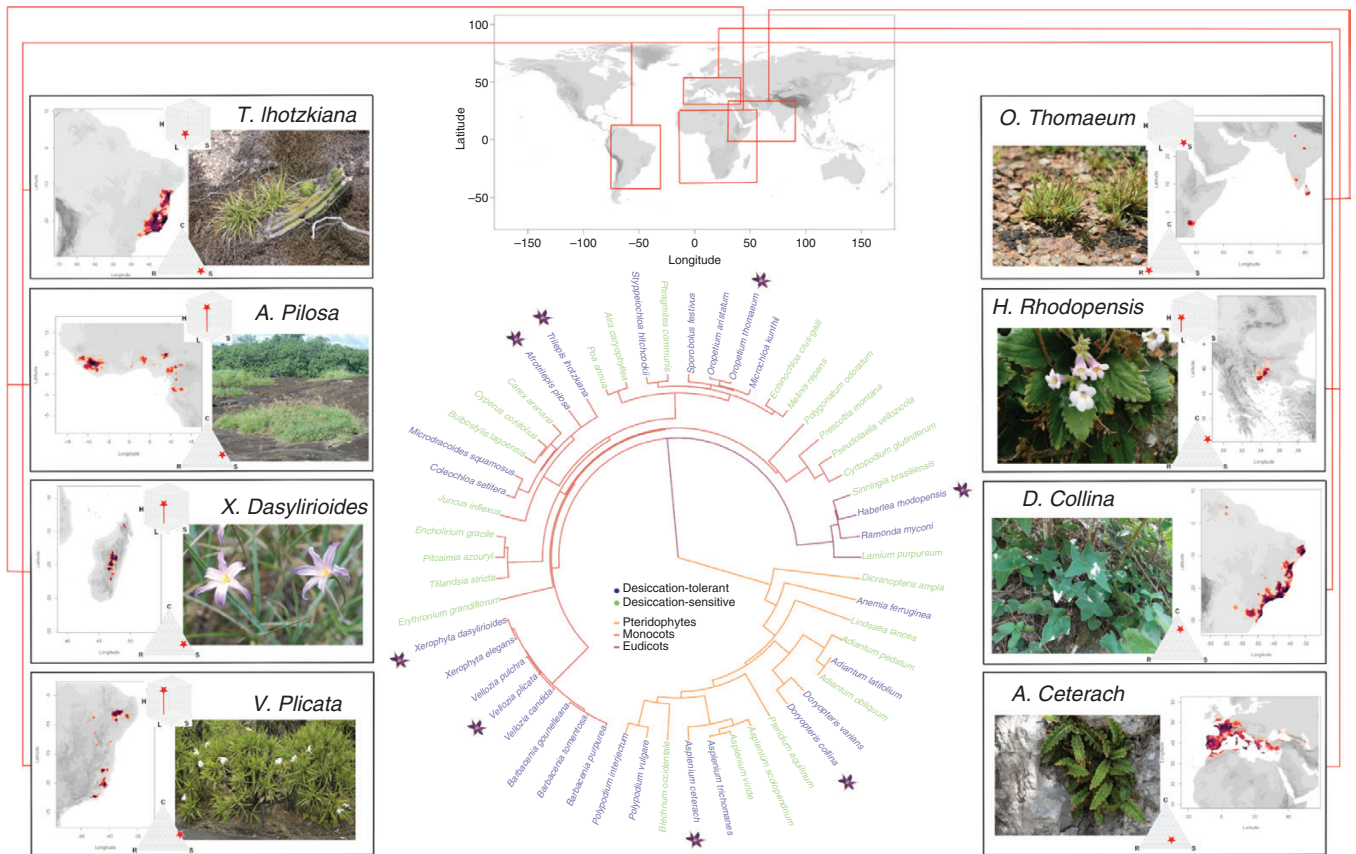
FIG. 6. The diversity of desiccation-tolerant vascular plants, in relation to their phylogenetic and geographical distribution, morphology and ecological strategies.

86.2 %, respectively). Drought leading to a disturbance for these species is corroborated by their high SLA, besides low H and SM (*O. aristatum*: SLA = 49, H = 83 and SM = 0.042; *O. thomaeum*: SLA = 55.2, H = 45 and SM = 0.225). Desiccation tolerance would allow their leaves to survive quick water shortages, when drought acts as a stressful factor. However, their leaf traits favour quicker returns on biomass investment and shorter life cycles, reaching reproduction before long-term droughts lead to disturbance. This is compatible with the fact that these species occur in geographical regions with more extensive and intensive drought events in the dry season and short dry periods in the wet season. Therefore, the alternative functional designs within DT plants could promote the diversity of ecological strategies found among them and suggest that their occurrence is not driven by a common selective force, such as water deficit as a stressful constraint.

Rather than solely water deficit, we suggest that desiccation tolerance could bring advantages to dealing with the quick and pronounced variation in water availability. This is supported by the almost absence of DT plants in deserts (Fahmy *et al.*, 2006; Porembski *et al.*, 2021) and their strong correlation with habitats characterized by marked moisture fluctuations (i.e. rock outcrops; Porembski and Barthlott, 2000; Gaff and Oliver, 2013). Our results are in agreement with these expectations. Although we did not assess moisture fluctuations, we found a low average probability of occurrence of DT plants under extreme dryness (0.32 % according to species EIV_M).

The higher temporal variation in the availability of a given resource is expected to benefit species with a more generalist response to different levels of this resource (Lynch and Gabriel, 1987; Sexton *et al.*, 2017). This is because species from highly variable environments are expected to mitigate the selective pressures promoted by the circumstances to which they are subjected (Wilson and Yoshimura, 1994; Callaway *et al.*, 2003). For example, a habitat in which organisms experience enough water to grow, but cannot avoid the negative effects of drought periods, is considered to favour species that can cope with water abundance and deficiency. In this case, DT plants exhibit traits that allow compatible growth and reproduction when water is available, plus the survival of photosynthetic tissues when water is unavailable (Oliver and Bewley, 1996; Zhang *et al.*, 2018; do Nascimento *et al.*, 2020). This is consistent with the plastic responses of DT plants to water availability (do Nascimento *et al.*, 2020) and their need to hold a positive carbon balance under repeated desiccation–rehydration cycles (Alpert, 2005). Therefore, the occurrence of DT plants in such habitats could imply ecological strategies that fit both contrasting environmental situations they experience instead of an exclusive adaptation for only one facet of the environment.

Our results showed that the view of DT plants as a homogeneous group of plants in how they deal with drought and the simple correlation of desiccation tolerance with water deficit might be a mistaken generalization. Considerable knowledge about DT plants has been gathered, and paradigms have been

consolidated. However, we need new studies that challenge the accepted paradigms that might be constraining scientific progress regarding the ecological aspects of DT plants. We argue that alternative functional designs should be considered when the responses of DT plants to water deficit conditions are investigated. Also, we encourage new studies that seek for a better understanding of how our results might vary within the most diverse phylogenetic lineages. Besides drought promoting environmental stress, we suggest that the low water availability intensifying competition between plants or long droughts leading to biomass loss might have also played an important evolutionary role for some DT species. Among vascular plants, desiccation tolerance has independently re-evolved multiple times, and it is therefore plausible that the importance of those evolutionary processes changes according to the distinct phylogenetic lineages in which DT plants are found. A better understanding of the responses of DT plants to the ecological processes that shape their occurrences across environments would substantially aid the development of more robust ecological assumptions for these species.

SUPPLEMENTARY DATA

Supplementary data are available online at https://academic.oup.com/aob and consist of the following.

Table S1: list of desiccation-tolerant vascular plants and phylogenetically related desiccation-sensitive plants used as model species in this study.

Table S2: ecological specialization and water deficit affinity scores for species.

Table S3: ecological specialization and water deficit affinity scores for species.

Table S4: ANCOVA summary table for species' ecological convergence.

Table S5: ANCOVA summary table for species' ecological specialization and water deficit affinity scores.

Table S6. ANCOVA summary table for determining significant differences between desiccation-tolerant and desiccation-sensitive plants in relation to their ecological strategies, when controlling for their phylogenetic groups.

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