Dryland tree data for the Southwest region of Madagascar: alpha-level data can support policy decisions for conserving and restoring ecosystems of arid and semiarid regions

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ABSTRACT
We present an eco-geographical dataset of the 355 tree species (156 genera, 55 families) found in the driest coastal portion of the spiny forest-thickets of southwestern Madagascar. This coastal strip harbors one of the richest and most endangered dryland tree floras in the world, both in terms of overall species diversity and of endemism. After describing the biophysical and socio-economic setting of this semiarid coastal region, we discuss this region's diverse and rich tree flora in the context of the recent expansion of the protected area network in Madagascar and the growing engagement and commitment to ecological restoration. Our database, DTsMada (short for Desert Trees of Madagascar), is part of a larger 'work-in-progress', namely an eco-geographical database on desert and dryland trees of the world. DTsMada draws heavily on the Catalogue of the Vascular Plants of Madagascar (MacCat) project, in which floristic, ecological and endemism parameters are compiled, together with available conservation status assessments based on IUCN Red List criteria. Both are projects within the plant systematics database, Tropicos\textsuperscript{®}, developed at Missouri Botanical Garden and maintained on the Garden's website. To highlight the need for greater study of the interactions between biological, bioclimatic, and anthropogenic determinants of current and potentially changing biogeographical patterns and community dynamics in the tree strata of vegetation in the study area, we consider four contrasting groups of native trees: Adansonia spp. (Malvaceae), Pachypodium spp. (Apocynaceae), Baudouinia spp. (Fabaceae), and all 11 species in the 4 genera of Didiereaceae in Madagascar. We discuss DTsMada as a prototype dataset of alpha level information vital for effective conservation, landscape planning, sustainable use and management, and ecological restoration of degraded arid and semiarid ecosystems, in Madagascar and elsewhere.

RÉSUMÉ
Nous présentons un ensemble de données éco-géographiques sur les 355 espèces d'arbres (156 genres, 55 familles) présentes dans les fourrés et forêts épauillées de la frange côtière aride et semiaride du Sud-Ouest de Madagascar. Cette région possède un des ensembles d'arbres de climat sec les plus riches (en termes de diversité spécifique et d'endémisme) et les plus menacés au monde. Après une description du cadre biophysique et de la situation socio-économique de cette région, nous présentons cette flore régionale dans le contexte de la récente expansion du réseau de des aires protégées de Madagascar et de l'engagement croissant dans le domaine de la restauration écologique. Notre base de données DTsMada (raccourci de « Desert Trees - Madagascar », en anglais) s'inscrit dans le cadre d'une base de données éco-géographique plus large que nous développons, regroupant les espèces d'arbres des régions arides et semiarides du monde entier, avec un accent particulier mis sur leur utilisation dans la conservation, gestion et restauration écologique. Nombre des informations présentées dans DTsMada proviennent du projet MacCat (Catalogue des plantes vasculaires de Madagascar) qui regroupe des données floristiques et écologiques, et les statuts d'endémisme et de conservation des espèces végétales, basés sur les critères de l'IUCN.

Ces deux projets font partie de la base de données taxonomique Tropicos\textsuperscript{®}, du Jardin Botanique du Missouri. Pour souligner le besoin de disposer de plus d'études pour comprendre : les interactions entre les facteurs biologiques, bioclimatiques et anthropiques qui affectent la biogéographie et les dynamiques des communautés dans les strates arborées de la végétation dans la région étudiée, qu'il s'agisse de la situation actuelle ou celle d'un futur qui sera éventuellement modifié, nous considérons quatre groupes bien différents d'espèces d'arbres in-
INTRODUCTION

Seasonally dry inter-tropical forests, woodlands, and thickets are among the most highly threatened and least well-studied terrestrial ecosystems on Earth (Underwood et al. 2015). They are as rich in both plant and animal species and more productive than other dryland ecosystems and many mesic ones (Aronson et al. 2003), yet their importance—for both biodiversity conservation and delivery of ecosystem services—is often underestimated. The drylands—including the hyperarid, arid, semiarid, and dry-subhumid biomes that occupy >40% of the Earth’s land surface (Reed and Stringer 2016)—are often treated as if they have little lasting value to people. This in turn tends to lead to a spiral of degradation leading to potentially catastrophic consequences for over two billion people who live in these regions (Reynolds et al. 2007; Lal et al. 2012).

There are two underlying factors that contribute to degradation. Firstly, the unsustainable extraction of woody biomass and palatable fodder through a process called ‘artificial negative selection’ (Burkhart 1976). The most desirable timber trees are progressively harvested and removed, thus leading to replacement by less desirable individuals of the species, and more generally to species of inferior ecological quality and timber value compared to the ones removed through selective extraction. Similarly, the hardest-wooded trees that people can exploit are generally extracted for charcoal production first—e.g., Baudouinia rouxvillei in southwest Madagascar—while soft-wooded trees (such as Baobabs) are left behind until people have no other choice left but to use them for fiber and wood. Similar patterns of extraction generally apply to forage and fodder consumption, especially when population density is high and people are very poor (Randamalala et al. 2016). Secondly, the impact of the ‘shifting baseline syndrome’ proposed by fisheries scientist Paul (1995), a term coined to describe the gradual lowering of expectations of the quality and quantity of fishery resources with each new generation of people. Although conceived and applied in relation to ocean fish stocks over the past 100 years (Paul 1995), arguably it applies to dryland ecosystem trees and other valuable resources as well. Many dryland ecosystems and arboreal formations in southwestern Madagascar and elsewhere, were once much more abundant and diverse than they are today (Feige et al. 2001; Le Floc’h and Aronson 2013).

Relative to its size (587,000 km²), Madagascar has a remarkable array of bioclimates which were the subject of an intensive study by Comet (1974), and vegetation types (Moat and Smith 2007). The island is rich in number of species and in the level of endemism recorded in all groups of organisms. Of the ca. 11,400 described species of vascular plants in the country, 95% are angiosperms, and among these, almost 96% are indigenous, with only ca. 400 non-native, naturalized species known. Of the indigenous angiosperm flora ca. 84% have been recorded recently as endemic (Callmander et al. 2011, Rabarimanarivo et al. 2014). However, every year between 50 and 100 new plant species are described, and it is projected that 2,200 or more species of higher plants endemic to Madagascar remain to be described (Phillipson, unpubl. data), which would bring the total number of described species to more than 13,600, with vascular plant species endemism for Madagascar close to 90% (Phillipson 1994, 1996, 2006, Lowry II et al. 1997). Relatively little is known about either historical or contemporary impacts of human land and resource use on the flora and vegetation in Madagascar. In contrast, wild animal–plant interactions have received some attention from evolutionary ecologists working on broad time scales (Gautier et al. 2012). For example, Bond and Silander (2007) suggested that various branch and foliage characteristics present in over 20 plant lineages endemic to Madagascar may have evolved as anti-browsing adaptations and for dispersal by elephant birds or aepyornithids and other large herbivores now long extinct. Grubb (2003) suggested that the spines covering the stems of most or all Malagasy Diidereaceae, and whose length parallels leaf length, are an evolutionary adaptation to protect the leaves against arboreal primates. They noted that members of the same family in Africa have no spines. More recently, Crowley and Godfrey (2013) found that giant lemurs may have played a key role in the evolution of spines in this group of plants.

The southwestern dry forests and spiny thickets are everywhere highly fragmented due to over-exploitation of wood, bark and fiber by local people, especially for charcoal production, which remains the main source of cooking fuel in Toliara, and other cities throughout the country (Vielledent et al. 2018). Harper et al. (2007) estimated that at least 28% of the surface area of forest and spiny thicket was lost between 1950 and 2000, and that in 2000 only 4 million hectares of this vegetation still existed, of which less than half occurred in the coastal area on which we focus in this paper (Figure 1).

Prior to 2003, less than 3% of southwestern Madagascar was included in the national network of protected areas. In that year, former President Ravalomanana launched the so-called Durban Vision process to increase the area in Madagascar available for biodiversity management three-fold, from 17,000 km² to over 60,000 km² (ca. 10% of Madagascar’s total land area) within 10 years (Virah-Sawmy et al. 2014). The subsequent program to implement the vision process, through the Système d’Aires Protégées de Madagascar (SAPM), has resulted in the formal establishment of 85 additional protected areas by government decree issued in April and May 2015, as well as significant additions to existing areas. The total number and surface area of the protected area network has been extended to 122 sites covering just over 71,000 km² (Gardner et al. 2018). Four long-established protected areas in southwestern Madagascar contain areas of dry spiny forest and thicket. These are the Andohanaha National Park and the Beza Mahafaly Special Reserve, Tsmanampetsotsa National Park, the area of which has been recently dramatically increased from 432 km² to 2,627 km², and the much smaller (63 km²) Cap Sainte Marie Reserve (Figure 2). In addition, this vegetation type is also represented in certain of the newly established protected areas in the southwest (SAPM 2018) (Figure 2).

The objective of this paper is to present a database of a poorly-studied tree flora that will be part of a worldwide study and an on-line database linked to it, that will cover dryland and desert trees of the world. The global database we are building, and this specific component of it, which we call DTsMada (short for Desert
Trees of Madagascar, represent alpha-level information for those
engaged in conservation, planning, ecological restoration, and
long-term ecosystem management in megadiverse areas not only
in Madagascar (Birkinshaw et al. 2013), but also in drylands world-
wide. Such databases can provide information in a systematic
fashion, and insights, to assist fundamental and applied research,
including intentional community reassembly (Verdu et al. 2009,
Castillo et al. 2010) through planning for protection and natural re-
genation, and active interventions aimed at ecological restora-
tion.

METHODS

STUDY AREA. Here we consider the tree flora of the coastal
strip of southwestern Madagascar; which is the driest part
(mean precipitation 350–450 mm per annum) of the country, with
a notably erratic distribution of rainfall, seasonally, annually and
spatially (Bonque 1975). This area corresponds to the Elage sous
Coastal fog contributes additional moisture here (Dewar and
Richard 2007), but its role has not been well studied. The forma-
tions found here include ‘dry spiny forest-thicket’, ‘degraded dry
spiny forest’, and ‘coastal bushland’, as mapped in the Atlas of the
vegetation of Madagascar (Moat and Smith 2007). While there are
many NGOs and a number of community-based conservation,
restoration, and sustainable development projects in Madagascar,
especially in the humid, eastern part of the country (Roelens et al.
2010, Birkinshaw et al. 2013), far less attention is being paid to the
unique and highly threatened ecosystems in the drier regions
(Waelder et al. 2015). This contribution is part of an on-going study
and database we are assembling on dryland trees of the world (Le
Floch and Aronson 2013). We consider the ecology, diversity and
distribution, conservation status, horticultural and silvicultural
prospects, and the various uses by people of dryland trees to be
essential information for all who work for conservation, ecological
restoration, and long-term sustainable ecosystem management in
Madagascar, and elsewhere.

The soils of southwestern Madagascar are not diverse, re-
flecting the relatively simple geology of the region, generally com-
prising of superficial lithosols and regosols (Cornet 1974). The
most conspicuous geological features in the region are the ter-
tary limestone outcrops that extend from Morombe in the north-
west of the region to the extreme south, and which form a series of
plateau areas separated by the main river basins draining from the
highlands and western slopes of the interior to the southwest coast—namely from south to north the Menarahandra, Linta, Oni-
lahy, Fihenomana, and Mangoky rivers. A generally narrow coastal
strip to the west of the limestone outcrops represents a series of
ancient, so-called ‘esopronen’ dunes (Du Puy and Moat 1996),
consisting of consolidated calcareous sandstones derived from the
limestone plateau. To the north of Tolitika, the Mikena area and
at certain sites south of this city, an extensive coastal dune sys-
tem, varying in width from five to 50 km, overlies the calcareous
sandstone formations that reach the surface further inland. In the
south, the Karibola plateau with its calcareous lithosols abuts
the rugged basaltic territory of the Androy people, which is adja-
cent to the volcanic formations that abruptly delimit the dry southwest region from the more humid areas of Madagascar to the east.

Only two of the four long-established protected areas mentioned above harbour dry spiny forest and thicket within our study area (Tamanampetsotra National Park and Cap Sainte Marie Reserve). However five of the new protected areas established in 2015 (Gardner et al. 2018) contain dry spiny forest and thicket and lie largely within our study area. These include; (1) Mikae, between Morombe and the Manombo River, (2) Ranobe PK32, between the Manombo and Ifiherana Rivers, (3) Tsinyriaka, between the mouth of the Onilahy River and Toliara, and (4) Amoron-i-Onilahy, along the lower Onilahy basin.

Today spiny thicket, deciduous forest and woodland form a highly fragmented patchwork in southwestern Madagascar, but they were formerly more abundant and had much stronger ecological connections across the region and to the much larger dry bioclimatic region to the north that encompasses most of the western half of Madagascar (Moat and Smith 2007, Vieilledent et al. 2018). The two dominant groups of the forest canopy are tree Euphorbias, and members of the four genera of Didiereaceae occurring in Madagascar, (Alluaudia, Alluaudiopsis, Didierea, and Decarya) all of which are to a large degree endemic to this region. Vegetation cover is quite variable, with poor study correlations to soils, available nutrients in the soils, and substrate types (Moat and Smith 2007). Mills et al. (2012) suggest that woody plants in particular are sensitive to nutrient status of soils in arid and semiarid regions.

In his seminal treatment of the bioclimate of Madagascar, which recognized a total of 29 bioclimatic units mapped across the whole of Madagascar, Antoine Comoret distinguished a subarid (subaziale) region in southwestern Madagascar (Comoret 1974). With only 350–650 mm mean annual precipitation, this region represents the driest of the five major bioclimatic ‘levels’ (étages) he recognized. Within the subarid region, Comoret (1974) recognized three bioclimatic ‘sub-levels’ (sous-étages) based on increasing hydric deficit. The term ‘subarid’ (or sub-arid) is rarely used in English, as compared to ‘semiarid’, a term widely employed by the FAO and other UN agencies, and which has a similar meaning. A semiarid zone is formally defined as having an aridity index of 0.20–0.50 (i.e., annual precipitation divided by evapotranspiration, which is often denoted as PET) (Comoret 1974). These conditions prevail only in the driest part of Comoret’s subarid region, the predominantly coastal area of 16,200 km² that is the main subject of this article (Figure 1), and is dominated by southwestern dry spiny thicket (Moat and Smith, 2007).

For simplicity, we use the term ‘semiarid’ in the context of our study area, which serves to distinguish it from the remainder of Comoret’s subarid region, and henceforth refer to it as the ‘semiarid zone’ (Table 1). The two larger, less arid and predominantly inland areas recognized by Comoret in his subarid region do not have truly semiarid climates, and for these we retain the term subarid. We shall refer to the less arid, northeastermost area as the ‘upper subarid zone’ and the southern area, which has a more gradual transition to the semiarid zone as the ‘lower subarid zone’ (Figure 1) within Comoret’s Étage Subaride.

The semiarid zone consists of the sandy littoral strip along the southwestern coast and the lowest elevation portion of the limestone escarpment leading up to the Karimbola plateau. It stretches from the mouth of the Mangoky River, just north of the town of Morombe, located about 220 km north of Toliara, to Cap Sainte Marie (alias Cape Vohimena) at the southernmost tip of Madagascar. From there it extends east to the Manambovo River near the town of Tsimo, then beyond to the mouth of the Ranofosy River, just south of Andohahela National Park, 25 km west of Tôlagnaro (alias Fort Dauphin). That small area in the southeast constitutes an isolated rainshadow semi-desert with exceptionally high local endemism.

An important feature of the region is its erratic rainfall. Rainless periods can persist for as long as 12 months, during which a significant water deficit accumulates for most plants, and the entire annual precipitation is often concentrated in one or two short heavy storms. The coastal strip is the driest portion of the region but it is a zone where the contribution of fog to total precipitation is significant, even during the generally dry months April to October (Donque 1975). Comet (1974) had access to data from eight stations in the dry southwest when preparing his bioclimatic map, only three are situated within the semiarid zone. A more recent synthesis of data was provided by Oldeman (1990) (Table 2).

Still, reliable long-term data on weather and climate are lacking.

Plant species diversity and endemism: Focusing on the diversity and endemism of vascular plant species of the semiarid zone, based on data extracted from the Madagascar Catalogue (2018), a total of 930 native vascular plant species in 107 plant families have been recorded, of which roughly 23% are endemic to the area. Summary data on the diversity of the better represented families is provided in Table 1.

Considering global tree diversity, a striking feature is the large number of taxonomic groups to which they belong including tree ferns, Gymnosperms and within the angiosperms—six families of monocots and 75 families of dicots (Thomas 2014). The range of 4

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<th>Endemic species</th>
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life forms and life history strategies among trees is also large, notably in dryland ecosystems where drought, nutrient status in soils, and unpredictable weather and climate provide strong selection pressure on desert trees and all other forms of organisms. This is particularly true in the drylands of southwest Madagascar.

Dryland trees: in our global database project, and for the dry southwest Malagasy tree flora considered here (Figure 51), we find it necessary to develop our own definition of dryland trees given that none of the numerous definitions presented previously seems entirely satisfactory for our study areas. We use elements from the definitions offered by Shreve and Wiggins (1951), Bernhardt (2000), Feigl et al. (2001), and Schatz (2000, 2001) to complement the following definition: in the context of drylands, trees are long-lived plants which develop at least one sturdy long-lived trunk, from one to 20 meters or more in height. There may be additional vertical stems, but after cutting, burning, or brows- ing, it may be difficult or impossible to distinguish which stem was initially the main stem.

This definition includes longevity and the presence of a single, primary trunk, whether tall or short, as opposed to the multi-branching life forms found in shrubs. Even in the absence of human impacts, many dryland trees—like some montane and arctic tundra trees—never attain five meters in height. Examples abound in the drylands of Africa and Madagascar, in genera such as Acacia, Adenium, Aloe, Commiphora, Cyphostemma, Euphorbia, and Morinda. Similarly, in many groups of Australian trees, lignotubers and other underground organs have evolved to allow trees to survive drought, fire, and severe grazing (Nicolle 2006).

To underscore the spectrum of life forms and taxonomic groups in which they occur, we use names such as 'monocot tree', 'dwarf tree', 'bottle tree', or 'arboreal cactus' when a dryland tree deviates from standard notions of trees. Dwarf trees, candelabra tree euphorbs, and monocot trees—those without lignified stems—can be recognized as special category of desert trees. In the evolutionary ecology of desert and dryland trees, succulence also merits special attention as it occurs in leaves and young stems, but also in tree trunks (and roots), producing a condition called pachycaul (alias bottle trees). In the dry southwest and other drylands, there are also many other adaptations to drought and unpredictability observed in trees (and other plants) such as ultra-rapid leaf shedding during drought, and thorns or spines.

In preparing the distribution maps presented in this article, we followed Cornel (1974) and Schatz (2000) for bioclimatic regions, and for vegetation cover and protected areas, we followed Moat and Smith (2007), and supplemented their maps by other recent unpublished data. For species distribution, we used the Tropicos® database. Regarding taxonomy, we followed the ongoing Catalogue of Vascular Plants of Madagascar project (http://www.tropicos.org/project/mada) and Angiosperm Phylogeny Group (2016).

DATA SAMPLING AND ANALYSIS. The second lead-author has conducted numerous field trips in southwest Madagascar over the past 28 years. Shorter trips devoted to this study have been undertaken by the first and third authors since 2002. Field observations of the information used to complete the various fields in the database for the trees included were supplemented by consultation of the Catalogue of the Plants of Madagascar database (Madagascar Catalogue (MadCat) 2018), literature searches, and careful review of herbarium specimens of the taxa considered for the MadCat database, in the herbaria at the National Museum of Natural History in Paris, France, and at the National Herbarium at Tizimazaza, Antananarivo, Madagascar, as well as the Royal Botanic Gardens Kew, UK, and Missouri Botanical Garden, USA.

Included in DTSMada are data regarding species distribution, bioclimate, habitat categories and endemcity derived from the Madagascar Catalogue (2018). Additionally, we note endemcity to the semi-arid zone, based on MadCat, and our study of herbarium specimens and field observations. We also note presence or absence of a series of eco-physiological features thought to be of functional and adaptive significance, based on herbarium specimens and our own field observations. These include: the pachycaul (swollen trunk) life form (e.g., Acontochyla), stem succulence (e.g., Dideronaeae), leaf succulence (e.g., Aloe), and the presence of spines or thorns. Further, we note the presence of unusual bark characteristics such as peeling (e.g., most Commiphora), and leaf duration (deciduous, evergreen or semi-deciduous). Data for conservation risk assessments for some taxa have been obtained from the IUCN Red List of Threatened Species (IUCN 2018) and the Red List published by the IUCN Malagasy Plant Specialist Group (2011) (Table 2). Assessments published in 1994 used earlier criteria that are no longer regarded as valid (e.g., examples of criteria 1, 2, 3), with some of the assessments still being provisional, i.e., having not yet been validated by the IUCN Red List authority. Additional adaptive traits recorded in the DTSMada database include sexual system (hermaphroditic, monococious or dioecious), long distance dispersal syndromes (e.g., anemochory, the ability to cope with the worst of the season), where the species is most commonly found, and height range (m) at maturity.

RESULTS AND DISCUSSION. The semi-arid zone harbors 355 documented tree species in 156 genera and 55 families in a total area of approximately 16,200 km². Endemism is also high; a total of 31% (89.9%) of the tree species recorded from this zone are endemic to Madagascar, and 76 species (21.4% of the tree flora) are restricted to the zone, and a further 111 are confined to the dry southwest. Therefore, based on our results, 187 (52.7%) of the 355 tree species identified in our study area are regional endemics. Furthermore, two genera (12%) are strictly endemic to the semi-arid zone (Alluaudiaopsis and Salvadorodopsis), a total of 12 genera (7.7%) are endemic to the dry southwest, and 38 genera (24.4%) of the 156 present are endemic to Madagascar (Table 3). More than half (52.7%) of the tree flora in the broader subarid region as a whole (sensu Cornel 1974) is endemic to that region and more than a fifth is endemic to the semi-arid zone.

In order to illustrate some of the biogeographical patterns and life history traits that occur in the arboreal flora of the semi-
and zone, we now present four case studies of three genera with many endemic species, each in a different, widespread tropical family, and the four Malagasy genera of Didiereaceae.

CASE STUDY 1. The genus Adansonia (Malvaceae): Adansonia comprises eight species, of which six are endemic to Madagascar (Cron et al. 2016). Like Pachypodium, this iconic group shows a clear distribution pattern in various dry areas of sub-Saharan Africa and Madagascar, but with a single species, A. gregorii F. Muell., endemic to the Kimberley ranges in northwestern Australia (Baum 1995, Baum et al. 1998, Leong Pock Tsy et al. 2009). As discussed by Raveloson et al. (2014), Baobabs are comparable to lemurs in their iconic value and the importance of strengthening educational and conservation measures for their protection and integration in far-reaching programs of conservation and sustainable development. To this call to action, we would add a third component, namely ecological restoration.

Adansonia za is widespread throughout the subarid and dry bioclimatic regions of Madagascar. A. granddieri is coastal in distribution and is certainly the best represented species within the subarid zone (Figure 3). The other three Malagasy species, A. suarezensis, A. perrieri, and A. madagascaricensis, are concentrated in the north and northwest, and do not occur in the dry southwest. It seems that A. digitata, the most widespread Baobab having a vast range in Africa, was intentionally introduced to Madagascar from sub-Saharan Africa where it is native, and is cultivated, never wild, in Madagascar, India, and Australia (Baum 1995, Pettigrew et al. 2012). However, in southern Oman and Yemen it appears to have been introduced more than 1000 years ago and now occurs as an escape from cultivation in few localities (Aronsohn et al. 2017).

In Madagascar as in Africa, Adansonia digitata shows polypley and its distribution is linked to villages, both active and abandoned (Leong Pock Tsy et al. 2009). Adansonia species in general tend to be left uncult by people clearing areas for agriculture because their wood is of little use for construction, firewood, or charcoal, and because the trunks are a valuable source of moisture for livestock in periods of prolonged drought when stems can be cut and fed to animals. The tree has many other domestic uses as well, including fiber from the bark used for various purposes. Furthermore, there are strong ritual or spiritual uses and connotations associated with this widespread, iconic group of bottle trees (Leong Pock Tsy et al. 2009). As a result the trees are exposed to human-mediated evolutionary pressures and opportunities that may result in the patterns of hybridization brought to light by Leong Pock Tsy et al. (2013).

CASE STUDY 2. The genus Pachypodium (Apocynaceae): The 25 species of the pachycaul genus Pachypodium, like those of Adansonia, are mostly concentrated in Madagascar. According to Rapaniano and Leeuwenberg (1999), no less than 20 species are endemic to Madagascar while five occur in Angola, Mozambique, South Africa, Swaziland, and Zimbabwe. The genus shows an extraordinary amplitude of life forms and habitats, ranging from nearly prostrate shrubs in granitic hills of central Madagascar to succulent trees 4-6 m tall in the canyons of the Gariep river (P. namaquorum), near the South African border with Namibia. In Madagascar, five species enter the semiarid zone (Figure 4). These include four trees—P. geayi, P. lamerei, P. meridionale, and P. mkea, and also the shrub species, P. cactipes.

Three of the four arboreal species of Pachypodium in Madagascar occur in the semiarid zone yet extend into the subarid region as a whole, while a single species, only recently discovered, is endemic to the coastal areas of the zone between Toliara and Morombe, where it is partially sympatric with the other tree species (Lüthy 2003). The well-known dwarf species P. brevicaule is endemic to quartzite outcrops in central Madagascar and does not occur in the dry southwest. Pachypodium brevicaule and other species are much sought after as ornamentals for the horticultural trade, which has led to over-harvesting and reduction of its range. The natural populations of certain species have also
been modified due to translocation within Madagascar and illegal commerce overseas (Sajeve et al. 2007). All Malagasy species of the genus are listed in CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora)—three in Appendix I, and all others in Appendix II (Sajeve et al. 2007).

CASE STUDY 3. The four Malagasy genera of Didiereaceae: We consider the Didiereaceae, which are similar in appearance to various primitive cacti and are grouped with them in the order Caryophyllales (The Angiosperm Phylogeny Group 2016). In Madagascar, there are 11 species in four genera—Alluaudia, Alluaudiodopsis, Decarya, and Didiera. Until recently, this family was considered to be endemic to Madagascar, however based on molecular studies (The Angiosperm Phylogeny Group 2016), it now also includes 11 African species in three genera formerly placed in Portulacaceae—Ceraria (six species), Calyptrotheca (two species), and Portulacaria (three species). Notably, all these African taxa are mainly shrubs—or rarely small trees—many with broad distributions. In contrast, most of the 11 taxa in Madagascar are unequivocally trees, all endemic to the island and all occur within the semiarid zone, to which five species are endemic. In fact, only two species, Alluaudia humberti and A. dumas, occur beyond the subarid region, having outlying populations in the center-south of the country near the town of Iosy (Figure 5). Among the four Malagasy genera, Alluaudiodopsis appears to be the most ancient (Applequist and Wallace 2000) and, as in Adansonia, various episodes of polyploidization within the genus seem to have occurred.

Like the well-known Spekboom of southern Africa (Portulacaria afra), many Malagasy Didiereaceae can be reproduced from cuttings or, for those species where it is possible, stanchions (i.e., very large cuttings, typically 50–200 cm long). These rooted cuttings can grow quickly and serve as dense living fences (Figure 5). This is true especially for Didiera madagascariensis and Alluaudia procera. Additionally, Alluaudia ascendsens produces relatively sturdy wood that is cut into wide, thin boards used as sheathing to cover exterior walls of houses (Schatz 2000). It is possible that the distribution of some or all of these trees was modified and extended by intentional use and transport by people. Moreover, the thick stems of several species are used for firewood, and young leaves of some species are highly palatable to livestock. Didiera madagascariensis is a fast-growing, pioneer colonizer of sandy habitats that could be of particular value in ecological restoration and rehabilitation.

CASE STUDY 4. Baudouinia (Fabaceae): This is a hardwood tree that once was more abundant. Baudouinia rouxvillei H. Perrier, a small to medium-sized tree, with wood that is highly prized by wood-workers. It is restricted to a small area of the Mahafaly Plateau between the Fiheronana River in the north and the Itambobo corridor southwest of Betoky, where it occurs in low, deciduous woodland and scrubland on limestone 100–300 m above sea level. Historically, it was an offense to cut the wood, as it was reserved for the King; the translation of the local name—Manjakabety—means ‘King’s wood’ or ‘King of the Earth’ (Du Puy 2002). Yet that taboo was insufficient. Already in
ACKNOWLEDGEMENTS

We warmly thank Thibaud Aronson for his valiant help with the manuscript and data base and Raonajany Andriaharanamanjaka Fanomezantsoa for his timely help with figures. We warmly thank all of the remarkable team of Missouri Botanical Garden Madagascar. We are also grateful to the editors, Pete Lowry, and two anonymous reviewers for their lucid comments on previous versions of the manuscript.

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SUPPLEMENTARY MATERIAL
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Figure S1. Spiny forest-thicket in the Dry Southwest region of Madagascar.
Figure S2. Use of Semiand Zone trees by local communities.
Figure S3. Exemplary taxa and morphological adaptations.
Tablo S1. Summary of names used by Comet (1974), Schatz (2000) and the present authors for each biogeographic area.
Tablo S2. Climatic data for the driest stations of the coastal zone of the Dry Southwest region of Madagascar.
Tablo S3. Ecogeographical database for the dry southwest Malagasy tree flora.
Figure S1. Spiny forest-thicket in the Dry Southwest region of Madagascar. A. (Top left) Somewhat degraded community just south of Morombe on coastal white sand with locally dominant “dwarf” Adansonia grandidieri that nevertheless tower above spiny succulent Didiera madagascariensis and succulent Euphorbia trees. B. (Right). The Ranobe Forest north of Toliara, dominated by deciduous trees and shrubs, including a large individual of Commiphora mafaidoha with conspicuously flaking bark, and also succulent Euphorbia trees and shrubs. C. (Bottom left) Spiny thicket near Itampolo on coastal yellow sands with the locally endemic and abundant spiny succulent Alluaudia montagnacii, which is growing here with various species of deciduous trees and shrubs, including the locally endemic Lemuropism edule, and various species of Grewia.

Figure S2. Use of Semiarid Zone trees by local communities. A. (Left) Branches of Didierea madagascariensis cut and planted to form a living fence to enclose livestock and to deter unwanted visitors in a Vezo village North of Toliara. Different species of Didiereaceae are used throughout the region according to availability. B. (Right) Artisanal charcoal production taking place within a clearing in the Ranobe Forest north of Toliara to meet the needs of villagers and townsfolk alike. Trees with the most sought-after wood are selectively felled, until the resource is exhausted. Then the production operation moves to another site. This is a prime example of artificial negative selection (see text).
Figure S3. Exemplary taxa and morphological adaptations. A. (Left) *Aloe vaotsanda* in the extreme south-west near Itampolo is one of five tree-like species of this genus occurring in the Semiarid Zone. Here, this rare species grows in a degraded community with the common *Euphorbia stenoclada*. Both species are locally dominant over the smaller deciduous trees and shrubs, and are characterised by succulent leaves in the case of the *Aloe*, and succulent branches in the case of the *Euphorbia*. B. (Right) *Pachypodium geayi* towers above smaller trees and shrubs in the Beza Mahafaly Reserve, and is an example of a "bottle" tree; its trunk armed with sharp clustered spines.
Table S1. Summary of names used by Cornet (1974), Schatz (2000) and the present authors for each biogeographic area.

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Table S2. Climatic data for the driest stations of the coastal zone of the Dry Southwest region of Madagascar (Oldeman 1990). (Meteorological stations are listed from north-west to south-east (see also Figure 1). Latitude and longitude coordinates correspond to the weather stations mentioned in Column 1)

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<th>Average number of rainy days per year</th>
<th>Mean annual temperature (°C)</th>
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Other stations in the Dry Southwest

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Table S3. Summary of the data available for the 355 known species of trees of the semi-arid zone of Southwest Madagascar. (data for selected morphological traits are also shown indicating correlation of each to degrees of endemism; *IUCN Redlist threat categories are also given, where appropriate: CR = Critically Endangered, EN = Endangered, VU = Vulnerable, NT = Near Threatened, LC = Least Concern, empty cells for taxa which have not been evaluated; ** cf. references; *** data include two levels of endemism: BC14 endemic = endemic to the dry southwest as a whole, sub-arid endemic = endemic to the semi-arid zone)

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## Supplementary Material

### Table 1: Dryland tree data for the southwest region of Madagascar: alpha-level data can support policy decisions for conserving and restoring ecosystems of arid and semiarid regions.

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MPSG = IUCN Madagascar Plant Specialist Group

