

Conservation of Phylogenetic Diversity in Madagascar's Largest Endemic Plant Family, Sarcolaenaceae

Anaëlle Soulebeau, Roseli Pellens, Porter P. Lowry II, Xavier Aubriot, Margaret E.K. Evans, and Thomas Haevermans

Abstract Madagascar is renowned for its impressive species richness and high level of endemism, which led to the island being recognized as one of the world's most important biodiversity hotspots. As in many other regions, Madagascar's biodiversity is highly threatened by unsustainable anthropogenic disturbance, leading to widespread habitat loss and degradation. Although the country has significantly expanded its network of protected areas (PAs), current protocols for identifying priority areas are based on traditional measures that could fail to ensure maximal

A. Soulebeau (✉) • T. Haevermans

Institut de Systématique, Evolution, Biodiversité, ISYEB – UMR 7205 CNRS MNHN
UPMC EPHE, Muséum National d'Histoire Naturelle, Sorbonne Universités,
57 rue Cuvier, CP 50, 75005 Paris, France
e-mail: asoulebeau@mnhn.fr; haever@mnhn.fr

R. Pellens

Institut de Systématique, Evolution, Biodiversité, ISYEB – UMR 7205 CNRS MNHN
UPMC EPHE, Muséum National d'Histoire Naturelle, Sorbonne Universités,
45 rue Buffon, CP 50, 75005 Paris, France
e-mail: pellens@mnhn.fr

P.P. Lowry II

Institut de Systématique, Evolution, Biodiversité, ISYEB – UMR 7205 CNRS MNHN
UPMC EPHE, Muséum National d'Histoire Naturelle, Sorbonne Universités,
57 rue Cuvier, CP 50, 75005 Paris, France

Missouri Botanical Garden, PO Box 299, St. Louis, MO 63166-0299, USA
e-mail: pete.lowry@mobot.org

X. Aubriot

Institut de Systématique, Evolution, Biodiversité, ISYEB – UMR 7205 CNRS MNHN
UPMC EPHE, Muséum National d'Histoire Naturelle, Sorbonne Universités,
57 rue Cuvier, CP 50, 75005 Paris, France

Department of Life Sciences, Natural History Museum,
Cromwell Road, London SW7 5BD, UK
e-mail: x.aubriot@gmail.com

© The Author(s) 2016

R. Pellens, P. Grandcolas (eds.), *Biodiversity Conservation and Phylogenetic Systematics*, Topics in Biodiversity and Conservation 14,
DOI 10.1007/978-3-319-22461-9_18

355

inclusion of the country's biodiversity. In this study, we use Madagascar's largest endemic plant family, Sarcolaenaceae, as a model to identify areas with high diversity and to explore the potential conservation importance of these areas. Using phylogenetic information and species distribution data, we employ three metrics to study geographic patterns of diversity: species richness, Phylogenetic Diversity (PD) and Mean Phylogenetic Diversity (MPD). The distributions of species richness and PD show considerable spatial congruence, with the highest values found in a narrow localized region in the central-northern portion of the eastern humid forest. MPD is comparatively uniform spatially, suggesting that the balanced nature of the phylogenetic tree plays a role in the observed congruence between PD and species richness. The current network of PAs includes a large part of the family's biodiversity, and three PAs (Ankeniheny Zahamena Forest Corridor, the Bongolava Forest Corridor and the Itremo Massif) together contain almost 85 % of the PD. Our results suggest that PD could be a valuable source of complementary information for determining the contribution of Madagascar's existing network of PAs toward protecting the country's biodiversity and for identifying priority areas for the establishment of new parks and reserves.

Keywords Protected areas • Extinction • Endemism • Biodiversity • Species richness

Introduction

Among the areas identified by biologists and conservationists as biodiversity hotspots (Myers et al. 2000; Myers 2003), Madagascar is one of the most important because of its exceptionally high levels of species diversity and endemism, along with an unprecedented rate of habitat loss due to anthropogenic activities, leading to species extinction (Goodman and Benstead 2005; Callmänder et al. 2011; Buerki et al. 2013). Less than 10 % of the original natural habitats present on the island before human colonization are still intact (Myers et al. 2000). Although the conservation of Madagascar's biodiversity is a high priority, the dearth of reliable information for identifying priority sites in need of protection complicates the establishment of a robust national conservation program and policy.

M.E.K. Evans

Institut de Systématique, Evolution, Biodiversité, ISYEB – UMR 7205 CNRS MNHN
UPMC EPHE, Muséum National d'Histoire Naturelle, Sorbonne Universités,
57 rue Cuvier, CP 50, 75005 Paris, France

Laboratory of Tree Ring Research, University of Arizona,
Bryant Bannister Building, 1215 East Lowell St, Tucson, AZ 85721, USA
e-mail: mekevans@email.arizona.edu

In Madagascar, as in many other regions of the world, species richness and the number of endemic species are the parameters most frequently used to define priorities for biodiversity conservation (Callmander et al. 2007; Kremen et al. 2008). However, as illustrated throughout this book, phylogenetic diversity is another important element that should be taken into consideration, for two main reasons. First, phylogenetic diversity takes into account not only the number of species or endemics in an area but also the evolutionary distinctiveness of those species, such that a site with a legume, an orchid and a fern would be considered to have higher phylogenetic diversity than another site with three species belonging to just one of these groups (Vane-Wright et al. 1991; Faith 1992). Second, measures of phylogenetic diversity are useful in conservation decision-making because extinctions are not random – in many groups where one species is vulnerable, several other related species will tend to be as well. The use of phylogenetic diversity as a criterion in conservation planning thus reduces the risk of losing entire groups or lineages (see Yessoufou and Davies, chapter “[Reconsidering the Loss of Evolutionary History: How Does Non-random Extinction Prune the Tree-of-Life?](#)”).

We might then ask to what extent does Madagascar's system of protected areas help protect key features of the biodiversity within a clade, including not only the number of species, but also phylogenetic and ecological diversity. Patterns in biodiversity distribution can vary considerably from one lineage to another, as shown by two recently published studies on the conservation of biodiversity in Madagascar. While Isambert et al. (2011) showed a striking difference in the spatial distribution of the number of endemic species and phylogenetic diversity of adepghan water beetles, Buerki et al. (2015) revealed a strong congruence between species richness and phylogenetic diversity in the plant family Fabaceae.

Here we use Sarcolaenaceae, the largest plant family endemic to Madagascar, as a case study to identify areas of high phylogenetic diversity and to assess whether the current network of protected areas provides adequate conservation of that diversity.

Madagascar

Madagascar, located in the Indian Ocean off the coast of southeastern Africa, is well known for its rich and highly endemic flora and fauna (Myers et al. 2000; Myers 2003; Goodman and Benstead 2005). This large continental island separated from mainland Africa ca. 165 Million Years Before Present (MYBP) as part of a block that also included Antarctica and India, subsequently becoming detached from the latter two by 80 MYBP (Schettino and Scotese 2005; Jöns et al. 2009). The resulting long isolation has played a key role in the development and maintenance of Madagascar's striking biota, which exhibits affinities with neighboring Africa, but is also home to groups thought to have reached Madagascar by long-distance dispersal, with their closest relatives occurring in more distant areas such as India, Sri Lanka, Southeast Asia, Australia, New Caledonia and America (Leroy 1978; Schatz

1995; Yoder and Nowak 2006; Warren et al. 2010; Gautier et al. 2012; Buerki et al. 2013; Torsvik et al. 2013).

The evolution of Madagascar's biota has also been driven by the tremendous diversity of environments found on the island, which is underscored by the fact that it has one of the world's highest rates of vertebrate beta-diversity (Holt et al. 2013). The landscape is characterized by a mountainous interior that extends the entire north-south length of the island (ca. 1600 km) resulting in an often sharp altitudinal gradient from the coasts to well over 1000 m in large areas, with many massifs reaching above 1500 m and several dozen peaks surpassing 2000 m, the highest being Maromokotro in the Tsaratanana massif (2876 m). The climate is characterized by a strong precipitation gradient from perennially humid areas on the mountain slopes in the northeastern part of the island, where rainfall may exceed 6000 mm in some years (Thorstrom et al. 1997 in Rakotoarisoa and Be 2004), to a subarid zone in the southwest, which receives less than 300 mm of rain per year and can go without precipitation for 10 months or more (Cornet 1974; Goodman and Benstead 2003). Madagascar's ecosystems in turn reflect the island's relief and climate, ranging from perhumid tropical and montane forests in the east to subhumid and dry formations in the center and west, and subarid ecosystems in the southwest, often with fairly sharp, well delimited boundaries between them. Compounding the spatial arrangement of these biomes is the fact that they are thought to be of different ages. For instance, the spiny subarid vegetation of the southwest is regarded as comparatively old (Paleogene, 23–66 MYBP) while the Sambirano humid forest is likely the youngest biome (Late Miocene, 8 MYBP), originating with the advent of a Monsoon regime in Asia following the uplift of the Himalayas (Wells 2003).

As mentioned above, two particularly striking features of the Malagasy flora are its remarkable species richness and its high level of endemism. A recent assessment indicated that some 11,220 described native vascular plant species are currently recognized, belonging to 1730 genera and 243 families, and that 82 % of these species are endemic (Callmander et al. 2011). Moreover, based on recent taxonomic revisions in a wide range of families (Madagascar Catalogue 2015), an additional ca. 2200 species have been described in the last few years or are awaiting description, nearly all of which will be found to be endemic, along with an estimated 600 more species still to be discovered, thus increasing the total number of native species to ca. 14,000 and the level of endemism to well over 85 % (P. Phillipson personal communication). Equally striking is the level of lineage diversification in Madagascar's flora. The 30 most species-rich families include almost 70 % of the total vascular plant flora as well as 30 % of the genera present on the island, and 38 families include 10 or more genera (Gautier et al. 2012). Moreover, more than 320 genera (19 %) and a total of 5 families are endemic to the island (Callmander et al. 2011; Buerki et al. 2013), Sarcolaenaceae being the largest of these endemic families.

Understanding the origin and diversification of lineages in Madagascar requires consideration of the interplay among the complex eco-geography and geological history of the island, the varying dispersal abilities of the members of the lineages present there, and Madagascar's proximity to potential source areas, in particular the African continent but also Asia and areas beyond. Many studies have been pub-

lished on the evolutionary and ecological processes that have shaped diversity in Madagascar's fauna, but very little attention has been given to its flora. One of the most notable features, still to be explored, is the spatial distribution of plant species richness on the island and the drivers underlying this distribution. Some have suggested that abiotic factors have played an important role, e.g. bio-climate, substrate type, elevation or paleo-precipitation (Yoder and Nowak 2006; Pearson and Raxworthy 2009; Agnarsson and Kuntner 2012; Buerki et al. 2013; Mercier and Wilmé 2013; Rakotoarinivo et al. 2013). Others have explored the role of potential key innovations in species diversification and niche expansion (Vary et al. 2011; Evans et al. 2014; Moore and Robertson 2014).

Biodiversity Conservation in Madagascar

As mentioned earlier, Madagascar is recognized as one of world's 'hottest' biodiversity hotspots (Myers et al. 2000; Myers 2003; Goodman and Benstead 2005) because its large, diverse and highly endemic biota is severely threatened by unsustainable practices such as shifting agriculture, uncontrolled burning and extensive charcoal production, all of which place intense pressure on the island's remaining natural areas. Over the last three decades a major effort has been made to expand and strengthen the system of protected areas, which now includes ca. 5.7–5.9 million hectares of terrestrial parks and reserves, many of which were established during the last 15 years (Kremen et al. 2008, <http://atlas.rebioma.net>). Despite these efforts, however, deforestation and habitat degradation have continued at an alarming rate as the human population has doubled in the last 25 years, reaching an estimated 22.4 million by mid-2014 (Population Reference Bureau 2015). More than three-quarters of the population lives below the poverty level (World Bank 2015) and almost all Malagasy are directly or indirectly dependent on the island's natural resources as a major source of food, shelter, fuel, and traditional medicine. Studies of Madagascar's forest cover using aerial photographs and Landsat images have estimated a decline in area of 40 % since the 1950s, with a rate of forest loss of 0.9 % per year between 1990 and 2000 (Harper et al. 2007). Organized, large-scale illegal exploitation of precious hardwoods and endangered plant and animal species increased dramatically during the last political crisis (roughly 2009–2014), adding to an already alarming situation (Schuurman and Lowry II 2009; Waeber 2009; Caramel 2015). Furthermore, because a high proportion of Madagascar's species have restricted geographic ranges, they are particularly vulnerable to changes in forest cover. For instance, in a study of 2243 species in 12 different taxonomic groups (including both plants and invertebrates), Allnutt et al. (2008) estimated that 9.2 % of them were driven to extinction between 1950 and 2000 due to forest loss, in addition to the 32.9 % thought to have gone extinct prior to 1950.

Beyond these alarming conclusions, it remains to be seen to what extent the present system of protected areas can effectively preserve what remains of Madagascar's unique biodiversity. Does the system include the full array of species, and do they have populations large enough to be viable over time?

Sarcoalaenaceae as a Model Group

Sarcoalaenaceae are ideally suited for such a study of phylogenetic diversity because (1) the taxonomy and distribution of its members are particularly well understood and documented, (2) its genera vary in size and its species have a wide range of eco-geographic preferences, and (3) a well-resolved phylogeny is available based on a large, representative sample of species that includes members of all ten genera (Haevermans et al. [in prep](#)).

Sarcoalaenaceae comprise 71 species of shrubs and trees belonging to 10 genera (Madagascar Catalogue [2015](#)), each of which has been the subject of a recent taxonomic revision (Hong-Wa [2009](#); Lowry II et al. [1999](#), [2000](#), [2002](#); Randrianasolo and Miller [1994](#), [1999](#); Schatz et al. [2000](#), [2001](#)), followed by the description of several newly discovered species (Lowry II and Rabehevitra [2006](#); Rabehevitra and Lowry II [2009](#); Lowry II et al. [2014](#)). Members of the family are found almost throughout the island, with the notable exception of the subarid southwest, and the distribution of each species has been carefully mapped using the locality information associated with herbarium collections (Ramananjanahary et al. [2010](#); Madagascar Catalogue [2015](#)). Based on the collections in the herbaria of Paris Museum and the Missouri Botanical Garden, we estimate that more than 2000 specimens are available for the family, with an average of 30 geographic occurrences per species and a total number of collections ranging from more than 300 for common, widespread species such as *Leptolaena pauciflora* Baker to just one or a few for species known from a single locality such as *Leptolaena masoalensis* G.E. Schatz & Lowry II, *Schizolaena capuronii* Lowry II et al. and *Schizolaena raymondii* Lowry II and Rabehevitra. The genera of Sarcoalaenaceae vary considerably in size, from *Schizolaena* with 22 species, *Sarcoalaena* with 8 described species (as well as 6 that remain to be described), to *Mediusella* and *Eremolaena*, which include just 2 and 3 species respectively (Madagascar Catalogue [2015](#)). A little more than half of the species in the family have a restricted geographic distribution, known from fewer than ten localities, and several genera are largely or entirely restricted to a particular climatic region, such as *Eremolaena*, *Leptolaena* *Rhodolaena* and *Schizolaena* which are found primarily or exclusively in humid areas, and *Mediusella* and *Xerochlamys*, which occur only in drier habitats.

The goal of this chapter is to identify areas with the highest levels of phylogenetic diversity of Sarcoalaenaceae and to evaluate the degree to which that diversity is captured in existing protected areas. Toward that end, we first show how members of the ten genera are distributed and analyze the geographic distribution of three important diversity measures: species richness, Phylogenetic Diversity (PD) and Mean Phylogenetic Diversity (MPD). We then compare the distribution of these diversity statistics to Madagascar's system of protected areas and point out areas of greatest importance for conservation of phylogenetic diversity in Sarcoalaenaceae.

Material and Methods

Phylogenetic Data

To estimate phylogenetic diversity we used the plastid and nuclear phylogeny of Sarcolaenaceae produced by Haevermans et al. ([in prep](#)). The taxon sampling includes 47 species belonging to the family, for a total of 91 Operational Taxonomic Units (OTUs). All ten genera were represented and 66 % of the species were sampled, thereby capturing most of the taxonomic and morphological/ecological diversity and covering the full geographic distribution of Sarcolaenaceae.

In addition to the 47 Sarcolaenaceae sampled, 6 species were selected from their sister group, Dipterocarpaceae, and 1 species from the next most-closely related family, Cistaceae (Dayanandan et al. 1999; Ducouso et al. 2004; Haevermans et al. [in prep](#)), all of which served as outgroup taxa. Sequence data were obtained from one nuclear (ITS) and three plastid (*rbcL*, *psbA-trnH*, and *psaA-ORF170*) markers (Haevermans et al. [in prep](#)). We performed a Bayesian dating analysis using BEAST v1.7.2 (Drummond et al. 2012) under the uncorrelated lognormal relaxed clock model with a Yule prior on speciation. Data were partitioned according to the number of DNA regions and we applied to each partition the GTR+ I+G substitution model, for reasons outlined by Huelsenbeck and Rannala (2004). An individual MCMC run was conducted for 20×10^6 generations, with sampling every 1,000 iterations, thus generating 20,000 chronograms. We discarded the first 25 % of samples as burn-in. Mixing of the chains and their convergence were verified in Tracer 1.4 (Rambaut and Drummond 2007). Using Logcombiner, we merged the remaining 15,000 trees and produced a maximum clade credibility (MCC) chronogram using TreeAnnotator. We applied two temporal constraints to calibrate the tree, one at the split between Dipterocarpaceae and Sarcolaenaceae based on Wikström et al. (2001), and another for the age of the stem-group of the clade comprising *Leptolaena*, *Mediusella*, *Sarcolaena*, *Xerochlamys* and *Xyloolaena* based on the estimated age of a fossil pollen attributable to this group (Coetzee and Muller 1984).

In order to assess the cladogenesis process in Sarcolaenaceae, we measured the degree of imbalance of the Sarcolaenaceae consensus tree topology using the R package *apTreeshape* (Bortolussi et al. 2006), in conjunction with the R package *ape* (Paradis et al. 2004). The imbalance was estimated by calculating the Colless's index (Mooers and Heard 1997). We compared this experimental value against those obtained for 500 simulated trees built under the Equal Rate Markov (ERM) Yule model or the PDA (Proportional to Distinguishable Arrangement) model in which each tree is equally probable (Mooers and Heard 1997), using the function *colless.test()* implemented in R package *apTreeshape* (Bortolussi et al. 2006). We used the “less” and “greater” alternatives to test whether the tree is less unbalanced or more unbalanced than predicted by the null model.

Measures and Analysis

We estimated the area of each species' geographic distribution by creating a minimum convex polygon based on 2148 occurrence points, 1899 of them corresponding to species included in the phylogeny (using ArcMap version 10.2). Occurrences of species with less than three points (for which polygons cannot be generated) were directly assigned to ¼ degree grid cells (each covering 30×30 min) overlaid on a map of Madagascar. Then, a global polygon for the entire family was produced by overlaying all the species polygons, with limits calculated to exclude the sea. Species richness (the number of recorded species) was then calculated in each grid cell, along with two measures of phylogenetic diversity, Faith's PD (Faith 1992) and Mean Phylogenetic Diversity (MPD). PD is a group measure of phylogenetic diversity given by the minimum spanning path along the tree linking all species occurring in a grid cell (see Faith chapter "The PD Phylogenetic Diversity Framework: Linking Evolutionary History to Feature Diversity for Biodiversity Conservation"). For cells with only one species, the PD value corresponds to the branch length from the tip to the root of the tree. MPD is the mean distance (i.e., mean branch length) between all pairs of species occurring in a given grid cell; this measure provides information on phylogenetic relatedness of the set of species occurring in that cell, controlling for species richness. These two measures were computed using the R package *picante* (Kembel et al. 2010). The distributions of the three measures (species richness, PD and MPD) were then overlaid on the polygon of Sarcolaenaceae occurrence and plotted on a map of Madagascar, which results in parts of the island not being represented in the overall polygon. The resulting maps were compared to the most recent map of protected areas (PA) in Madagascar (<http://atlas.rebioma.net/>). This enabled us to identify whether the cells containing the highest level of PD correspond to those occupied by PAs, and to determine which, if any, cells with high values of PD are located out of the current coverage of Madagascar's PA network.

Results

Sarcolaenaceae species occur in a wide range of forest ecosystems in Madagascar, from remnant littoral forests scattered along the entire east coast to montane forests on the highest massifs and woodlands in the center, and from the north to the south of the island. By contrast, very few occurrences have been recorded in deciduous seasonally dry forest of the west and none at all from deciduous dry forests and scrubland in the south and southwest (Fig. 1a). By plotting the points for each of the ten genera (Fig. 1b), it can be seen that eastern littoral forest and low- and mid-altitude evergreen humid forests have the greatest diversity, with species in several genera.

The Colless's index obtained when estimating the balance of the Sarcolaenaceae phylogenetic tree is 93, with non-significant p-values for all tests, except when using a PDA model under the "less" alternative (p-value <0.05). These results sug-

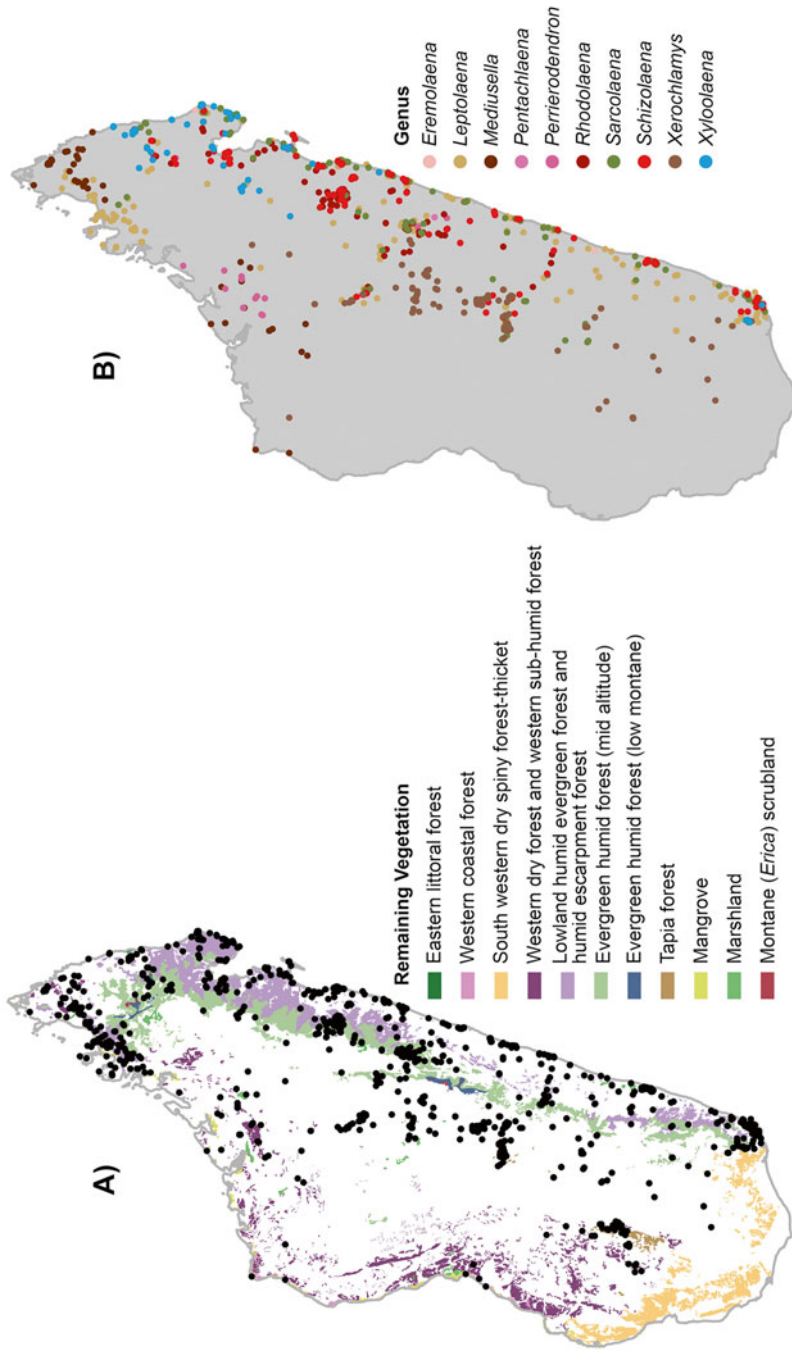


Fig. 1 Points of occurrence of Sarcolaenaceae in Madagascar. (a) Points of occurrence of 69 species of Sarcolaenaceae in the remaining vegetation of Madagascar. The vegetation map layer is adapted from the vegetation map of Faramelala (1988, 1995), available on ArcGis 10.2. (b) Points of occurrence of 47 species used in this phylogenetic analysis according to the genera they belong. Colors of the same hue indicate close related genera

gest that the Sarcolaenaceae consensus tree is significantly more balanced than one built under a PDA model. The evolutionary history of Sarcolaenaceae thus seems to be characterized by processes that have operated evenly among clades.

Species richness and Phylogenetic Diversity (PD) vary markedly, from high in eastern Madagascar to low in the west, and to a lesser degree along a north-south gradient (Fig. 2a, b). These two variables show a high degree of spatial congruence (Fig. 2a, b). The areas with the highest values of both species richness and PD are concentrated in the central-northern portion of the eastern escarpment, in regions with both low- and mid-altitude evergreen humid forest. By contrast, Mean Phylogenetic Diversity (MPD) varies much less than species richness and PD (Fig. 2c) and a comparison among the distributions of all three variables does not suggest that cells with higher PD values harbor sets of species that are more distantly related to one another than those found in cells with lower values of PD. The cells with the highest values of MPD, mostly located in the northwestern and northeastern parts of the island (Fig. 2c), have comparatively low values of PD, indicating the occurrence of a limited number of species that are evolutionarily distinct.

Forty-five percent of the cells occupied by Sarcolaenaceae contain at least part of a protected area (Fig. 3a) and the system of PAs is comparatively better represented in cells with higher values of species richness (Fig. 3b) and PD (Fig. 3c). By contrast, most of the cells lacking any PA correspond to those with the lowest values of species richness and PD. All lineages of Sarcolaenaceae and 97.6 % of the total PD are thus found in cells that contain PAs.

Figure 4 shows the PD values for each protected area (Fig. 4a), indicating that areas with the highest PD values in Sarcolaenaceae are concentrated in grid cells in the central-northern portion of the eastern escarpment, centered in the sites comprising the Ankeniheny Zahamena Forest Corridor (Fig. 4b) which contain 64 % of the Sarcolaenaceae's PD. These cells include eight out of ten lineages and all lineages deeply branched. Two lineages are not represented in the Ankeniheny Zahamena Forest Corridor: The genus *Xerochlamys*, which is found from the central region to the south, and the genus *Mediusella* which occurs in the extreme north and in the northeast (see Fig. 1b). Some other PAs exhibit a high level of heterogeneity in PD with parts that show high PD and others that display low PD values. It is the case for Midongy du Sud (Southeast Madagascar), Masoala (perhumid forest in Northeast Madagascar) and the Itremo massif (Central Highlands) (Fig. 4c–e). Interestingly, a few PAs are located in cells with low species richness and PD, but with high value of MPD, in particular Behara-Tranomaro in the southeast (Fig. 4f) and the Bongolava Forest Corridor in the northwest (Fig. 4g).

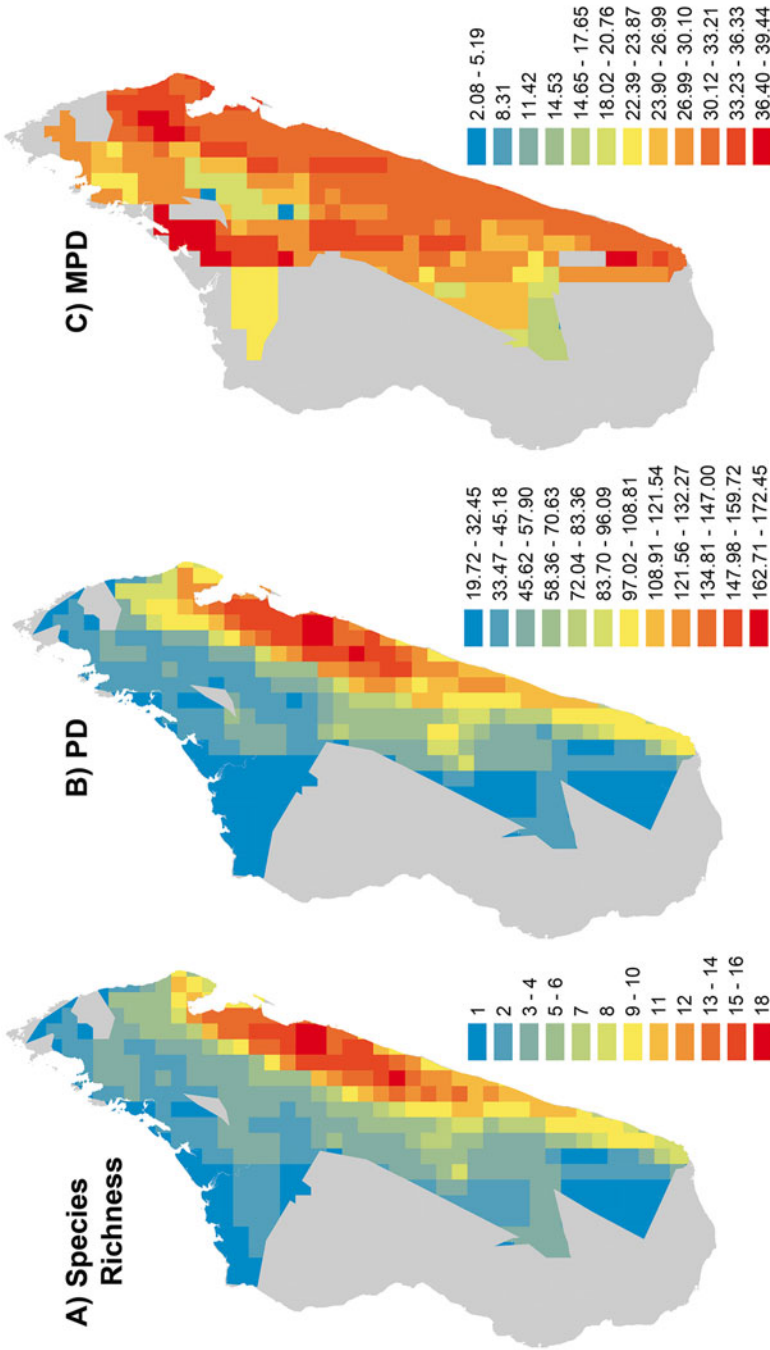


Fig. 2 (a) Distribution of the species richness of Sarcolaenaceae in Madagascar; (b) patterns of distribution of the phylogenetic diversity (Faith's PD), and (c) Mean Phylogenetic Distance (MPD)

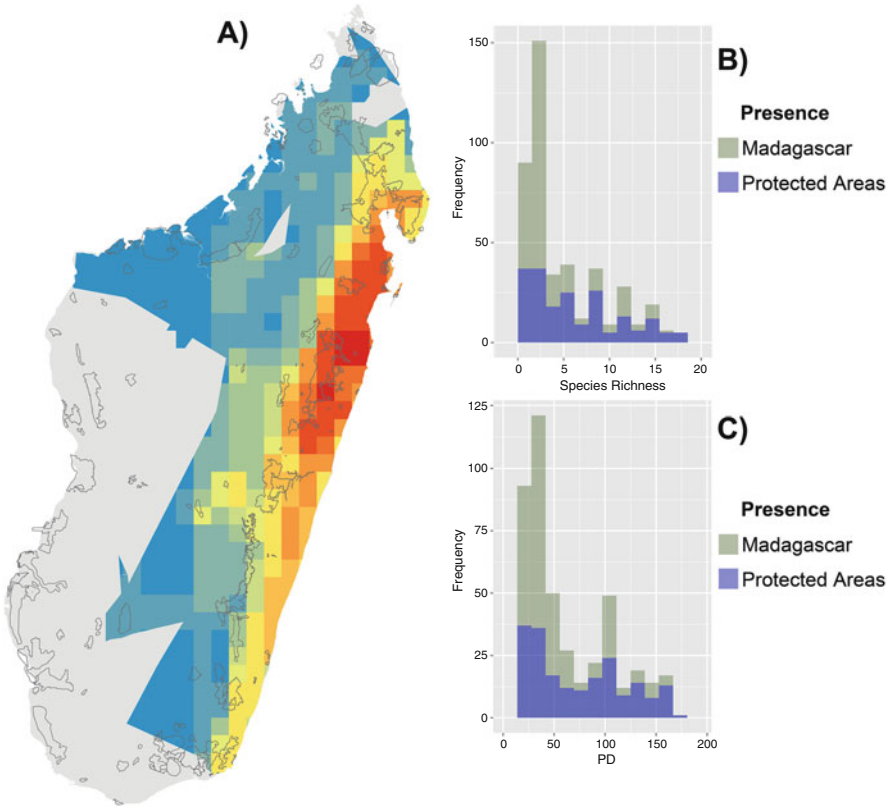


Fig. 3 (a) PD of Sarcolaenaceae in the network of protected areas in Madagascar; (b) Frequency of species richness and PD (c) all over Madagascar, and in the cells including protected areas

Discussion

Sarcolaenaceae as a Model Group for Conservation in Madagascar

As mentioned above, Madagascar's biodiversity is among the most distinctive and highly endemic in the world, and the multiple threats it faces result in it being among the most threatened as well. There is thus a strong need to evaluate the effectiveness of conservation efforts, in particular the existing network of protected areas in Madagascar, with respect to their ability to ensure the survival of biodiversity, as measured not only by species richness but also in terms of phylogenetic diversity. In particular, PD is assumed to serve as a valuable tool for developing conservation policies, but to date very few studies have explored it for Madagascar (Sechrest et al. 2002; Magnuson-Ford et al. 2010; Isambert et al. 2011), only one of which

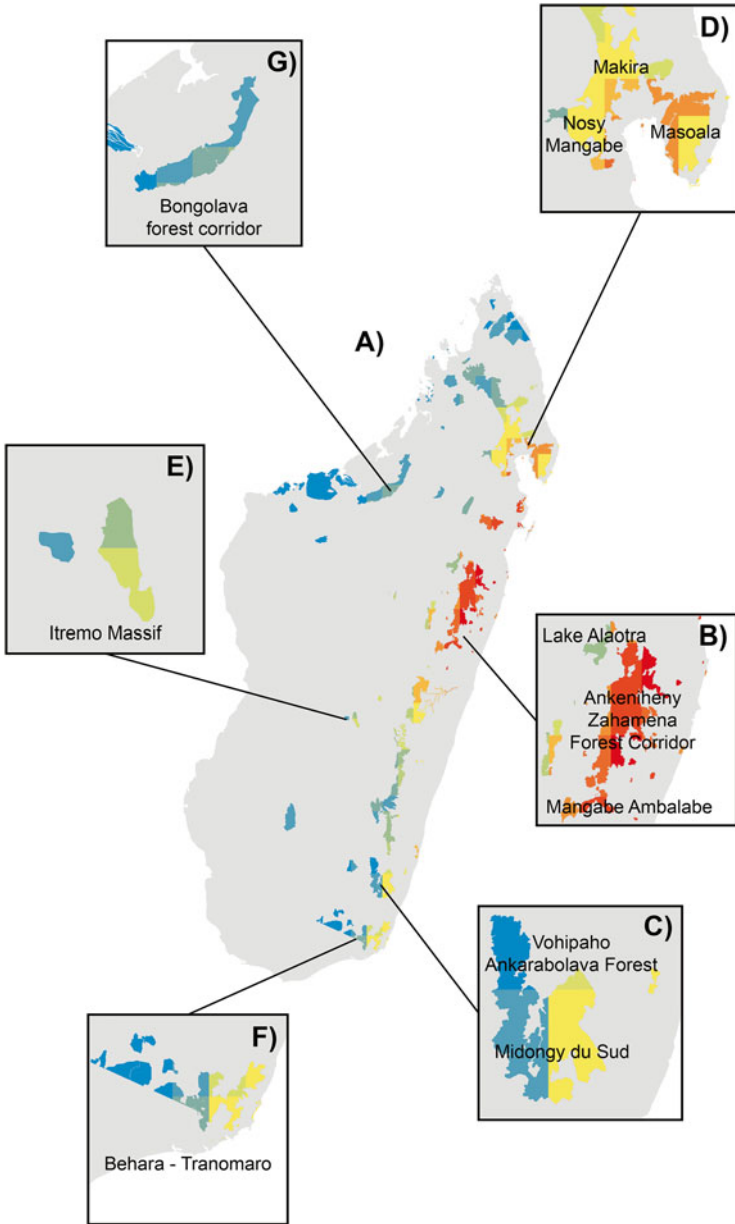


Fig. 4 (a) PD of Sarcolaenaceae in the Malagasy system of protected areas; (b) Ankeniheny Zahamena Forest Corridor; (c) Midongy du Sud; (d) Mangabe/Masoala; (e) Itremo massif; (f) Behara-Tranomaro; (g) Bongolava Forest Corridor

involving plants (Buerki et al. 2015). In that respect, we focused on Sarcolaenaceae in order to help provide a better understanding of the potential value of PD for conserving Madagascar's biodiversity.

A robust analysis of PD requires a dated phylogeny based on dense taxon sampling, as well as reliable data on the distribution of each species. For Sarcolaenaceae, our sampling comprised nearly 70 % of the total species diversity, with good representation from each of the ten genera in the family. We used the most up-to-date and reliable distributional information, based on more than 2000 occurrence points from the collections kept in the herbaria of the Paris Museum and of the Missouri Botanical Garden examined for recent taxonomic revisions and data from the ca. 40–50 new collections made each year since. The result presented in Fig. 2 provides the first insights into the distribution of species richness and PD for Madagascar's largest endemic plant family, showing that both measures of diversity are highest in areas with humid forest and lowest in dry forests and subarid thickets.

Measures of Biodiversity and Madagascar's Network of Protected Areas

Our results show a high level of congruence between the distribution of species richness (Fig. 2a) and PD (Fig. 2b). Although not a rule, congruence between species richness and PD is often observed (see for example, Arponen and Zupan, chapter “[Representing Hotspots of Evolutionary History in Systematic Conservation Planning for European Mammals](#)” and Chazot et al. chapter “[Patterns of Species, Phylogenetic and Mimicry Diversity of Clearwing Butterflies in the Neotropics](#)”). This is primarily due to the fact that they both increase as more species are included (see Nipperess, chapter “[The Rarefaction of Phylogenetic Diversity: Formulation, Extension and Application](#)”). But tree shape and the structure of geographic distributions also contribute to variation in congruence between these two statistics. The more balanced a tree is, the more similar each species' contribution will be to overall PD. Likewise, the more species from different parts of the tree co-occur, the higher the congruence between species richness and PD (Rodrigues et al. 2005).

Sarcolaenaceae present a case where both of these factors are at play. The phylogenetic tree is balanced, as shown by Colless's index, yielding little variation among species in PD values. Moreover, the areas with the highest level of species richness contain species belonging to several genera (Fig. 1b) rather than many species in a single genus, as would be expected if overall diversity were the result of radiation of a single lineage within a given eco-geographic zone. Sarcolaenaceae thus present a situation very different from that observed in Malagasy adaphagan water beetles by Isambert et al. (2011) but highly similar to that observed in Fabaceae by Buerki et al. (2015), where the distributions of PD and species richness are highly congruent.

In contrast, MPD is independent of species richness, and high values of MPD indicate the presence of distantly-related species co-occurring in a particular area. The balanced nature of the phylogenetic tree partly explains the low variation in Mean Phylogenetic Diversity (MPD) across Madagascar (Fig. 2c). This measure provides additional insight into the distribution of phylogenetic diversity, being of particular interest in those areas with low species richness and low values of PD. In this case, high values of MPD could indicate areas in which ecological convergence has occurred in separate lineages of Sarcolaenaceae. We note, however, the absence of areas that concurrently exhibit low species diversity and high values of PD, although some areas do have low species diversity and low PD but high MPD.

The most important areas for conserving PD in Sarcolaenaceae are concentrated in the central-northern portion of Madagascar's Eastern region, including and adjacent to the eastern edge of the Ankeniheny Zahamena Forest Corridor (Figs. 3 and 4b). However, as this area does not include any representatives of *Xerochlamys* and *Mediusella*, and because the distributions of these two genera do not overlap, the ideal strategy for protecting all lineages of Sarcolaenaceae and to maximize conservation of PD for this family, would be to include two additional protected areas: the Bongolava Forest Corridor in the northwest (Fig. 4g) and the Itremo Massif (Fig. 4e). Taken together, these three regions contain 84.9 % of the PD of Sarcolaenaceae. It is also of critical importance to consider preserving sites with high MPD values because (1) they harbor distantly related species that do not share the same evolutionary history, (2) might be impacted by different threats, and (3) require different conservation procedures. Buerki and colleagues (2015) recently suggested that the current distribution of MPD in endemic Malagasy legumes could be explained by a range of factors, such as the role of watersheds and dispersal corridors during past climatic changes, as well as by the evolutionary history of the group's most important dispersers, viz. extant and extinct lemurs. They conclude by advocating that a sound conservation plan should incorporate, in addition to the traditional biodiversity measures (species richness, PD and MPD), a detailed investigation of the biotic and abiotic factor that play (or have played) a role in the dynamics of each ecosystem.

The trends observed in the PD of Sarcolaenaceae differ significantly from those observed in Malagasy legumes by Buerki et al. (2015), where high values of species richness and PD are found in the subhumid highlands and lower values in humid eastern forests. However, the Bongolava Forest Corridor (Fig. 4g) and Midongy du Sud (Fig. 4c) are two sites where MPD values are high for Sarcolaenaceae that were regarded by Wilmé et al. (2006) and Buerki et al. (2015) as low- and high-elevation watersheds, respectively, and considered by them to represent potential refugia during the Quaternary climatic shifts. The list of important areas for conserving Sarcolaenaceae would thus also include the Bongolava Forest Corridor, Midongy du Sud, along with Makira and Masoala in the northeast and the eco-geographically diverse Behara-Tranomaro-Andohahela-Tsotongambarika area in the southeast, which spans a sharp ecotone from humid forest in the east to subarid tundra in the west (Fig. 4).

The recent expansion of Madagascar's network of protected areas has strengthened conservation in several areas that exhibit high levels of PD for Sarcolaenaceae, such as Makira, Pointe à Larrée, the Ankeniheny Zahamena and Fandriana Marolambo Forest Corridors, Ambalabe and Alan'Agalazaha (Fig. 4), all receiving legal protection within the last 5 years. Our results show that while Madagascar's present system of PAs was not designed to protect the phylogenetic diversity of Sarcolaenaceae, it nevertheless does a very good job of this, as indicated by the fact that 97.6 % of the total PD is included in cells that contain PAs. Furthermore, recent studies have shown that Sarcolaenaceae are part of a cohort of woody groups that are host to a diverse array of ectomycorrhizal fungi, which also includes members of two other endemic families, Asteropeiaceae and Sphaerosepalaceae, as well as the Malagasy species of the widespread tropical genus *Uapaca* (Phyllanthaceae), all of which are likewise endemic (Ducouso et al. 2008). Our results suggest that the overall distribution of Sarcolaenaceae (Fig. 1) might be constrained by aridity. As the presence of ectomycorrhizal fungi has been documented in the family, the spatial distribution of Sarcolaenaceae might also be limited by the dispersal ability of the associated fungi. This ecological interaction should therefore be taken into account when seeking to conserve the full diversity of this plant family. Members of these groups often co-occur and form an important component of the local vegetation, which suggests that habitat loss in areas rich in Sarcolaenaceae may also impact members of these other groups. The integration of information on the phylogenetic diversity of Sarcolaenaceae into conservation planning could thus also lead to species protection in these associated groups.

Conclusion

As indicated earlier, the type of analysis presented here requires a dated phylogeny based on sampling that is representative of the study group, as well as reliable data on the distribution of each species. For Sarcolaenaceae, our sampling comprised ca. 70 % of the total species diversity, with good representation from each of the 10 genera in the family. We were also able to access reliable distributional information from recent taxonomic revisions augmented by ongoing identifications made of subsequently collected material. Our study has shown the potential value of determining the spatial distribution of species richness, PD and MPD for understanding whether the current network of protected areas provides adequate conservation of these important biodiversity values and for identifying gaps in the existing network that should be targeted for the establishment of new PAs. The study presented here suggests that it may be worthwhile to expand this approach to other endemic Malagasy clades that contain a sufficient number of well-delimited species and are present in a range of eco-geographic zones. By carefully selecting study groups it should be possible to cover regions of Madagascar in which Sarcolaenaceae are poorly represented or absent and thereby generate results from a set of lineages that are collectively representative of the Malagasy flora as a whole. It would then be

possible to deliver another valuable source of information – phylogenetic diversity – to the set of criteria used to assess the value and effectiveness of Madagascar's existing network of PAs and to identify priority areas for the establishment of new parks and reserves.

Acknowledgments Anaëlle Soulebeau is funded by a doctoral grant from Doctoral School ED227, Ministère de la Recherche, at the Muséum National d'Histoire Naturelle (Paris, France). The laboratory work was supported by the ANR-funded project EVORANGE (ANR-09-PEXT-011) and agreement No. 2005/67 between Genoscope and the MNHN under the project "Macrophylogeny of life" directed by Guillaume Lecointre. We thank Nicolas Chazot and Benoit Lefeuvre for their help with the R script and GIS analysis, and Philippe Grandcolas and Sven Buerki for comments that helped to improve this manuscript.

Open Access This chapter is distributed under the terms of the Creative Commons Attribution-Noncommercial 2.5 License (<http://creativecommons.org/licenses/by-nc/2.5/>) which permits any noncommercial use, distribution, and reproduction in any medium, provided the original author(s) and source are credited.

The images or other third party material in this chapter are included in the work's Creative Commons license, unless indicated otherwise in the credit line; if such material is not included in the work's Creative Commons license and the respective action is not permitted by statutory regulation, users will need to obtain permission from the license holder to duplicate, adapt or reproduce the material.

References

- Agnarsson I, Kuntner M (2012) The generation of a biodiversity hotspot: biogeography and phylogeography of the western Indian Ocean islands. In: Anamthawat-Jonsson K (ed) Current topics in phylogenetics and phylogeography of terrestrial and aquatic systems. InTech Publishers, Rijeka, pp 33–82
- Allnutt TF, Ferrier S, Manion G et al (2008) A method for quantifying biodiversity loss and its application to a 50-year record of deforestation across Madagascar. *Conserv Lett* 1(4):173–181
- Atlas numérique du Système des Aires Protégées de Madagascar (2015). <http://atlas.rebioma.net/>. Accessed 30 Jan 2014
- Bortolussi N, Durand E, Blum et al (2006) apTreeshape: statistical analysis of phylogenetic tree shape. *Bioinformatics* 22(3):363–364
- Buerki S, Devey DS, Callmander MW et al (2013) Spatio-temporal history of the endemic genera of Madagascar. *Bot J Linn Soc* 171(2):304–329
- Buerki S, Callmander MW, Bachman S et al (2015) Incorporating evolutionary history into conservation planning in biodiversity hotspots. *Philos Trans R Soc Lond B Biol Sci* 370(1662):20140014
- Callmander MW, Schatz GE, Lowry II PP et al (2007) Identification of priority areas for plant conservation in Madagascar using Red List criteria: rare and threatened Pandanaceae indicate sites in need of protection. *Oryx* 41(02):168–176
- Callmander MW, Phillipson PB, Schatz GE et al (2011) The endemic and non-endemic vascular flora of Madagascar updated. *Plant Ecol Evol* 144:121–125
- Caramel F (2015) Bolabola, le bois qui saigne. De Madagascar à la Chine, le scandaleux trafic du bois de rose. http://www.lemonde.fr/planete/article/2015/01/24/bolabola-le-bois-qui-saigne_4562855_3244.html. Accessed 16 Feb 2015

- Coetzee JA, Muller J (1984) The phylogeographic significance of some extinct Gondwana pollen types from the Tertiary of the southwestern Cape (South Africa). *Ann Mo Bot Gard* 71:1088–1099
- Cornet A (1974) Essai de cartographie bioclimatique à Madagascar. Notice Explicative de l'ORSTOM 55:1–38
- Dayanandan S, Ashton PS, Williams SM et al (1999) Phylogeny of the tropical tree family Dipterocarpaceae based on nucleotide sequences of the chloroplast *rbcL* gene. *Am J Bot* 86(8):1182–1190
- Drummond AJ, Suchard MA, Xie D et al (2012) Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Mol Biol Evol* 29(8):1969–1973
- Ducoussou M, Béna G, Bourgeois C et al (2004) The last common ancestor of Sarcolaenaceae and Asian dipterocarp trees was ectomycorrhizal before the India-Madagascar separation, about 88 million years ago. *Mol Ecol* 13(1):231–236
- Ducoussou M, Ramanankierana H, Duponnois R et al (2008) Mycorrhizal status of native trees and shrubs from eastern Madagascar littoral forests with special emphasis on one new ectomycorrhizal endemic family, the Asteropeiaceae. *New Phytol* 178(2):233–238
- Evans M, Aubriot X, Hearn D et al (2014) Insights on the evolution of plant succulence from a remarkable radiation in Madagascar (*Euphorbia*). *Syst Biol* 63(5):698–711. doi:10.1093/sysbio/syu035
- Faith DP (1992) Conservation evaluation and phylogenetic diversity. *Biol Conserv* 61(1):1–10
- Faramalala MH (1988) Étude de la Végétation de Madagascar à l'aide des Données spatiales. Doctoral Thesis, Univ. Paul Sabatier de Toulouse, 167 p. + map at 1:1,000,000
- Faramalala MH (1995) Formations Végétales et Domaine Forestier National de Madagascar. Conservation International (et al.), 1 map
- Gautier L, Chatelain C, Callmander MW et al (2012) Richness, similarity and specificity of Madagascar flora compared with sub-Saharan Africa. *Plant Ecol Evol* 145(1):55–64
- Goodman SM, Benstead J (eds) (2003) The natural history of Madagascar. University of Chicago Press, Chicago
- Goodman SM, Benstead JP (2005) Updated estimates of biotic diversity and endemism for Madagascar. *Oryx* 39:73–77
- Haevermans T, Schatz GE, Applequist W et al Molecular phylogenetics of Sarcolaenaceae (Malvales), Madagascar's largest endemic plant family. (in preparation)
- Harper GJ, Steininger MK, Tucker CJ et al (2007) Fifty years of deforestation and forest fragmentation in Madagascar. *Environ Conserv* 34(04):325–333
- Holt BG, Lessard JP, Borregaard MK et al (2013) An update of Wallace's zoogeographic regions of the world. *Science* 339(6115):74–78
- Hong-Wa C (2009) Endemic families of Madagascar. XII. Resurrection and taxonomic revision of the genera *Mediusella* (Cavaco) Hutchinson and *Xerochlamys* Baker (Sarcolaenaceae). *Adansonia* 31(2):311–339
- Huelsenbeck JP, Rannala B (2004) Frequentist properties of Bayesian posterior probabilities of phylogenetic trees under simple and complex substitution models. *Syst Biol* 53(6):904–913
- Isambert B, Bergsten J, Monaghan MT et al (2011) Endemism and evolutionary history in conflict over Madagascar's freshwater conservation priorities. *Biol Conserv* 144(6):1902–1909
- Jöns N, Emmel B, Schenk V et al (2009) From orogenesis to passive margin—the cooling history of the Bemarivo Belt (N Madagascar), a multi-thermochronometer approach. *Gondwana Res* 16(1):72–81
- Kembel SW, Cowan PD, Helmus MR et al (2010) Picante: R tools for integrating phylogenies and ecology. *Bioinformatics* 26:1463–1464
- Kremen C, Cameron A, Moilanen A et al (2008) Aligning conservation priorities across taxa in Madagascar, a biodiversity hotspot, with high-resolution planning tools. *Science* 320:222–226
- Leroy JF (1978) Composition, origin, and affinities of the Madagascan vascular flora. *Ann Mo Bot Gard* 65:535–589

- Lowry II PP, Rabehevitra D (2006) Endemic families of Madagascar. IX. A new littoral forest species of *Schizolaena* (Sarcolaenaceae). *Adansonia* 3(28):149–153
- Lowry II PP, Schatz GE, Leroy JF et al (1999) Endemic families of Madagascar. III. A synoptic revision of *Schizolaena* (Sarcolaenaceae). *Adansonia* 3(21):183–212
- Lowry II PP, Haevermans T, Labat JN et al (2000) Endemic families of Madagascar. V. A synoptic revision of *Eremolaena*, *Pentachlaena* and *Perrierodendron* (Sarcolaenaceae). *Adansonia* 3(22):11–31
- Lowry II PP, Schatz GE, Wolf AE (2002) Endemic families of Madagascar. VIII. A synoptic revision of *Xyloolaena* Baill. (Sarcolaenaceae). *Adansonia* 3(24):7–19
- Lowry II PP, Nusbaumer N, Randrianasolo A et al (2014) Endemic families of Madagascar. XIII. New, restricted range species of *Eremolaena* Baill. and *Schizolaena* Thouars (Sarcolaenaceae). *Candollea* 69:183–193
- Madagascar Catalogue (2015) Catalogue of the vascular plants of Madagascar. Missouri Botanical Garden, St. Louis. <http://www.efloras.org/madagascar>. Accessed 30 Jan 2015
- Magnuson-Ford K, Mooers A, Paquette SR et al (2010) Comparing strategies to preserve evolutionary diversity. *J Theor Biol* 266(1):107–116
- Mercier JL, Wilmé L (2013) The Eco-Geo-Clim model: explaining Madagascar's endemism. *Madag Conserv Dev* 8(2):63–68
- Mooers AO, Heard SB (1997) Inferring evolutionary process from phylogenetic tree shape. *Q Rev Biol* 72(1):31–54
- Moore W, Robertson JA (2014) Explosive adaptive radiation and extreme phenotypic diversity within ant-nest beetles. *Curr Biol* 24(20):2435–2439
- Myers N (2003) Biodiversity hotspots revisited. *Bioscience* 53(10):916–917
- Myers N, Mittermeier RA, Mittermeier CG et al (2000) Biodiversity hotspots for conservation priorities. *Nature* 403:853–858
- Paradis E, Claude J, Strimmer K (2004) APE: analyses of phylogenetics and evolution in R language. *Bioinformatics* 20(2):289–290
- Pearson RG, Raxworthy CJ (2009) The evolution of local endemism in Madagascar: watershed versus climatic gradient hypotheses evaluated by null biogeographic models. *Evolution* 63(4):959–967
- Population Reference Bureau (2015). <http://www.prb.org/>. Accessed 30 Jan 2015
- Rabehevitra D, Lowry II PP (2009) Endemic families of Madagascar. XI. A new critically endangered species of *Schizolaena* (Sarcolaenaceae) from tapia woodland in South-Central Madagascar. *Adansonia* 3(31):149–155
- Rakotoarinivo M, Blach-Overgaard A, Baker WJ et al (2013) Palaeo-precipitation is a major determinant of palm species richness patterns across Madagascar: a tropical biodiversity hotspot. *Proc R Soc Lond B* 280(1757):20123048
- Rakotoarisoa JE, Be B (2004) Breeding and foraging behaviour and habitat characteristics of the scaly ground-roller *Geobiastes squamigerus* in Madagascar. *Ostrich-J Afr Ornithol* 75(1–2):25–31
- Ramananjahary RH, Frasier CL, Lowry II PP et al (2010) Madagascar's endemic plant families species guide – Guide Des Espèces de Plantes Appartenant Aux Familles Endémiques de Madagascar. Botanical Garden Press, Missouri
- Rambaut A, Drummond AJ (2007) Tracer ver. 1.4. <http://beast.bio.ed.ac.uk/Tracer>. Accessed 30 Sept 2013
- Randrianasolo A, Miller JS (1994) *Sarcolaena isaloensis*, a new species of Sarcolaenaceae from Isalo, south-central Madagascar. *Novon* 4:290–292
- Randrianasolo A, Miller JS (1999) Taxonomic revision of the genus *Sarcolaena* (Sarcolaenaceae). *Ann Mo Bot Gard* 86:702–722
- Rodrigues ASL, Brooks T, Gaston KJ (2005) Integrating the phylogenetic diversity in the selection of priority areas for conservation: does it make a difference? In: Purvis A, Gittleman JL, Brooks T (eds) *Phylogeny and conservation*, vol 8, Conservation biology. Cambridge University Press, London, pp 101–119

- Schatz GE (1995) Malagasy/Indo-Malesian phytogeographic connections. In: Lourenço WR (ed) *Biogéographie de Madagascar*. Orstom, Paris, pp 73–83
- Schatz GE, Lowry II PP, Wolf AE (2000) Endemic families of Madagascar. VI. A synoptic revision of *Rhodolaena* (Sarcocaulaceae). *Adansonia* 3(22):239–252
- Schatz GE, Lowry II PP, Wolf AE (2001) Endemic families of Madagascar. VII. A synoptic revision of *Leptolaena* Thouars sensu stricto (Sarcocaulaceae). *Adansonia* 3(23):171–189
- Schettino A, Scotese CR (2005) Apparent polar wander paths for the major continents (200 Ma to the present day): a palaeomagnetic reference frame for global plate tectonic reconstructions. *Geophys J Int* 163(2):727–759
- Schuurman D, Lowry II PP (2009) The Madagascar rosewood massacre. *Madag Conserv Dev* 4(2):98–102
- Sechrest W, Brooks TM, da Fonseca GA et al (2002) Hotspots and the conservation of evolutionary history. *PNAS* 99(4):2067–2071
- Torsvik TH, Amundsen H, Hartz EH et al (2013) A Precambrian microcontinent in the Indian Ocean. *Nat Geosci* 6(3):223–227
- Vane-Wright RI, Humphries CJ, Williams PH (1991) What to protect? – systematics and the agony of choice. *Biol Cons* 55(3):235–254
- Vary LB, Gillen DL, Randrianjanahary M et al (2011) Dioecy, monoecy, and their ecological correlates in the littoral forest of Madagascar. *Biotropica* 43(5):582–590
- Waeber PO (2009) Madagascar – ‘down the river without a paddle’ or ‘turning the corner’? *Madag Conserv Dev* 4(2):72–74
- Warren BH, Strasberg D, Bruggemann JH et al (2010) Why does the biota of the Madagascar region have such a strong Asiatic flavour? *Cladistics* 26(5):526–538
- Wells NA (2003) Some hypotheses on the Mesozoic and Cenozoic paleoenvironmental history of Madagascar. In: Goodman SM, Benstead JP (eds) *Natural history of Madagascar*. The University of Chicago Press, Chicago, pp 16–34
- Wikström N, Savolainen V, Chase MW (2001) Evolution of the angiosperms: calibrating the family tree. *Proc R Soc B* 268(1482):2211–2220
- Wilmé L, Goodman SM, Ganzhorn JU (2006) Biogeographic evolution of Madagascar’s microendemic biota. *Science* 312:1063–1065. doi:10.1126/science.1122806
- World Bank (2015). <http://data.worldbank.org/country/madagascar>. Accessed 15 Jan 2015
- Yoder AD, Nowak MD (2006) Has vicariance or dispersal been the predominant biogeographic force in Madagascar? Only time will tell. *Annu Rev Ecol Evol Syst* 37:405–431