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ORIGINAL PAPER

Myrtaceae in the Atlantic forest: their role as a 'model' group

Eve J. Lucas[1] · Mariana O. Bünger[2]

Abstract Myrtaceae is one of the richest families in the Atlantic Forest, a priority biodiversity hotspot that continues to be highly threatened, subject to rapid urbanisation and high levels of resource exploitation. Authors have suggested that individual lineages can be used as models to study biome evolution and ecology and to provide data for conservation planning in these areas. Here we review how Myrtaceae fit the 'model' criteria and examine the family's distribution throughout the Brazilian Atlantic Forest answering the questions: What is the ecological representation of Myrtaceae in the Atlantic Forest?; What is the current taxonomic situation of Myrtaceae in the biome?; What is the current phylogenetic understanding in the family?; Does the historical timeframe of the lineage coincide with that of the biome?; Can Myrtaceae be used to discuss species diversity hotspots within the Atlantic forests?; What is the role of Myrtaceae in conservation strategy? And finally, Can Myrtaceae be used as a 'model' taxon? The concept of the 'model taxon' is also discussed. The review concludes that taxonomic and phlyogenetic understanding in Myrtaceae are rapidly increasing, giving hope that taxonomic stability, easy species identification and management are realistic in a way unthinkable only a few decades ago. Myrtaceae function well as a 'model' within the Atlantic forest but fit some criteria better than others. Taxa can qualify as 'models' representing different times and pressures in the history of a given biome; each tells its own story. For future 'model' group studies to have maximum impact and implementation for evolutionary studies and conservation strategy, synthetic studies of multiple 'model' groups using multiple approaches

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Communicated by Jefferson Prado, Pedro V. Eisenlohr and Ary T. de Oliveira-Filho.

✉ Eve J. Lucas
e.lucas@kew.org

Mariana O. Bünger
maribunger@gmail.com

[1] Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3AE, UK

[2] Laboratório de Sistemática Vegetal, Departamento de Botânica, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais, Belo Horizonte, MG CEP 31270-901, Brazil

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are required; only then can a predictive understanding of past and future processes in the biomes concerned, be glimpsed.

Keywords Biodiversity · Hotspots · Myrteae · Conservation · Phylogeny · Speciation

Introduction

The Brazilian Atlantic coastal forest is one of five UNESCO priority biodiversity hotspots (Conservation International 2015) yet continues to be highly threatened, subject to rapid urbanisation and high levels of resource exploitation. This biome originally extended to c. 1.3 million km^2 (INPE and IBAMA 1990) but the last three centuries have seen the habitat increasingly destroyed for logging, mining, agriculture and urbanization. Industrialisation of agriculture and increased access in the last 50 years by road and air have had huge impact until today only c. 8 % of the original forest cover now remains (Pacto Mata Atlantica 2014). However, the Atlantic rainforest remains rich in diversity, supporting c. 14,000 plant species (Forzza et al. 2012) of which around half are endemic (Critical Ecosystems Partnership Fund 2014). Similarly high levels of diversity are found in other biological groups such as mammals (Fonseca et al. 1999) and birds (Harris et al. 2005). An overall increase in the number of environmentally protected areas in Brazil since the 1930s has culminated in ca. 8.75 % of the Atlantic forest (here on referred to as AF) currently under protection; a positive trend (Drummond et al. 2010). Difficulties of implementing and maintaining these areas on the ground however, are a continuous cause for concern.

Murray-Smith et al. (2009; described in more detail below) suggest that model lineages can be used to compare species diversity hotspots within the AF and to predict their conservation value. Couvreur and Baker (2013) suggest criteria to determine if a lineage is suitable for the study of biome evolution and ecology in a tropical forest biome: (1) it should be ecologically representative of the biome under investigation, (2) species taxonomy and distributions of the lineage should be well-documented, (3) comprehensive phylogenetic hypotheses of the lineage should be available, and (4) the historical timeframe of the lineage should coincide with that of the biome.

This paper reviews these assertions in the case of the woody dicot family Myrtaceae and examines the family's distribution throughout the Brazilian AF. Contemporary understanding of the evolutionary history and biogeography of the family is summarised and its role in the context of AF evolution is examined. The role of the family in influencing conservation strategy is reviewed as is the concept of the 'model' lineage.

Ecological representation of Myrtaceae in the Atlantic forest

Myrtaceae is the fourth most species-rich woody plant family in Brazil (928 species) behind Fabaceae, Rubiaceae and Melastomataceae (Forzza et al. 2010) and is highly representative of a variety of biomes of the Neotropics including the AF. It is reported to be the most (Oliveira-Filho and Fontes 2000) or second most (Stehman et al. 2009) species-rich woody family in the AF biome after Leguminosae, becoming dominant in particular vegetation types such as the dense, ombrophilous forests of southern Bahia (Mori et al. 1983). Duarte et al. (2014) use phylobetadiversity in the AF to demonstrate that the dense
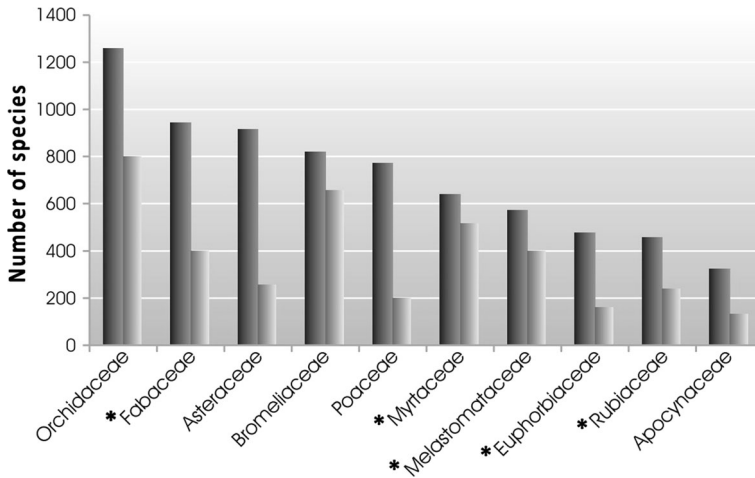
Fig. 1 Distribution of species richness and endemism of the ten most important angiosperm families in the AF. *Dark bars* represent total species, *pale bars* represent endemic species, woody families are marked with an *asterisk* (Stehman et al. 2009)

AF physiognomy is positively correlated with high numbers of Myrtaceae and other Myrtalean groups. Stehmann et al. (2009) show Myrtaceae to be the woody family with most endemism in the biome (Fig. 1). Further evidence that Myrtaceae represents total tree species diversity in the AF comes from the study of Murray-Smith et al. (2009). The latter study was based on AF tree data (Oliveira-Filho 2015) consisting of tree species checklists from 439 sites across the biome. A Spearman correlation was used to compare the 12 most species rich families across all sites against total number of species for (1) all sites and (2) AF subcategories: dense rainforest, semi deciduous forest, deciduous forest, Araucaria forest, and coastal forest. Results found Myrtaceae were well correlated and therefore could be considered a reliable indicator family of total tree diversity for the whole AF biome as well as in every vegetation subcategory. That study concluded that in general, Myrtaceae was better correlated with total diversity than the most speciose family, Leguminosae; more speciose than the best indicator family, Rubiaceae; and much richer and better known than another high scoring indicator family, Lauraceae (Murray-Smith et al. 2009). Neotropical Myrtaceae show a wide range of pollination and seed dispersal systems (Gressler et al. 2006) and significant variation in fruit (particularly embryo and seed) morphology (Landrum and Kawasaki 1997) that allow speciation to be examined from the perspective of fruiting syndromes (Pizo 2002) and other responses to pressure from the niche's macro-fauna. Phenological studies of the group suggest the potential for using the family within the AF, to understand more general ecological responses to climatic changes such as flowering and fruiting periods (Staggemeier et al. 2010, 2015). Studies of the genetics of populations of AF Myrtaceae taxa with widespread distributions (e.g. De Carvalho 2013) demonstrate the use of the family to model evolutionary processes at the level of the species.

Well documented Myrtaceae taxonomy and distributions

The taxonomy of Myrtaceae is summarised by a global checklist that includes distributional data (World Checklist of Myrtaceae (WCSP) 2015). Following this reference,

Myrtaceae comprises c. 5800 species (WCSP 2015) with centres of diversity in Australia, Southeast Asia, tropical and subtropical America and a small representation in Africa (Wilson et al. 2001). The latest classification of the family was proposed by Wilson et al. (2005); a DNA-based phylogeny was used to divide Myrtaceae into two subfamilies: Psiloxyloideae and Myrtoideae containing 2:15 tribes respectively. All neotropical Myrtaceae (bar one: monospecific genus *Tepualia*) belong to subfamily Myrtoideae and tribe Myrteae DC. (sensu Wilson et al. 2005); these are trees or occasionally shrubs with a Pantropical distribution. Myrteae comprises 52 genera (Wilson 2011) and c. 2500 species (World Checklist of Myrtaceae 2015). For its size, Myrtaceae is unusual in having four genera of over 500 species; two of these (*Myrcia* (sensu Lucas et al. 2011) and *Eugenia* (sensu Mazine et al. 2014), with >700 spp. and >1050 spp. respectively (WCSP 2015)), are predominantly from tropical rainforest and are ubiquitous in the AF biome. Numbers of AF species per genus are contrasted against the same numbers both in Brazil and globally in Table 1. Until ca. 10 years ago, taxonomic disorder within tribe Myrteae was immense at both the genus and the species level, particularly in the large genera with low morphological variation. This gave Myrtaceae a 'difficult' reputation; Landrum and Kawasaki (1997) estimated that less than half of the Brazilian species had been treated by recent studies. Today that proportion is rising as a result of monographic work (e.g. Mazine 2006; Santos 2014) based on clades generated by DNA-based phylogenies (e.g. Mazine 2006; Mazine et al. 2014; Lucas et al. 2011). Confusion does continue in some groups and even now, only a fraction of available names have complete diagnoses. Extrapolation from the basic estimates of available species descriptions of AF species presented in Table 1 suggest that still only ca. 40 % of both Brazilian and AF species are described in recent monographs; numbers that will increase further if regional accounts (e.g. Sobral 2003) are included. However, perspectives from DNA-based phylogenies (e.g. Lucas et al. 2007, 2011; Murillo-A et al. 2012; Mazine et al. 2014) and large scale check listing projects (Sobral et al. 2015; WCSP 2015) have clarified generic taxonomy of Myrteae and synonymised a significant proportion of superfluous names. These efforts have resulted in taxonomic deflation and provide taxonomic frameworks on which smaller, mixed monographic/phylogenetic studies are now based (e.g. Faria-Júnior 2014; Santos 2014; Staggemeier et al. 2015). Increased interest and activity in the group has underpinned acceleration in publication of new species in the biome (Table 1; Fig. 2). This taxonomic acceleration is most acute in the AF and neighbouring cerrado savanna biomes due to their proximity to active, resource rich universities, ironically in the very cities that have contributed to the destruction of the biome.

Phylogenetic understanding

The most recent phylogenies at the generic level in tribe Myrteae (Lucas et al. 2007; Costa 2009; de Carvalho 2013; Murillo-A et al. 2013) have answered long-standing questions about generic delimitation such as (for example) whether *Myrcia* and related genera are monophyletic, whether *Hexachlamys* has a separate origin from *Eugenia* or whether *Psidium* is monophyletic relative to *Campomanesia*. De Carvalho (2013) provides a time-calibrated tree of the tribe. While these studies produce hypotheses for relationships between these well supported genera, statistical support is low along the back-bones of the resulting trees and relationships between genera are incompletely resolved. Questions that remain to be answered concern the relationships of the main subtribal and sub-generic clades to each other.

Table 1 Global (WCSP 2015), Brazilian (Sobral et al. 2015) and AF (Stehman et al. 2009) Myrtaceae

|	Global (spp.)[a]	Brazilian (spp.)	AF (spp.)	Modern monographs	New (spp.) since last taxonomic treatment: global (spp.)/Brazilian (spp.)/AF (spp.)	Global (spp.)/Brazilian (spp.) to be treated	Global (spp.) with taxonomic descriptions	AF (spp.) with taxonomic descriptions
Acca	3	1	1	–	–	–	–	1
Accara[a]	1	1	1	–	–	–	–	1
Blepharocalyx	4	4	3	Landrum (1986)	1/1/0	1/1	3	3
Calycolpus	15	9	2	Landrum (2010)	0	0	15	2
Curitiba[a]	1	1	1	–	0	0	1	1
Campomanesia	40	40	28	Landrum (1986)	10/10/2	10/10	40	28
Eugenia	1100	385	241	Mazine (2006) (sect. *Racemosae*); Faria-Júnior (2014) (clades 4 and 2; Bünger[b] (sect. *Phyllocalyx*); Coutinho[b] (sect. *Eugenia*); Giaretta[b] (sect. *Calycorectes*)	106/42 (since 2006)/29	ca. 900/205	ca. 160	ca. 120
Myrceugenia	48	31	28	Landrum (1981)	3/3/0	3/3	40	28
Myrcia	600	ca. 400	320	Lucas et al. (sect. *Aulomyrcia*, unpublis. res.); Lima Lourenço (AF *Calyptranthes*)[b]; Fortes-Santos (clade 7); Amorim[b] (clade 3); Lima dos Santos[b] (clade 5); Fernandes Lima[b] (clade 4)	100/32/32	ca. 250/200	ca. 250	ca. 100
Myrcianthes	37	8	5	Griffo 1992	8/2/1	8/2	29	5
Myrciaria	30	22	15	Sobral (1993)	6/6/2	6/6	27	15
Myrrhinium	1	1	1	–	–	–	1	1
Neomitranthes	16	16	16	Souza 2009	3/3/3	3/3	16	16
Pimenta	23	1	1	Landrum (1986)	2/0/0	2/0	15	1
Plinia	67	32	28	–	0/2/2 (since 2008)	–	40	28
Psidium	ca. 100	59	32	–	0/3/3 (since 2008)	–	100	0
Siphoneugena	13	9	7	Proença (1990)	4/2/0	4/2	9	7

Table 1 continued

	Global (spp.)[a]	Brazilian (spp.)	AF (spp.)	Modern monographs	New (spp.) since last taxonomic treatment: global (spp.)/Brazilian (spp.)/AF (spp.)	Global (spp.)/Brazilian (spp.) to be treated	Global (spp.) with taxonomic descriptions	AF (spp.) with taxonomic descriptions
Total	2099	1020	730		229/106/74	1187/432	786	337

[a] Signifies taxa endemic to the AF biome. *Calyptranthes*, *Gomidesia* and *Marlierea* are included in *Myrcia* (sensu Lucas et al. 2011). Numbered *Eugenia* clades refer to Mazine et al. (2014), numbered *Myrcia* clades refer to Lucas et al. (2011)

[b] Signifies a monograph underway. New species numbers were taken from IPNI (2015). A treated species is defined as a species with a description in a modern (since 1900) monograph
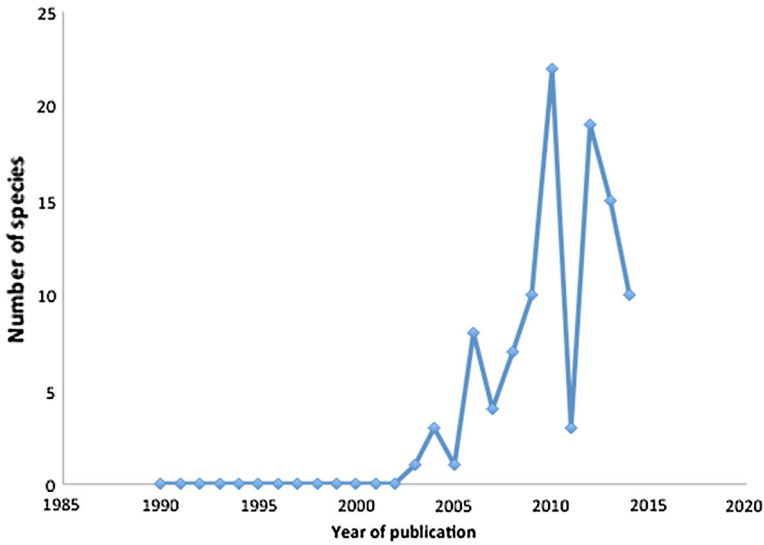
Fig. 2 Numbers of new species of Myrtaceae published (104 total) from Brazil since 1990 (IPNI 2015)
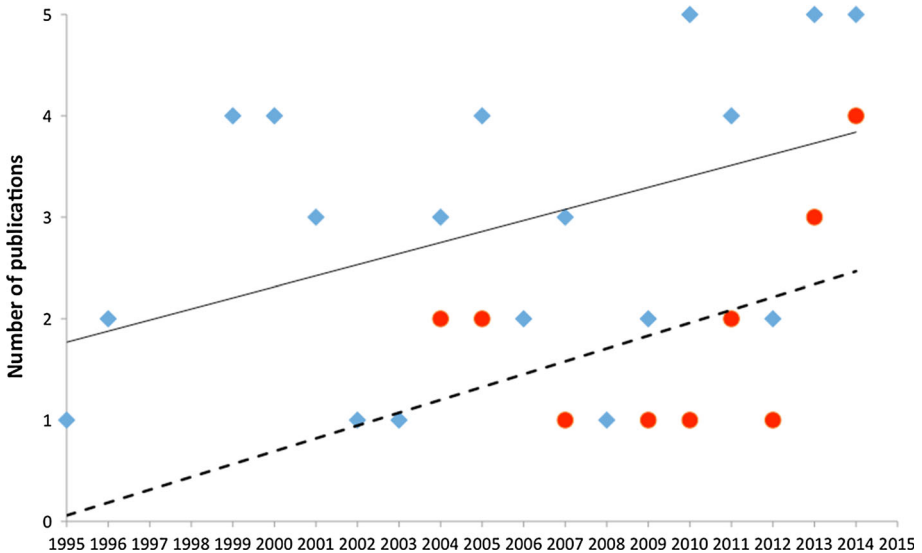
Fig. 3 DNA-based phylo-systematic studies of Myrtaceae (*diamonds*) and Myrteae (*circles*) completed between 1995 and 2014. Linear regressions over publication numbers by year represent Myrtaceae (*solid line*) and Myrteae (*dotted line*)

Nevertheless, the last 15 years have seen a significant increase in molecular based studies in both Myrtaceae and Myrteae. A search using Google Scholar using the default criteria returned a total of 55 phylo-systematic studies (DNA-based phylogenies also concerned with systematics) between 1990 and 2014. Of these, 18 studies concern tribe Myrteae. Figure 3 demonstrates an increasing rate of such studies for both Myrtaceae and

Myrteae; from 2004 there was a rapid increase in publications on tribe Myrteae as a proportion of total works on Myrtaceae (currently nearly 50 %). With multiple studies in preparation at the time of writing, a further increase in studies seems likely e.g.: *Eugenia* sect. *Umbellateae*; *Eugenia* sect. *Phyllocalyx*; *Eugenia* sect. *Eugenia*; *Eugenia* sect. *Calycorectes*; *Myrcia* sect. *Guianensis*; *Myrcia* sect. *Gomidesia* ; *Myrcia* sect. *Myrcia*; *Calyptranthes*; Myrteae.

Historical timeframe of the lineage should coincide with that of the biome

After the separation of the Gondwanan supercontinent and opening of the South Atlantic Ocean during the Mesozoic (250–65 Ma.), South America underwent a long period of geological isolation that resulted in high levels of endemism in its humid forests (Burnham and Graham 1999). In the early part of this period, the area that today supports the AF date back to the evolution forest was a landscape of metamorphic hills and plateaus interspersed with tectonic faults and basic intrusions (Almeida and Carneiro 1998). A process of erosion and uplift in the Paleocene (c. 70 Ma.) produced the parallel ridges of the Serra do Mar and Serra da Mantiqueira in the Paleocene (c. 70 Ma.; Almeida and Carneiro 1998) that today induce high levels of precipitation from Atlantic Ocean weather systems that sustain the Atlantic Rainforest. During the late Paleocene and Eocene (c. 50 Ma.) a continuous band of humid subtropical forests covered the north of South America (Ortiz-Jaureguizar and Cladera 2006) extending to 40°S at its largest expansion. This expansive South American forest subsequently underwent disjunction as a result of climate and habitat changes resulting from the arrival and retreat of shallow oceanic transgressions that covered parts of Patagonia, Bolivia and Peru in the Eocene to Oligocene (55–24 Ma.) and again in the late Oligocene to mid-Miocene (26–11 Ma.; Ortiz-Jaureguizar and Cladera 2006). These vicariant events allowed ancestors of current extant taxa to diverge in the forest areas in which they remained. A further suite of geological events such as the rise of the Andes (ca. 23 Ma–present), the consequential formation of the dry biomes in the centre of the continent as well as expansion and contraction of forest patches during the climatic fluctuations of the Pleistocene (ca. <1–2 Ma.; Carnaval and Moritz 2008) caused further habitat fragmentation and distinction of current Neotropical biomes.

Synthetic study of the evolution of the Neotropical terrestrial biota (Morrone 2013) supports these geological patterns, concluding that the Neotropical region can today be divided into three evolutionary distinct subregions. The Chacoan subregion includes the AF, cerrado and southeastern Amazonia. The Chacoan and Amazonian subregions are found to share a direct origin that then shares an origin with the Antillean subregion. This suggests that within the Neotropical region the Caribbean flora is the most similar to the expansive forests of the Eocene with the Amazonian and Chacoan subregions (sensu Morrone 2013) subsequently diverging and the AF and cerrado floras emerging from South East Amazonia.

Sytsma et al. (2004) used Penalised Likelihood rate smoothing (Sanderson 2002) to suggest the origins of Myrtaceae date to the Cretaceous (86 Ma.) and that Myrteae lineages subsequently migrated from what is now Western Australia to South America via land bridge connections to Antarctica ca. 70 Ma. This pattern is supported by DIVA analysis (Ronquist 1997) of the Myrteae phylogeny (Lucas et al. 2007) that shows the oldest, species-depauperate lineage Myrteae to be sister to the mega-diverse Neotropical clade and to have an Australasian origin. The timing suggested by Sytsma et al. (2004) is

considerably different from that found by Biffin et al. (2010) using BEAST (Drummond and Rambaut 2007) who found the age of the Myrteae crown node to be 10–30 Ma. younger. More recently, de Carvalho (2013) also used BEAST to date an enhanced Myrteae phylogeny and found the origin of the tribe to be ca. 60 Ma. Differences between ages are likely due to little available fossil evidence, with available data used differently when constraining phylogenetic tree nodes for dating as discussed further below.

At their furthest southern extension, the continuous band of Neotropical humid sub-tropical forests mixed with temperate elements of the southernmost parts of the continent (Palazzesi and Barreda 2007). Lucas et al. (2007) suggests that after initial colonisation of the southernmost parts of South America elements of the sub-Antarctic sub-province including ancestral Myrteae moved north via these humid forests and eventually reached the most northern parts of the continent.

Within tribe Myrteae, a variety of even more recent phylo-biogeographic studies demonstrate the evolution of the component parts of the tribe against what is known of the geological events that shaped existing Neotropical biomes. Thornhill et al. (2012) used macro and micro (pollen) fossils suggest a mean age of ca. 51 Ma for tribe Myrteae. Staggemeier et al. (2015) and Santos (2014) date the origin of *Myrcia* finding mean dates of 31 and 27 Ma., respectively. Bünger et al. (in prep.) date *Eugenia* to 35 Ma. De Carvalho (2013) find dates 5–10 Ma. younger, as do Biffin et al. (2010) and Thornhill et al. (2012) although these last two works are based on relatively few Myrteae species. All of these studies report large confidence intervals (e.g. Santos (2014) 95 % HPD 21–36 Ma). It is not clear whether discrepancies in dates are due to differences in sample size, fossil calibrations or both of these factors. All studies however indicate high rates of speciation during the Miocene that lead to the inflated numbers of species found today in Myrteae (developed in detail by De Carvalho et al. in prep.) and found in such high numbers in the AF and associated biomes. At the subgeneric level, Bünger et al. (in prep.) note that older lineages of *Eugenia* are represented by more geographically widespread species. Apparently more recent lineages are species more likely to occur in centres of endemism like the Serra do Mar in Paraná, São Paulo and Rio de Janeiro State. Within *Myrcia*, Staggemeier et al. (2015) find an AF clade to be ca. 28 Ma old; the study also suggests that lower species diversification rates occur within species from areas considered climatic refugia (Carnaval and Moritz 2008) although range expansion in unstable areas resulted in higher colonisation of adjacent refugia leading to higher plant diversity in the Bahian refuge. Results suggest that the Bahian refuge acts as a biodiversity museum and centre of species accumulation, maintaining the high species diversity in the central corridor of the AF.

Can Myrtaceae be used to compare species diversity hotspots within the Atlantic forest and to predict their conservation value?

The AF is a global biodiversity hotspot as defined by Myers (2000), i.e. an area of exceptional species diversity under extreme environmental threat. Within 35 existing global hotspots (Conservation International 2015), Mittermeier et al. (2005) consider local hotspots should meet three criteria: (1) to be of a small enough size to be manageable, (2) to be representative of the major hotspot in which it occurs and (3) to be highly threatened. In addition to demonstrating the use of Myrtaceae as an indicator of total tree species diversity in the AF, Murray-Smith et al. (2009) used a thorough sample of key herbarium datasets of *Myrcia* (sensu Lucas et al. (2011) including *Calyptranthes*, *Gomidesia* and *Marlierea*) to observe

distribution of species diversity in the biome. Murray-Smith et al. (2009) produced predictive species-distribution models for each species using Maxent (Phillips et al. 2006) and complementarity analysis using DIVA-GIS (Hijmans et al. 2005) was performed on 35 km^2 grid cells overlaid on the observed data. These analyses revealed *Myrcia* to have two centres of species diversity (1) in coastal Bahia and Espírito Santo (BA-ES) and (2) in the coastal forests of Rio de Janeiro and São Paulo (RJ-SP). High diversity was also found in coastal Paraná and Santa Catarina. Predicted species distribution maps were stacked and summed and overlaid with an outline of remaining forest fragments derived from satellite imagery (SPOT VGT; Harris et al. 2005) followed by the World Database on Protected Areas shapefile (WDPA 2004). Areas of high species diversity and high or low level of threat could therefore be assessed. Results identified ten 35 km^2 grid cells as local hotspots of *Myrcia* diversity, six from RJ-SP and four from BA-ES. Of these, squares with the highest quality forest but with least environmental protection encompassed the Morro do Cururupé Ecological Reserve (grid square: 32 % forest, 0.003 % protected; Bahia), the Itariri State Forest Reserve (grid square: 69 % forest, 26 % protected; São Paulo) and the Santa Lúcia Biological Station/ Mestre Álvaro Biological Reserve (grid square: 41 % forest, 3 % protected; Espírito Santo).

The role of Myrtaceae in conservation strategy

As well as the hotspots study discussed above, Rigueira et al. (2013) used Myrtaceae to identify a relationship between the amount of available habitat and Myrtaceae species richness, to identify species extinction thresholds. They found that forest with less than 25 % tree cover presented an approximately six-fold reduction in Myrtaceae species richness compared with landscapes with forest cover greater than 40 %. Rigueira et al. (2013) frame their findings as a recommendation for conservation strategists to consider minimal amounts of available habitat to ensure conservation of the forest ecosystem, species and intrinsic ecological processes. Such metrics for decision making in environmental management or recommendations of areas for conservation such as presented by Murray-Smith et al. (2009) would ideally be firmly on the radar of those concerned with conservation planning.

The conservation hotspots highlighted by Murray-Smith et al. (2009) included protected areas featured in the World Database on Protected Areas shapefile (WDPA 2004). This resource is now available through IUCN and UNEP-WCMC (2015), the 'most comprehensive global database on terrestrial and marine protected areas', however two of the three protected areas listed in 2004 are no longer recovered by a search of the database preventing follow-on assessment of the fate of these regions. The Mestre Álvaro Biological Reserve is listed by IUCN and UNEP-WCMC (2015) but no update information is available. A websearch reveals various mentions of the Santa Lúcia Biological Station but without comment of its status or threats. To our knowledge, no conservation action has taken place as a direct result of the Rigueira et al. (2013) or Murray-Smith et al. (2009) studies.

Can Myrtaceae be used as a 'model' taxon?

Myrtaceae in the AF clearly fit the 'model group' criteria of Couvreur and Baker (2013) but fit some criteria better than others. Myrtaceae are doubtless ecologically representative of the AF biome in its present form. Myrtaceae taxonomy at the generic level is now stable, particularly as statistically supported, morphologically credible groups of species

correspond on the whole to classical generic concepts; their existence should resist future taxonomic fashions. AF Myrtaceae species level taxonomy enjoys some of the most complete checklisted taxonomy; detailed monographic treatments underway will soon culminate in modern treatments for groups previously considered taxonomically very difficult. While AF Myrtaceae taxonomy is not at present comparable in organisation to some other key groups that enjoy family monographs or data rich on-line e-taxonomy platforms (e.g. Palmae, Leguminosae), information is being compiled on Myrtaceae at an accelerated pace (Figs. 2, 3). As well as the publication of key monographs in preparation, the next 5 years should witness a gathering of on-line resources and an equivalent stabilisation in taxonomic understanding. Phylogenetic understanding of Myrtaceae is also increasing with a dated phylogeny including all genera of tribe Myrteae in preparation to build on the nearly complete versions already available. Intensive phylogenetic studies in the largest clades will culminate with the majority of AF species being accounted for; the same study aims to date timing and rates of speciation within the tribe. As is the case for Palmae (Couvreur and Baker 2013), phlyogenetic analyses of Myrteae provide evolutionary hypotheses for the full history of the AF biome and not at 'only lower levels, which tend to be limited to recent timeframes and often emphasize rapid radiations'.

The historical timeframe of Myrteae clearly does coincide with the evolution of the AF biome. Patterns of Myrtaceae biogeography reflect a major Gondwanan pathway in which families of plants have colonised the biome (Vicentini 2007). However, different groups have taken different routes and one taxon cannot reflect the whole history of the biome. In addition to its highly endemic flora and taxa with Gondwanan origins, the AF flora bears evidence of floristic intrusions from Laurasia via land bridges with North America (Pennington and Dick 2004). The result is a biome with a unique mix of floras with distinct biogeographic and phylogenetic origins (Duarte et al. 2014). From its Gondwanan origins, AF Myrtaceae underwent Oligocene/Miocene speciation explosion that corresponds to patterns found in other groups of Angiosperms (e.g. Compositae; Funk et al. 2005, *Inga*; Richardson et al. 2001) and is consistent with a period of expansion followed by fragmentation in Neotropical forests. The model by which a group has attained extreme levels of species diversity recently by a process of hyper-diversification, as experienced by AF Myrtaceae, has been coined the 'cradle' model (Richardson et al. 2001). The alternative, when species accumulate at a steady rate since their origin (e.g. Palms; Couvreur and Baker 2013, *Symphonia* (Dick and Heuertz 2008)), is known as a 'museum' model (Richardson et al. 2001). The AF flora therefore is comprised of lineages from a variety of sources as well as from both old and recently diverged lineages.

Comparing the suitability of Myrteae against the 'model' criteria, there is one aspect in which Myrteae performs poorly. The fossil record of Myrteae is unfortunately rather depauperate. The most commonly used Myrteae fossil is of fruit of the genus *Paleomyrtinaea* from the late Palaeocene of North Dakota and early Eocene of British Columbia (Pigg et al. 1993), known only from fruit. Additional Myrteae fossil pollen of *Myrtaceidites* has been reported by Thornhill et al. (2012) from the Cretaceous of Gabon that are already being used to make dating studies more reliable (Thornhill et al. 2012). Beyond this, only sterile material of leaves has been suggested for Myrteae. The fossil record of Palmae by contrast is extensive and thorough. Encouragingly, the criteria that Myrtaceae meet less well are related to insufficient levels of data that are being collected and generated at an ever increasing pace. We suggest that Myrtaceae already functions well as an indicator group but that its use will increase as its nomenclature stabilises further and its fossil record improves.

In one aspect, Myrteae might be seen to have an advantage as 'model' taxa. Palmae is a medium sized family of approximately 2500 worldwide species with average sized genera wheras the tribe Myrteae has an equivalent number of species within South America alone. This species richness and ubiquity may make the group more perceptive to environmental change in the biomes of the Neotropics and provide a more sensitive 'memory' of past events to be reflected in any predictive model.

Regarding conservation strategy, Myrtaceae have been implicated in various conservation-focused studies. Unfortunately, the step between making recommendations and those recommendations being implemented on the ground is a difficult one without objective targets and/or direct channels to federal decision makers and advisory non-governmental bodies. The result is that patterns, evidence and recommendations for conservation based on single or few studies are often lost and political inertia and missed opportunity often result. Ultimately, it is anticipated that these smaller scale studies feed into a wider understanding and a critical mass of data from multiple case-studies and multiple scales that allows a biome-wide perspectives for conservation that cannot be ignored.

How useful is the 'model taxon' concept?

The use of a single or few species to extrapolate general spatial diversity of species is relatively common in a variety of groups (e.g. Cardoso et al. 2004; spiders, Pearman and Weber 2007; butterflies) but is less common in plants. Results are frequently used to prioritise areas for conservation and can provide ecologists and conservation practitioners with information on current species diversity in threatened habitats. As resources for full taxonomic surveys are limited, 'model' or 'indicator' species become more attractive to estimate the condition of a given habitat. Such assessments can be rapid habitat assessments (Cardoso et al. 2004) or more detailed ecological extrapolations such as niche modeling to predict areas of high diversity for conservation strategy (Trisurat 2009; forest tree distributions in South East Asia), of particular interest for predicting the reaction of a biome to macro-ecological events such as global warming. Use of an entire family or other larger taxon or lineage as a model to understand wider evolutionary patterns in tropical forests is also becoming more commonplace and in these cases, plants are most commonly employed (e.g. Murray-Smith et al. 2009; Daly et al. 2012; Couvreur and Baker 2013). Such studies are of particular interest as extrapolations based on orders of magnitude more species (in particular, as in Myrtaceae) will take into account more responses to past and present pressures on a biome. Daly et al. (2012) and Couvreur and Baker (2013) make convincing cases that the group in question is best placed to represent the biome as a whole and set out similar criteria for what makes a taxon or lineage 'model' and recount with examples, how their families (Burseraceae and Palmae respectively) fit. Neither study explicitly tests the fit of their groups against total diversity data. Murray-Smith et al. (2009) on the other hand, describe Myrtaceae as an 'indicator' of total tree species diversity without reference to 'model' criteria but do test the suitability of the group in its model role. Concerning the 'model' group criteria of Couvreur and Baker (2013), the criteria appear a good guide to qualification. A criterion that has not been considered by these authors is that of the size of the group. Groups of different sizes may be of use for different tasks but overall, we suggest that larger groups will provide a richer and more predictive pattern; future study of the effect of the size of the indicator group is likely to yield exciting

results. Ricketts et al. (1999) emphasise that the size of a given area and its latitude describe must also be taken into consideration when selecting indicator taxa as these will affect the strength of correlations among taxa as they vary.

Considering the use of the model lineages to date for extrapolation of historical biogeography, it is clear that due to the complex and markedly different histories of different lineages within an area, no one group can represent a particular biome in its entirety. As discussed, some families or groups may lend themselves better than others to the evolutionary story of a given biome, however different groups will better reflect different internal processes and different periods in the biome's history. To further harness the predictive potential of these and other model groups for any purpose, the next steps will be large scale, focused studies that survey potential model lineages from different biomes and kingdoms of the natural world. These studies should rigorously test the groups against the criteria discussed here and would test other factors such as the size of the group (number of species), size of the area and latitude. The survey would compare the historical biogeographies of the groups and select the best performing lineages with a diverse range of historical geography patterns. Distributional data from multiple such groups would then provide powerful synthetic, flexible models for holistic understanding of a given biome for a wide variety of applications, in particular for assessment of local areas within a biome, for conservation. The greatest challenge now facing practitioners integrating systematic and ecological studies of model groups with applied conservation is to ensure the conclusions of these works are heard and understood by those legislating conservation strategy. The synthetic study described above goes some way towards this but to harness the signals of past processes obtained from studies of model groups, for applied conservation action and modelling of future scenarios, a systematic review of such analyses based on methods, resulting patterns and practical implications for conservation is required. Such a synthesis would amplify the impact of model group studies and link even more directly to the front-line of natural habitat management.

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