



Evolutionary patterns in the assembly of fern diversity on the oceanic Mascarene Islands

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ABSTRACT

Aim To provide insights into the assembly and structure of biotic communities by exploring several processes of island biodiversity assembly: *in situ* speciation, immigration and ecological processes.

Location The Mascarene Islands.

Methods The phylogenetic relationships of 211 out of 232 Mascarene leptosporangiate fern species were reconstructed in relation to a global phylogeny of 400 leptosporangiate fern species to assess the importance of immigration versus *in situ* speciation and any deviation from randomness. Correlations between speciation and habit (terrestrial or epiphytic/lithophytic) were tested.

Results We inferred at least 197 colonization events onto the islands, accounting for > 80% of their leptosporangiate fern diversity. The phylogenetic structure of the assemblage of colonists was mostly overdispersed but aggregated at the tips of the phylogeny. Several families were more diverse on the islands than expected by their global richness. Among the 46 endemic species, up to 65% were inferred to have originated by cladogenesis, which in turn was found to be significantly related to a terrestrial habit.

Main conclusions Immigration has played a major role in the assembly of the fern flora on the Mascarene Islands. The overdispersion pattern supports the hypothesis of a dominant role of competitive interactions in the flora assembly, and we propose that most available niches were filled by species arriving via long-distance dispersal, preventing further immigration of closely related taxa. The over-representation of some families may reflect better colonization capacities, preadaptation to the Mascarene ecological niches, or ecological differentiation. Frequent colonization by long-distance dispersal has probably hampered *in situ* speciation in some habitats such as the epiphytic realm. Conversely, cladogenetic speciation appears to occur more frequently in terrestrial habitats.

Keywords

Cladogenesis, colonization, ferns, Indian Ocean, Mascarene Islands, Mauritius, oceanic islands, phylogenetic structure, Réunion, speciation.

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INTRODUCTION

Oceanic islands are much used as natural laboratories for the study of evolutionary processes (Losos & Ricklefs, 2009). With their distinct boundaries, oceanic islands are also ideal to investigate how genetic and species diversity are assembled at local scales (Emerson & Gillespie, 2008). A crucial question in studying the assembly of oceanic island diversity is

that of species origin by immigration versus *in situ* speciation (Emerson & Gillespie, 2008; Table 1). The assemblage of species having colonized the island (colonists) can then be seen as a subset of the diversity occurring in more or less nearby areas. As a result of both *in situ* speciation and the filtering of colonists, an insular assemblage is expected to exhibit a non-random or disharmonic structure compared with the regional species pool (Williamson, 1981). Several factors

Table 1 Hypotheses on the main processes involved in island community assembly and their predicted effects on the phylogenetic structure of island assemblages, assuming phylogenetic conservatism of traits and niche.

Origin of island species*	Hypotheses on processes	Predictions on phylogenetic structure
<i>In situ</i> speciation	Cladogenesis	(1) Phylogenetic clustering at tips
	When cladogenesis is important, the radiation of an initial colonist into a clade that occupies a variety of niches may inhibit the subsequent establishment of related dispersers (niche pre-emption; Silvertown, 2004; Silvertown <i>et al.</i> , 2005)	(2) Clustering at tips, global over-dispersion
Immigration	Variation in dispersal capacities, preadaptation to island environments, environmental filtering (at the local scale)†	(3) Phylogenetic clustering
	Interspecific interactions (competition)	(4) Phylogenetic overdispersion
	No dominant process	(5) Phylogenetic randomness

*Depends on various factors including isolation of island from source, age and area of island, and habitat heterogeneity.

†May also result from competitive exclusion based on differences in competitive abilities (Mayfield & Levine, 2010).

influence the composition of island biota, such as the capacities of dispersal, establishment and competition among species with similar habitat preferences, and, amongst other factors associated with the island, its isolation, age and the availability of habitats.

Phylogenetic studies are key to the study of the assembly of island diversity. First, they provide the framework to evaluate the importance of colonization versus *in situ* speciation. Second, the study of the phylogenetic structure of island assemblage can provide insights into the ecological processes involved. If deviating from a random relatedness, the biota on an island can be either more (i.e. phylogenetic clustering) or less (i.e. phylogenetic overdispersion) closely related than expected by chance. Various studies have addressed the question of island community structure before the advent of molecular phylogenetics (MacArthur & Wilson, 1967; Williamson, 1981), notably by analyses of species:genus ratios (Simberloff, 1970; Grant & Abbott, 1980). These studies led to the hypothesis that competition between related species (supposedly sharing similar ecological niches) may prevent the establishment of closely related species on the same island (leading to phylogenetic overdispersion). Alternatively, environmental filtering is expected to result in phylogenetic clustering. There has been much debate, however, as to the role of competition in shaping communities (Connor & Simberloff, 1980; Losos, 1995). More recently, the application of phylogenetic approaches has revitalized the study of community assembly by addressing the phylogenetic structure of communities (Webb *et al.*, 2002; Johnson & Stinchcombe, 2007; Mouquet *et al.*, 2012). However, few studies have investigated the phylogenetic structure of whole oceanic island assemblages. Cardillo *et al.* (2008) observed random phylogenetic structure in the mammal assemblages of many oceanic islands but also a few structured assemblages: phylogenetically overdispersed in ungulates and bats; clustered in carnivores and rodents. Reviewing several studies focused on islands in a broad sense, Emerson & Gillespie (2008) also found contrasting phylogenetic structures depending on the scale and age of the assemblages.

In this study, we aim to contribute to the understanding of the assembly of island diversity, by investigating the leptosporangiate fern flora of the Mascarene Islands. Located in the South West Indian Ocean hotspot of biodiversity and endemism, the Mascarene Islands consist of three main islands of volcanic origin: Réunion, Mauritius and Rodrigues. These islands differ in size, age and topography, but share tropical-oceanic climate and isolation from non-oceanic islands (Table 2). Oceanic islands are known to host a high proportion of ferns (Tryon, 1970; Smith, 1972; Kreft *et al.*, 2010) and the Mascarene Islands are no exception with 242 species (this study). Considering the estimate of 959 native flowering plants (Thébaud *et al.*, 2009), ferns contribute about 20% of the Mascarene vascular flora, a high ratio compared with the mean of 15% obtained for 106 islands (Kreft *et al.*, 2010) and the worldwide contribution of about 4% (Smith, 1972). The high contribution of ferns to the plant diversity on oceanic islands is arguably related to their high capacity for long-distance spore dispersal by wind, and the potential of solitary or isolated gametophytes to produce sporophytes through intragametophytic selfing (Tryon, 1970; Wolf *et al.*, 2001). Long-distance dispersal has been reported as the origin of several fern lineages occurring on islands (Schneider *et al.*, 2005; Shepherd *et al.*, 2009; Ranker *et al.*, 2010). However, recent research on fern dispersal has emphasized the strong influence of reproductive traits (Peck *et al.*, 1990; Ranker & Geiger, 2008; de Groot *et al.*, 2012).

Table 2 Main characteristics of the Mascarene Islands (only the three main islands are considered).

	Area (km ²)	Age (Ma)*	Max. elevation (m)	Distance to Madagascar (km)
Réunion	2500	2.1	3069	665
Mauritius	1865	7.8	826	800
Rodrigues	104	1.5	396	1370

*Age of most ancient dated lavas, but Rodrigues may be older.

Other characteristics related to habit are expected to have a role in island colonization based on the different ecological strategies displayed by the gametophytes of terrestrial versus epiphytic ferns (Dassler & Farrar, 2001; Watkins *et al.*, 2007).

In situ diversification appears to be important in the Mascarene Islands for both animals and angiosperms (Thébaud *et al.*, 2009; Le Péchon *et al.*, 2010; Strijk *et al.*, 2012), as well as for leptosporangiate ferns, as indicated by the relatively high level of endemism (19.8%; this study). Previous molecular studies have documented cases of speciation in the Mascarenes in *Alsophila* (Janssen *et al.*, 2008), *Elaphoglossum* (Rouhan *et al.*, 2004), *Lellingeria* (Ranker *et al.*, 2010), and *Megalastrum* (Rouhan & Moran, 2011). In contrast, no evidence for speciation was found in *Nephrolepis* (Hennequin *et al.*, 2010a). Extensive studies on the filmy ferns (Hymenophyllaceae) of the Mascarenes found a single endemic among 24 species (Ebihara *et al.*, 2004; Hennequin *et al.*, 2006, 2010b; Dubuisson *et al.*, 2013).

Both colonization from long-distance dispersal and *in situ* speciation have therefore influenced the assembly of the fern flora on the Mascarene Islands, but the relative contribution of each process remains to be evaluated, as does the importance of cladogenesis and anagenesis in speciation. To this end, we here compare the phylogenetic signature of the Mascarene leptosporangiate ferns with a global phylogeny of the lineage. We also test a series of predictions on the main processes of community assembly based on phylogenetic structure (Table 1). Identification of cladogenetic speciation is a prerequisite because it can strongly influence phylogenetic structure (Table 1, predictions 1 and 2). Speciation aside, species colonizing an island by immigration can show various patterns of phylogenetic structure. Assuming that traits influencing colonization capacities and niche/habitat preferences are phylogenetically conserved in the pool of species contributing to the community (Wiens *et al.*, 2010), these can be linked to contrasting processes (Table 1, predictions 3 and 4) or not (prediction 5). Finally, we aim to identify taxa responsible for the phylogenetic structure documented and explore differences in immigration/speciation success among Mascarene ferns.

MATERIALS AND METHODS

Taxonomic sampling

The leptosporangiate fern flora occurring in the Mascarenes was assessed based on published accounts (Lorence, 1976, 1978; Badré & Cadet, 1978; Badré, 2008; Grangaud, 2010), grey literature [the checklist of vascular flora of Réunion from Conservatoire Botanique National de Mascarin, 2010; the checklists and addenda available from E. Grangaud at <https://sites.google.com/site/fougeresmascareignes/>; personal communications by botanists (see Acknowledgements); and our own observations during fieldwork and herbarium study (Tables 3 & 4 and see Appendix S1 in Supporting Informa-

Table 3 Composition of the Mascarene leptosporangiate fern diversity in terms of total numbers, number of endemics and percentage endemism. The numbers in parentheses represent the number of species that have not been observed in recent years and were thus not available for our phylogenetic analyses.

	Mascarenes	Réunion	Mauritius	Rodrigues
Number of species	232	208 (17)	162 (25)	19 (2)
Number of endemics	46	15	13	1
% endemism	19.8	7.2	8.0	5.3

Table 4 Leptosporangiate fern families represented in the Mascarene Islands. Names are based on Smith *et al.* (2006) and Christenhusz *et al.* (2011) except for Arthropteridaceae (see Liu *et al.*, 2013). NMS, number of Mascarene species; NME, number of Mascarene endemics; GFD, global family diversity (= number of species) (Smith *et al.*, 2006); NMS/GFD, Mascarene species/global family diversity as a percentage; C-MD, contribution to Mascarene fern diversity; CF-GFD, contribution of family to global fern diversity. Families significantly over- or under-represented in the Mascarene Islands relative to their global diversity are marked by asterisks (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$).

	NMS	NME	GFD	NMS/ GFD	C-MD	CF- GFD
Families	232	46	8648	2.68		
Anemiaceae	1	0	100	1.0	0.4	1.1
Arthropteridaceae	3	0	20	15.0	1.5**	0.2
Aspleniaceae	23	3	700	3.3	11.5**	7.7
Athyriaceae	7	0	600	1.2	3.0**	7.7
Blechnaceae	5	1	200	2.5	2.2	2.2
Cyatheaceae	4	4	600	0.7	2.6**	6.6
Cystopteridaceae	1	0	30	3.3	0.4	0.2
Davalliaceae	2	0	65	3.1	0.7	0.7
Dennstaedtiaceae	8	0	170	4.7	3.0**	1.9
Dryopteridaceae	46	24	1693	2.7	19.3	18.8
Gleicheniaceae	5	0	125	4.0	2.2*	1.4
Hypodematiaceae	1	0	7	14.2	0.4	0.1
Hymenophyllaceae	24	1	600	4.0	8.2**	6.6
Lindsaeaceae	4	0	200	2.0	1.5	2.2
Lomariopsidaceae	3	2	70	4.3	1.5	0.8
Marsileaceae	1	0	75	1.3	0.4	0.8
Nephrolepidaceae	5	0	21	23.8	1.8***	0.2
Oleandraceae	1	0	12	8.3	0.4	0.1
Osmundaceae	1	0	20	5.0	0.7	1.7
Polypodiaceae	23	4	1200	1.9	9.2***	13.3
Pteridaceae	40	4	950	4.2	17.5***	10.5
Schizaeaceae	2	0	30	6.7	0.4	0.3
Tectariaceae	2	0	210	1.0	1.1*	2.3
Thelypteridaceae	21	3	950	2.2	7.8**	10.5

tion, with nomenclatural authorities for all species cited). Only 10 non-leptosporangiate ferns occur on the islands; none of these are endemic.

We restricted our study to the leptosporangiate ferns of the Mascarenes so that we could compare their phylogenetic structure with a global phylogeny, based on 400 leptosporan-

giate fern species, published by Schuettpelz & Pryer (2007). Their sampling has the twofold advantage of representing the global diversity of leptosporangiate ferns and, compared with the extensive sampling of Lehtonen (2011), to be sampled approximately in proportion to lineage species richness. We either generated, or obtained from GenBank, *rbcL* sequences for all but 24 of the 232 leptosporangiate species occurring in the Mascarenes. The missing species were mainly endemics known from a single or a few old collections. For three species of *Ctenitis* (Dryopteridaceae), we could not generate the *rbcL* sequence but we were able to generate sequences for *trnL-trnF* and *psbA-trnH*. Because we observed no sequence variation in the obtained plastid DNA regions among all Mascarene *Ctenitis* species (S. Hennequin *et al.*, unpublished), we included the three species in our dataset using the *rbcL* sequence shared by all other *Ctenitis* species in the Mascarene Islands.

Our Mascarene dataset thus included 211 species, assembled as follows: (1) we excluded all infraspecific taxa and exotic species; (2) we generated our own sequences for as many species as possible from Mascarene material; (3) we supplemented our own sequences with additional Mascarene sequences from GenBank as necessary; and (4), if no material/sequence was available for the Mascarenes, we used material or sequence from the closest possible region, i.e. the Indian Ocean region, then Africa, then more remote areas. Five species belonging to the Marattiaceae were included as outgroup taxa (two newly sequenced). Family classification follows Smith *et al.* (2006) and Christenhusz *et al.* (2011).

DNA sequencing

DNA was extracted from silica-dried material or from herbarium material following the modified CTAB method (Doyle & Doyle, 1987) plus DNA purification step using the Qiaquick PCR purification kit (Qiagen, Valencia, CA, USA). The *rbcL* gene was amplified and sequenced using the primers *rbcL1F* (Olmstead *et al.*, 1992) and *rbcL1351R* (Gastony & Rollo, 1995) plus the internal primers 645F and 663R (Schuettpelz & Pryer, 2007). After purification, PCR products were directly sequenced using BigDye Terminator kits and an ABI 3730 capillary DNA analyser (Applied Biosystems, Carlsbad, CA, USA). We newly generated 122 *rbcL* sequences (GenBank accession numbers KF992410–KF992531; Appendix S1).

Phylogenetic analyses

Sequences for Mascarene species were aligned with the *rbcL* sequences of the 400 species sample of Schuettpelz & Pryer (2007) using MACCLADE 4.03 (Maddison & Maddison, 2001). This resulted in a total number of 571 species, because the Schuettpelz & Pryer (2007) sampling already included species occurring in the Mascarenes (Appendix S1). The phylogenetic hypothesis was obtained by carrying out maximum likelihood (ML) analyses including rapid boot-

strap analyses using RAxML 7.2.8 via the RAxML black box at <http://embnet.vital-it.ch/raxml-bb/> (Stamatakis *et al.*, 2008). A gamma model of rate heterogeneity was applied, in accordance with the TVM+I+G model of sequence evolution determined by jMODELTEST 2.1.1 (Darriba *et al.*, 2012).

Evaluating immigration and *in situ* speciation

The number of colonization events was estimated by counting, using the phylogeny obtained, the number of clades solely composed of Mascarene species. *In situ* speciation was evaluated based on the number of endemics. Following Stuessy *et al.* (2006), we further quantified anagenesis (when the colonist species gives rise to only one species) versus cladogenesis (when at least two species result from a single colonization event) by counting the number of clades with only one endemic species versus those with more than one endemic species. This was performed at the archipelago scale. Our value for cladogenesis represents a maximum because increased taxon sampling may reveal that some cladogenetic events inferred here result, in fact, from independent colonizations, and cladogenesis at the archipelago scale may reflect anagenesis at the island scale.

Analyses of phylogenetic structure

Species pools and phylogenetic trees

The phylogenetic structure of the Mascarene fern flora (local species pool) was assessed by comparison with a global species pool corresponding to the sampling by Schuettpelz & Pryer (2007). We proceeded in two steps.

First, we used a species pool including all Mascarene taxa for which we had an *rbcL* sequence (similar to the sampling used for the initial phylogenetic analyses, i.e. 211 species; hereafter named 'all species' pool). The phylogenetic tree associated with this species pool is the 571-species tree previously mentioned. To investigate whether there was any difference between the Mascarene Islands, we also conducted separate analyses for Réunion and Mauritius. We did not explore the phylogenetic structure of the fern flora in Rodrigues, because it hosts only a small number of fern species (19).

In a second step, having identified colonization events on the phylogeny, we investigated the phylogenetic structure of colonist species only (197 species, named 'colonists only' pool). To obtain a phylogenetic tree including only these 197 species as Mascarene representatives, we re-ran phylogenetic analyses using this new sampling (now restricted to 551 species).

For these two steps, a small number of Mascarene species were missing from the local species pool, owing to the lack of DNA sequences (respectively, 21 and 11). To check the impact of the exclusion of these species from the phylogenetic structure analyses, we constructed a second species pool where they were included, for both analyses. To obtain the appropriate phylogenetic tree, we inserted the missing species

directly into the 571-species or 551-species trees using MES-QUITE 2.75 (Maddison & Maddison, 2011), using information on their phylogenetic placement from other phylogenetic studies. Species for which no information could be found (11 and 9, respectively) were placed at the base of the corresponding genus or family clade. In order to conserve branch length information, the branch leading to the included taxon was assigned the same length as the branch leading to its sister group.

As is required for these analyses and prior to running community structure analyses, the four phylogenetic trees used were transformed to ultrametric trees. This was done by nonparametric rate smoothing (Sanderson, 1997) implemented in TREEEDIT, version 1.0a10 (Rambaut & Charleston, 2002). In parallel, to test for any difference using another dating method, we conducted a Bayesian inference of divergence times, on the 571-species dataset, using BEAST 1.7.4 (Drummond *et al.*, 2012). The divergence of the crown group of leptosporangiate ferns (299 Ma) was used as constraint. The use of chronograms obtained either by NPRS or by BEAST led to similar phylogenetic structure results. Further analyses (on 'colonists only' and including missing species) were therefore conducted on trees ultrametrized by NPRS, which requires less computational time. In a final step in the preparation of trees, we pruned the five outgroup species (non-leptosporangiate ferns) from all trees.

Phylocom analyses

We calculated two measures of phylogenetic structure (Webb, 2000): (1) the net relatedness index (NRI), which quantifies the overall distribution of taxa on a phylogeny; and (2) the nearest taxon index (NTI), which quantifies the distribution of taxa near the tips of the phylogeny. For both indices, positive values indicate clustering and negative values indicate overdispersion. Analyses were carried out using the function 'comstruct' in PHYLOCOM 4.1 (Webb *et al.*, 2008). We tested each of the four randomization models implemented in PHYLOCOM, with 999 randomization runs.

We used the 'nodesig' algorithm as implemented in PHYLOCOM to identify the clades that contribute the most to the inferred patterns of phylogenetic structure. This function evaluates, using the list of species in the community and the phylogenetic tree used for 'comstruct', whether some clades have more, or fewer, representatives in the local community than expected by chance. This uses null model 2 (random draws of s species from the phylogeny terminals, where s is the number of species in a sample; Webb *et al.*, 2008).

Correlation tests

In order to investigate why some clades may be over-represented on the Mascarene Islands, we tested for correlation between habit [terrestrial or non-terrestrial (i.e. epiphytic or lithophytic)] and species origin by speciation (anagenesis

plus cladogenesis), or species origin by cladogenetic speciation. We used the Pagel94 module implemented in MES-QUITE, which tests for the independent evolution of two binary characters (Pagel, 1994).

RESULTS

Species richness

In total, 232 leptosporangiate fern species are known to have occurred on the Mascarene Islands within historical times, including 208 on Réunion, 162 on Mauritius, and 19 on Rodrigues (Table 3). Réunion and Mauritius share 145 species while 53 and 20 species, respectively, have only been recorded on Réunion and Mauritius. Rodrigues shares all its species with either one or both of the larger islands, except for one endemic species. In total, 46 (19.8%) species are endemic to the Mascarenes, with 32 on Réunion (including 15 that are endemic to only that island), 26 on Mauritius (including 13 endemic to only that island), and one on Rodrigues (endemic to only that island). The distribution of each Mascarene species is summarized in Appendix S1.

The fern families with the highest number of species in the Mascarenes (Table 4) are the Dryopteridaceae (46 species), Pteridaceae (40 species), Hymenophyllaceae (24 species), Polypodiaceae (23 species), Aspleniaceae (23 species) and Thelypteridaceae (21 species). The Dryopteridaceae shows the highest number of endemics (24 species). The number of species per family represented in the Mascarene Islands differs significantly from a random sample based on the global species numbers of these families (Table 4; G-test, $G_{adj} = 63.4$, $P < 0.001$). Seven families (Nephrolepidaceae, Arthropteridaceae, Dennstaedtiaceae, Pteridaceae, Gleicheniaceae, Hymenophyllaceae and Aspleniaceae) have significantly more species on the Mascarene Islands whereas five families (Athriaceae, Cyatheaceae, Polypodiaceae, Tectariaceae and Thelypteridaceae) are significantly under-represented. Twelve families show no significant deviations from their global representation.

Contribution of colonization and speciation

For the Mascarenes as a whole, we infer approximately 197 independent colonization events by leptosporangiate ferns (Fig. 1, Appendix S2) and deduce that 46 species evolved *in situ* from speciation processes following at least 20 colonization events. Among these 46 endemic species, at least 16 species have originated from anagenesis and up to 30 species have originated from cladogenesis. The clades for which we inferred cladogenesis belong to *Alsophila* (Cyatheaceae), *Amauropelta* (Thelypteridaceae), *Asplenium* (Aspleniaceae), and *Ctenitis*, *Dryopteris*, *Elaphoglossum* and *Megalastrum* (all Dryopteridaceae). Cladogenesis may also have occurred in *Lomariopsis* (Lomariopsidaceae), but DNA sequences are missing for two endemics. Our data also suggest cladogenesis

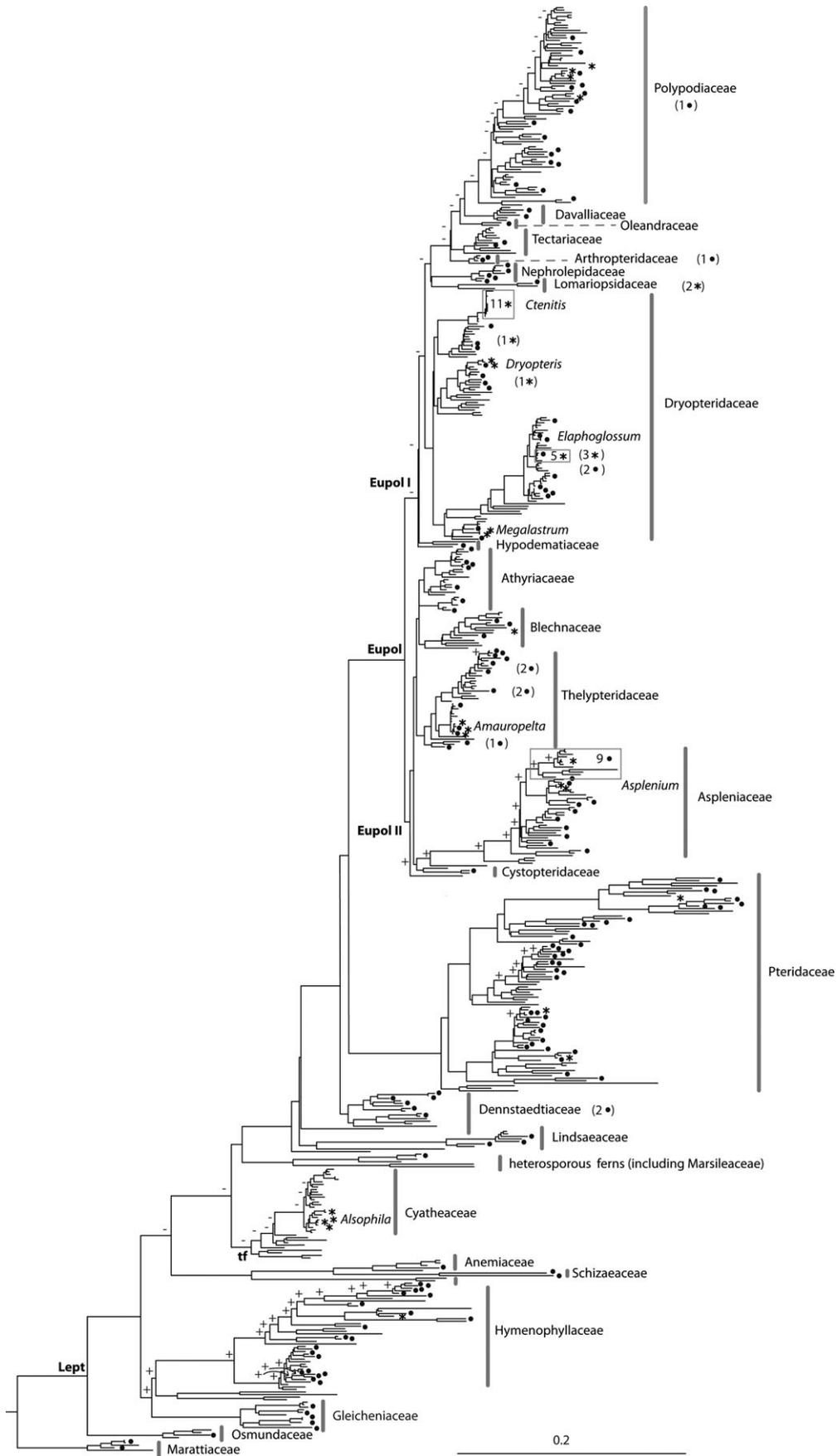


Figure 1 Phylogenetic hypothesis for leptosporangiate ferns inferred from maximum likelihood. Families occurring in the Mascarenes are indicated on the right; species occurring in the Mascarenes are identified by black dots (indigenous species) or stars (indigenous endemic species). In clades with many Mascarene representatives, the total number of indigenous/endemic species is indicated followed by a dot or a star, as appropriate, in a frame showing the clade involved. We further indicate, in parentheses and in their expected position (family or genus), the Mascarene species for which DNA data is still lacking followed by a dot or star as appropriate. Genera where we identify cladogenesis are also indicated. Nodes with respectively more or less descendants than expected as found by ‘nodesig’ are indicated as ‘+’ or ‘-’ (results for the ‘colonists only’ species pool). Lept = leptosporangiate ferns; Eupol = eupolypods; tf = tree ferns.

in *Ceradenia* (Polypodiaceae), but this was not confirmed with a broader sampling including Madagascan species [G. Rouhan, Muséum National d’Histoire Naturelle (MNHN), Paris, pers. comm.].

Phylogenetic structure of the Mascarene fern flora

No significant difference in the results was observed using the four randomization models of PHYLOCOM. We thus only report calculations obtained using model 2. For the ‘all species’ pool (including colonization and *in situ* speciation), we obtained negative NRI and positive NTI for all floras (i.e. the Mascarenes as a whole, and Réunion and Mauritius treated separately, Table 5). Calculations performed on the ‘colonists only’ species pool provided more negative NRI and slightly lower NTI values (Table 5). The tentative inclusion of the missing species did not alter this trend, although both NRI and NTI were slightly higher.

Table 5 Net relatedness index (NRI) and nearest taxon index (NTI) for the Mascarene leptosporangiate fern flora estimated from PHYLOCOM using various local species pools.

Community	All species		Colonists only			
	Number of taxa	NRI	NTI	Number of taxa	NRI	NTI
Mascarenes	211	-1.07	4.43	197	-1.15	3.8
Réunion	197	-1.08	3.62			
Mauritius	145	-1.88	2.77			

Table 6 Results of the ‘nodesig’ analyses using the two Mascarene leptosporangiate fern species pools. Presented results indicate families with significantly more (+) or less (-) Mascarene descendants than predicted by the null model. *indicates cladogenetic events, +/- indicates the presence of 1–5 significant deviated subtending nodes, ++/-- indicates the presence of 6–12 significant deviated subtending nodes.

Family	Node	All species	Colonists only	Life form
Hymenophyllaceae	<i>Crepidomanes</i>	++	++	Mainly epiphytic
	<i>Hymenophyllum</i>	+	+	Mainly epiphytic
Pteridaceae	Cheilanthoids	+	+	Terrestrial
Aspleniaceae	<i>Asplenium</i> *	++	++	Epiphytic or lithophytic
Thelypteridaceae	<i>Cyclosorus</i> subg. <i>Christella</i>	+	+	Terrestrial
	<i>Amauropelta</i> *	+		Terrestrial
Dryopteridaceae	<i>Ctenitis</i> *	++		Terrestrial
Cyatheaceae	Basal node	--	--	Terrestrial-tree habit
Polypodiaceae	Grammitid ferns	-	-	Mainly epiphytic
	Basal nodes	--	--	Mainly epiphytic

Clades with more representatives than expected by chance (Table 6, Fig. 1) were found in the Hymenophyllaceae (four nodes each in *Crepidomanes* and *Hymenophyllum*), Aspleniaceae (*Asplenium*), Thelypteridaceae (*Amauropelta*, *Cyclosorus* subg. *Christella*), Dryopteridaceae (*Ctenitis*), and Pteridaceae (cheilanthoid ferns). Clades with fewer descendants than expected by chance were found in the Cyatheaceae and Polypodiaceae.

Correlations between habit and speciation

Nearly all taxa undergoing cladogenesis on the Mascarene Islands occur in terrestrial habitats or are climbers rooted in the soil. The exceptions are some *Asplenium* species (occupying various habitats) and *Elaphoglossum*, which is mostly epiphytic to lithophytic. Terrestrial species represent nearly 85% of the species of cladogenetic origin, compared with nearly 58% in the whole indigenous flora (Table 7), and a significant correlation was found between terrestrial habit and cladogenetic speciation ($P < 0.001$). The endemics as a complete group (i.e. those of cladogenetic origin plus those of anagenetic origin) also have a larger proportion of terrestrial species than the whole indigenous flora (c. 70% vs. c. 58%) but no significant correlation was found between habit and speciation in general.

DISCUSSION

The recovered phylogeny was consistent with current phylogenetic hypotheses on ferns including some ambiguities in the context of deeper nodes (e.g. relationships of filmy ferns

Table 7 Comparison of the proportions of terrestrial and non-terrestrial (epiphytic or lithophytic) species in the indigenous, endemic and endemic species of cladogenetic origin in the Mascarene fern flora.

	Number of species	Number and percentage of terrestrial species (including climbers rooted in soil)	Number and percentage of non-terrestrial species	Number and percentage of species showing both growth forms
Indigenous species	232	134 (57.8%)	78 (33.6%)	20 (8.6%)
Endemic species (<i>in situ</i> speciation)	46	32 (69.6%)	9 (19.6%)	5 (10.9%)
Endemic species of cladogenetic origin	26*	22 (84.6%)	2 (7.7%)	2 (7.7%)

*This number only includes species for which a DNA sequence was obtained.

and gleichenoid ferns; Lehtonen, 2011; Schuettpelz & Pryer, 2007). The various values obtained in this study may be subject to changes by improved phylogenies and taxonomy, but we expect these changes to be slight.

The assembly of the Mascarene fern flora from immigration

Immigration has clearly played the major role in the assembly of the Mascarene fern flora, with at least 197 colonization events. A greater contribution from colonization than from *in situ* speciation was expected considering the high dispersal capacities of ferns and the relative proximity of the nearest source of species, Madagascar (Table 2). The documented overdispersion of the Mascarene indigenous fern flora is in agreement with the occurrence on these islands of all major leptosporangiate fern families (Table 4) and most major genera. Families with no representatives on the Mascarene Islands are families with few species that are also absent from Madagascar.

The documented overdispersion pattern also means that the Mascarene ferns are less closely related than would be expected by chance, suggesting that competitive interactions played an important role in the assembly of the Mascarene flora (Table 1, prediction 4). Considering the age and topography of Réunion and Mauritius, we suggest that both islands have reached at least the 'maturity' age of the general dynamic model of oceanic island biogeography (Whittaker *et al.*, 2008), and therefore are probably old enough to have filled their communities by the accumulation of species that arrived by long-distance dispersal plus those species that originated from *in situ* speciation thereafter. Although it remains to be tested, this argument is further supported at local scales, with numbers of species recorded on Réunion similar to richness values from tropical America and Asia (Kessler *et al.*, 2010, 2011). If verified, the ecological saturation in the Mascarene Islands is likely to promote strong competition among species and preclude further establishment of closely related species, in accordance with the general prediction by Emerson & Gillespie (2008, p. 626) that on remote islands, 'local overdispersion between close relatives [becomes] more important over time as communities are filled'. The competition hypothesis must, however, be nuanced with regard to the following points. First, it relies

on the assumption of niche conservatism, which was supported in some studies on ferns (Bystriakova *et al.*, 2010; Kluge & Kessler, 2011). Second, the impact of the source pool remains to be evaluated because its definition influences the phylogenetic structure recovered. A sampling covering all possible sources of colonists, especially the ferns of Madagascar, would ideally be required (Lessard *et al.*, 2011) but is not yet available. Last, the inference of ecological processes from phylogenetic structure (Table 1) is subject to controversy and remains to be refined; for example, other factors such as herbivores or stochastic disturbance may also influence the phylogenetic structure (Johnson & Stinchcombe, 2007).

The positive NTI values for the Mascarene indigenous flora and for each island, even for the colonist-only floras (thus excluding prediction 2), carries a signal of aggregation at the tips of the branches (Kembel & Hubbell, 2006). In combination with negative NRI, positive NTI indicates the presence of several clusters of indigenous species, evenly distributed in the tree. The hypothesis of environmental filtering at a finer taxonomic scale may explain these results. Evidence for environmental filtering has previously been reported for fern communities in temperate forests (Karst *et al.*, 2005) and along tropical elevation gradients (Kluge & Kessler, 2011). However, in the case of oceanic islands alternative factors, such as variation of traits influencing dispersal capacity, need to be considered (prediction 3).

The assembly of the Mascarene fern flora from *in situ* speciation

The dominant role played by long-distance dispersal in the assembly of the Mascarene fern flora does not negate the impact of speciation, as evidenced by the endemism level of 19.8%. This percentage is similar to that observed for the fern flora of the Marquesas Islands (Wagner & Lorence, 2002) but is low compared with the 77% endemism in the fern flora of the much more isolated Hawaiian Islands (Geiger *et al.*, 2007). It is also lower than the 45% endemism in the fern flora of Madagascar (Rakotondrainibe, 2003). This difference is likely to be due to the differences in history, area size, topographic complexity and overall fern diversity. Up to 65% of the Mascarene endemic species originated from cladogenesis. This percentage is close to the mean value

of 60% estimated for the whole pteridophyte flora of nine archipelagos and to the percentages estimated for pteridophytes of the Canaries, Juan Fernández and Tristan da Cunha by Patiño *et al.* (2014). This may be attributed to the topographical complexity of the Mascarenes and of these island systems, promoting habitat heterogeneity, disjunct populations and hence microallopatric speciation (Stuessy, 2007). Overall, the relative contribution of immigration, cladogenesis and anagenesis in the composition of the Mascarene fern flora is consistent with predictions from the unified model of island biogeography proposed by Rosindell & Phillimore (2011, Fig. 2c therein) for islands of similar area and isolation.

We identified cladogenetic events in *Ctenitis* (up to 11 species including *Heterogonium sieberianum*), *Amauropelta* (probably 3 species), *Asplenium* (at least 2 species), *Dryopteris* (2–3 species), and maybe *Lomariopsis* (2 species). Species involved are highlighted in Appendix S2. This is in addition to previously identified cladogenetic events in *Elaphoglossum* (Rouhan *et al.*, 2004; 3 species) and *Alsophila* (Janssen *et al.*, 2008; 4 species from two events), and one suggested for *Megalastrum* (Rouhan & Moran, 2011; 2 species). All these cladogenetic events are shared between Mascarene islands, apart from one restricted to Réunion (in *Alsophila*). The cladogenetic events newly revealed remain to be thoroughly documented using a taxonomic sampling covering the whole South West Indian Ocean region. Preliminary results suggest cladogenesis on the Mascarene Islands in *Ctenitis* (S. Hennequin *et al.*, unpublished) and *Amauropelta* (A. Salino *et al.*, unpublished), and ongoing differentiation processes in the *Asplenium daucifolium* and *A. nitens* complexes (H. Schneider *et al.*, unpublished).

Little is known about the drivers of cladogenesis in ferns, but several studies support the idea that colonization of new habitats and climatic fluctuations leading to habitat changes have been major drivers within the last 60 million years (Schneider *et al.*, 2005; Nagalingum *et al.*, 2007; Janssen *et al.*, 2008; Eiserhardt *et al.*, 2011; Wang *et al.*, 2012). Even less is known about the relation of niche differentiation and fern speciation (Bystrakova *et al.*, 2010). On oceanic islands, speciation is more likely to occur when the island has attained a level of topographic complexity generating various ecological niches, but also while these niches are still vacant. This corresponds to the ‘immaturity phase’ of the general dynamic model of oceanic island biogeography (Whittaker *et al.*, 2008) or the ‘early development phase’ of Stuessy (2007). To validate this hypothesis, we would need to accurately date the cladogenetic events revealed here, a major challenge on its own.

Differences in colonization and speciation successes

Our study indicates clear differences in colonization and speciation successes among fern lineages in the Mascarenes. Clades resulting from frequent colonization events notably occur in the Hymenophyllaceae (at least 22 colonization

events), Aspleniaceae (at least 21), and the cheilantheid ferns (at least 10) (Fig. 1, Tables 4 & 6). Three main processes may explain this pattern: (1) better colonization capacities; (2) preadaptation of these taxa to Mascarene habitats (i.e. having an ecological niche in the source area that will be available at some point in the Mascarenes), improving chances of establishment; and (3) reduced competition with co-colonizing congeners. All these groups are well represented in the African–Indian Ocean region, which may imply both higher chances of colonizing the Mascarenes and preadaptation, but this is not a general rule as other taxa that are well represented in the region were found to be under-represented in the Mascarenes (e.g. Cyatheaceae and grammitid ferns). Abundance of immigrant species in their source area should also be considered in future studies.

In tropical ferns, there appears to be a difference in ecological strategies, e.g. longevity and asexual reproduction, displayed by gametophytes of terrestrial and epiphytic species (Dassler & Farrar, 2001; Watkins *et al.*, 2007). Some strategies may enhance the probability of finding a mating partner in epiphytic habitats and, in turn, the ability of epiphytic species to colonize distant habitats. Epiphytes may also have higher dispersal capacities because, growing high up in trees, wind is likely to disperse their spores further, and they inhabit an inherently unstable environment that selects for good dispersers and colonizers. Such capacities may explain the over-representation of epiphytic filmy ferns belonging to *Hymenophyllum* and *Crepidomanes*. The Mascarene fern flora shows a high percentage of species growing as epiphytes or lithophytes (42% including the 8.6% having a variable habit, Table 7), compared with only 20% for South Africa and 26.3% for Madagascar (Dassler & Farrar, 2001). In contrast, the higher representation of terrestrial ferns among the endemics suggests that terrestrial ferns may generally be less successful colonists than epiphytic ones, resulting in a higher probability of undergoing *in situ* speciation and especially cladogenetic speciation. Additionally, epiphytic species may have less opportunity for allopatric speciation because they show lower beta diversity than terrestrial ferns, leading to less patchy populations.

A quite distinct pattern was found in *Asplenium* where many Mascarene species show close relationships. For example, *A. nitens*, *A. sulcatum*, *A. lividum*, *A. protensum* and *A. aethiopicum* belong to the *Tarachia* clade (Schneider *et al.*, 2005) but differ in their ecological preferences, ranging from epiphytic, hemiepiphytic, lithophytic and occasional terrestrial growth forms. Such ecological differentiation may provide opportunities to allow congeners to co-exist, as has been shown for the *Anolis* lizards on the Caribbean Islands (Losos *et al.*, 2003).

Clades with fewer representatives in the Mascarenes than expected by chance occur mainly in Cyatheaceae and Polypodiaceae, both of which are well represented on Madagascar. The failure of numerous closely related tree ferns to colonize the Mascarenes from Madagascar may be

due to limited dispersal capacity related to terrestrial habit or niche pre-emption. Within the Polypodiaceae, the under-representation of grammitids may be related to their biogeographical history.

CONCLUSIONS AND PERSPECTIVES

The Mascarene fern flora is a mix of colonist, cladogenetic and anagenetic species, making it quite distinct in composition from its most probable source, the fern flora of Madagascar. First, its assembly by immigration – the dominant process – was not random: the overdispersion pattern supports the hypothesis that competitive interactions may have played a dominant role in the flora assembly. However, the aggregation patterns observed at the tips of the phylogeny suggest the role of other processes at a finer taxonomic scale, such as variation in colonization. To confirm these results, future studies should aim to construct a source pool including all Madagascan species. Second, numerous *in situ* speciation events have occurred or are likely to be underway in the Mascarenes. Our study suggests differences in colonization or speciation success among taxonomic groups, which may be related to their habits.

The dataset assembled in this study, on a lineage and on an island system that are both inadequately investigated, will be of use to researchers attempting to model island biogeography. Further studies should also aim to assess the geographical origin of the Mascarene colonists, the tempo of colonization (including exchanges among the islands), and explore the cladogenetic events revealed in this study to elucidate aspects of fern speciation such as geographical isolation and niche differentiation. The characterization of ecological niches may be achieved by a thorough study of morphological traits and ecological specifications (Creese *et al.*, 2011), which would then allow testing for niche conservatism. Investigation of traits associated with colonization and speciation, at various scales (Peres-Neto *et al.*, 2012) and along ecological gradients (Savage & Cavender-Bares, 2012), is also expected to provide further insights into the ecological processes involved in the assembly of the Mascarene ferns.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 List of Mascarene leptosporangiate fern species and dataset used.

Appendix S2 Leptosporangiate fern phylogeny inferred from maximum likelihood.

BIOSKETCH

S. Hennequin is an assistant professor at the Université Pierre et Marie Curie in Paris. Her research focus is on systematics, biogeography and evolution of ferns. She is particularly interested in colonization and speciation in the islands of the South West Indian Ocean.

The authors share a strong research interest in the macroevolution of ferns. Together they are interested in understanding the factors shaping the spatial and temporal accumulation of plant diversity.

Author contributions: S.H. and H.S. designed and managed the project; S.H. carried out laboratory work and analyses; all contributed to fieldwork in the Mascarene Islands; S.L. provided critical information on, and material of, rare species of Mauritius. S.H., M.K. and H.S. led the writing with contributions from all authors.

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