The anagenetic world of spore-producing land plants

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Summary

- A fundamental challenge to our understanding of biodiversity is to explain why some groups of species diversify, whereas others do not. On islands, the gradual evolution of a new species from a founder event has been called 'anagenetic speciation'. This process does not lead to rapid and extensive speciation within lineages and has received little attention.
- Based on a survey of the endemic bryophyte, pteridophyte and spermatophyte floras of nine oceanic archipelagos, we show that anagenesis, as measured by the proportion of genera with single endemic species within a genus, is much higher in bryophytes (73%) and pteridophytes (65%) than in spermatophytes (55%).
- Anagenesis contributed 49% of bryophyte and 40% of endemic pteridophyte species, but only 17% of spermatophytes. The vast majority of endemic bryophytes and pteridophytes are restricted to subtropical evergreen laurel forests and failed to diversify in more open environments, in contrast with the pattern exhibited by spermatophytes.
- We propose that the dominance of anagenesis in island bryophytes and pteridophytes is a result of a mixture of intrinsic factors, notably their strong preference for (sub)tropical forest environments, and extrinsic factors, including the long-term macro-ecological stability of these habitats and the associated strong phylogenetic niche conservatism of their floras.

Introduction

A fundamental challenge to our understanding of biodiversity is to explain why some groups of species diversify, whereas others do not (Emerson & Kolm, 2005; Wagner *et al.*, 2012). The theory of 'punctuated equilibrium' (Gould & Eldredge, 1993) proposes that species change suddenly during short bursts associated with speciation ('cladogenetic change'; for a review, see Bokma, 2008). It is best exemplified on oceanic islands, where adaptive radiations have led to spectacular cases of endemic speciation (for reviews, see Losos & Ricklefs, 2009; Givnish, 2010). By contrast, speciation may also arise through the spatial isolation and progressive divergence of populations along the periphery of a species range ('budding' or 'peripheral speciation'; for a review, see Funk & Omland, 2003). On islands, the gradual evolution of a new species from a founder event has been called 'anagenetic speciation' (Stuessy *et al.*, 2006; Gehrke & Linder, 2011). This process does not lead to rapid and extensive speciation within lineages, as adaptive radiation may do, and has consequently received little attention. Nevertheless, anagenesis is much more important than previously thought, accounting for 7–88% of endemic seed plants on oceanic islands (Stuessy *et al.*, 2006).

High levels of anagenesis are promoted by extrinsic environmental conditions, including a low elevation range and low habitat heterogeneity (Stuessy *et al.*, 2006), and an intermediate distance from the mainland, as a result of the trade-off between the number of events potentially fostering anagenesis and the intensity of migration preventing speciation through undisrupted gene flow (Rosindell & Phillimore, 2011). Bryophytes and pteridophytes produce spores, which are much smaller than seeds and are hence likely to be wind dispersed over long distances (Wilkinson *et al.*, 2012). Spore-producing plants therefore appear to be even better candidates for anagenetic speciation than seed plants. Indeed, their high long-distance dispersal capacity might explain their failure to speciate on islands that are close to potential continental sources as a result of intense gene flow (Barrington, 1993; Vanderpoorten *et al.*, 2011). On more remote islands, multiple colonization events may promote anagenetic speciation as multiple island colonizations by congeneric species are thought to lead to non-radiating lineages, possibly as a result of the fast occupancy of all potential niches by the colonizers, which hampers the chances of subsequent radiation ('niche preemption' hypothesis; Silvertown, 2004).

Two additional features of bryophytes and pteridophytes suggest that they might exhibit unparalleled levels of anagenetic speciation. First, in contrast with the vast majority of seed plants, bryophytes and pteridophytes do not tend to develop ecotypes, but rather display an inherent broad ability to cope with

environmental variation. In pteridophytes, photosynthetic performance and ecological breadth have been shown to be associated with ecophysiological plasticity (Saldaña *et al.*, 2005; Huang *et al.*, 2011). In the fern *Athyrium filix-femina* (L) Roth., the absence of correlation between genetic and morphological variation along an elevational gradient points to phenotypic plasticity rather than genetic specialization (Schneller & Liebst, 2007). In the moss *Bryum argenteum* Hedw., plants from clean and heavily polluted environments exhibit indistinguishable growth responses to media supplemented with heavy metals (Shaw *et al.*, 1989; Shaw & Albright, 1990). In the desert moss *Syntrichia caninervis* Mitt., morphological variation of populations from extreme micro-habitats results from plasticity (Reynolds & McLetchie, 2011). This suggests that 'general purpose' genotypes (*sensu* Baker, 1965) confer on bryophytes an inherent high level of tolerance, making the evolution of specialized races unnecessary. Physiological and morphological plasticity therefore appears to be much more important than genetic specialization for bryophytes and pteridophytes (Shaw, 1992; Schneller & Liebst, 2007; Reynolds & McLetchie, 2011; but see Hutsemékers *et al.*, 2010; Richter *et al.*, 2012), potentially hampering the chances of adaptive radiation in response to habitat heterogeneity.

Second, sexual selection, one of the key drivers of rapid radiations in angiosperms (Givnish, 2010), may be less important as a result of the predominance of clonal reproduction in bryophytes (Longton & Schuster, 1983), which culminates on oceanic islands (Hutsemékers *et al.*, 2011; Karlin *et al.*, 2011; Patiño *et al.*, 2013a). This, together with the high rates of selfing in bisexual species (Eppley *et al.*, 2007; Hutsemékers *et al.*, 2013), decreases the chances of hybridization, and hence of the rapid increase in genetic variation and response to ecological selection that characterize many young adaptive radiations ('hybrid swarm hypothesis'; Seehausen, 2004).

Based on a survey of the endemic bryophyte, pteridophyte and seed plant floras of nine oceanic archipelagos, we report extremely high rates of anagenesis among the spore-producing land plant floras on oceanic islands, and discuss the reasons why, in contrast with seed plants, they largely failed to diversify.

Materials and Methods

Following Emerson & Kolm (2005), we used levels of endemism as a proxy for rates of speciation. A potential problem with this approach is that it assumes that endemic species evolved *in situ* (neoendemics). This is not necessarily the case as endemics may be the result of extinction in all other parts of a formerly more widespread range (palaeoendemics), inflating our index of diversification. However, this is likely to be balanced by species that evolved on islands, but became extinct or subsequently migrated to other areas, and therefore are not included in our calculations. In line with the high dispersal capacity of spore-producing plants, available phylogenetic information suggests that the proportion of palaeoendemics in oceanic island endemic floras is much lower than the proportion of neoendemics (Vanderpoorten *et al.*, 2011). Furthermore, although recurrent migrations between

islands and mainland have been reported in several instances (Hutsemékers *et al.*, 2011; Laenen *et al.*, 2011), phylogenetic evidence for the evolution of species on islands with subsequent continental back-colonization is currently lacking in spore-producing plants, so that this mechanism is not expected to substantially bias the calculated speciation rate.

Total numbers of endemic species were partitioned into two groups depending on speciation mode. Anagenesis was inferred when a single endemic species within a genus (single-species endemic; hereafter SSE) was recognized (Stuessy *et al.*, 2006). Cladogenesis was inferred when there were at least two congeneric endemic species (multiple-species endemic; hereafter MSE). Although islands have often been used as geographical units for counting the numbers of SSEs and MSEs (Whittaker & Fernández-Palacios, 2007), bryophytes and pteridophytes exhibit extremely low numbers of species endemic to a single island (Ranker *et al.*, 2000; Vanderpoorten *et al.*, 2011), even though they display speciation rates that are comparable with those reported in seed plants (Wall, 2005; Devos & Vanderpoorten, 2009; Schuettpelz & Pryer, 2009). For practical reasons, we therefore calculated the number of SSEs and MSEs at the archipelago scale. Nine oceanic archipelagos, for which critical and/or updated checklists for the three study plant groups are available, were investigated (Supporting Information Table S1).

Our rates of cladogenesis might be underestimates if cladogenetic endemic species go extinct or migrate to other areas. We are unable to quantify the effect of these two events, as information on extinctions is lacking, mainly because of the extremely poor fossil record in bryophytes, and there is so far no evidence for the migration of neoendemic island species to other areas (as described previously). However, two factors suggest that our rates of anagenesis represent minimum estimates. First, endemic congeneric species are not necessarily the result of cladogenesis following a single colonization event as they could each represent independent colonization events (Stuessy *et al.*, 2006). Second, cladogenesis at the archipelago level may reflect anagenetic speciation at a more restricted level as a radiation could be the result of allopatric speciation, with each species the result of anagenetic speciation on a different island.

Schaefer *et al.* (2011a) questioned the use of taxonomic checklists in biogeographical inferences and suggested that actual endemic diversification might be overlooked as a result of taxonomic shortcomings ('Linnean shortfall'; Brown & Lomolino, 1998). It is evident that the bryophyte floras are still much less well known than their angiosperm counterparts and that, as a result of their reduced morphologies, they are particularly prone to 'cryptic' speciation (e.g. Heinrichs *et al.*, 2011; Carter, 2012; Dong *et al.*, 2012; Medina *et al.*, 2012). However, the increase in the number of species resulting from molecular systematic studies is likely to be counter-balanced by mounting phylogenetic evidence refuting the circumscription of many bryophyte species and suggesting broader species circumscriptions (Vanderpoorten & Shaw, 2010). Population-level analyses in bryophyte species also revealed that the genetic diversity observed on islands mostly results from recurrent migration events from continental areas rather than by *in situ*

diversification (Vanderpoorten *et al.*, 2008; Hutsemékers *et al.*, 2011; Laenen *et al.*, 2011), further weakening the hypothesis of an overlooked diversification of *in situ* origin.

Information on habitat preferences in the endemic flora was retrieved for three archipelagos, namely the Canary Islands, Madeira and Azores, which form a biogeographical region referred to as Macaronesia (*sensu* Engler, 1879). Based on a literature review (Table S1), endemic species were assigned to one of six main ecosystem types defined by Domínguez Lozano *et al.* (2010): coastal vegetation, thermophilous woodlands, laurel forests, pine forests, summit scrublands and open areas (including rocky habitats and anthropogenic disturbed environments). Species and genera occurring in two or more ecosystems were scored as widespread.

Results

In the nine study archipelagos, the proportion of land plant genera exhibiting SSEs reaches 60%, but the overall proportion of species that are SSEs among archipelago endemic floras is substantially lower (21%). In bryophytes and pteridophytes, the predominance of anagenesis was evidenced by the higher proportion of genera with SSEs in bryophytes (73%) and pteridophytes (65%) than in seed plants (55%) (Fig. 1). Anagenesis contributed 49% of bryophyte and 40% of endemic pteridophyte species, but only 17% of seed plant species (Fig. 1).

Anagenesis was largely unrelated to distance from the mainland in bryophytes and pteridophytes (Fig. 2). For instance, high rates of anagenesis (70–80%) were observed in both archipelagos that are close to the nearest continent (e.g. Canaries) and in those located at > 2500 km from the nearest coasts (e.g. Hawaii, Tristan da Cunha) (Fig. 2; Table S2).

The partitioning of bryophyte, pteridophyte and seed plant endemic species across the main vegetation zones in Macaronesia reveals that the vast majority of endemic bryophyte and pteridophyte species are restricted to the subtropical evergreen laurel forest and apparently failed to diversify in more open environments, in contrast with the pattern exhibited by seed plants (Figs 3, S1). Thus, *c.* 80% of Madeiran SSEs in bryophytes and pteridophytes, and 80% of Azorean SSEs in bryophytes are laurel forest specialists (Fig. S1). These values are much lower in Madeiran (28%) and Azorean (22%) SSE seed plants. The trend is even more apparent when considering taxa that are endemic to the entire Macaronesian region (Fig. 3). Among SSE bryophytes and SSE pteridophytes endemic to Macaronesia, 87% and 50%, respectively, are restricted to the laurel forest in the Canaries, 92% and 75%, respectively, in Madeira, and 83% and 50%, respectively, in the Azores. Laurel forest lineages also account for a significant proportion of endemic seed plant SSE lineages (68% in the Canaries and 44% in Madeira; Fig. 3). Lineages of bryophytes, pteridophytes and, especially, seed plants that are restricted to laurel forests exhibit rates of cladogenesis which, in general, are substantially lower than those of anagenesis (Figs 3, S1). By contrast, the highest rates of cladogenesis in seed plants are observed in lineages that are found in more open environments or that are distributed across a number of ecological zones (Figs 3, S1).

Discussion

The 60% of land plant genera that exhibit SSEs and the substantially lower (21%) overall proportion of species that are SSEs suggest that anagenesis is the most common speciation pathway for lineages, but that a few genera contribute the bulk of endemic species richness in oceanic island floras by cladogenesis. In bryophytes and pteridophytes, the predominance of anagenesis was evidenced by the much higher proportion of genera with SSEs in bryophytes (73%) and the slightly higher percentage in pteridophytes (65%) than in seed plants (55%). Anagenesis contributed 49% of bryophyte and 40% of endemic pteridophyte species, but only 17% of seed plant species. Overall, therefore, anagenesis has played a much more substantial role in the evolution of endemic bryophyte and pteridophyte diversity on oceanic islands than in seed plants.

The extremely small numbers of total endemic species, and of endemics restricted to a single island in particular (Patiño *et al.*, 2013b), suggest that anagenetic patterns in bryophytes are driven by their high dispersal capacity, in line with the gene flow intensity (Rosindell & Phillimore, 2011) and niche pre-emption (Silvertown, 2004) hypotheses. However, this interpretation is not consistent with the fact that archipelagos located both close to and remotely distant from the mainland similarly exhibit high rates of anagenesis. The lack of relationship between rates of anagenesis and distance from the source is at first sight consistent with the hypothesis that spore dispersal patterns are better

Fig. 1 (a) Proportion of genera holding endemics, and (b) the proportion of endemic species in the bryophyte, pteridophyte and seed plant floras of nine oceanic archipelagos. Patterns of anagenesis (number of single-species endemics (SSEs) per archipelago, red) and cladogenesis (number of multiple-species endemics (MSEs) per archipelago, pink) are distinguished.

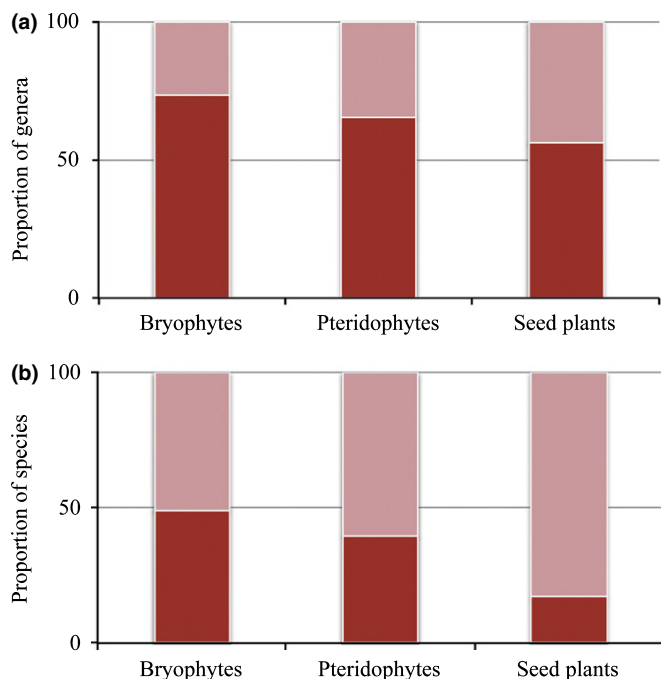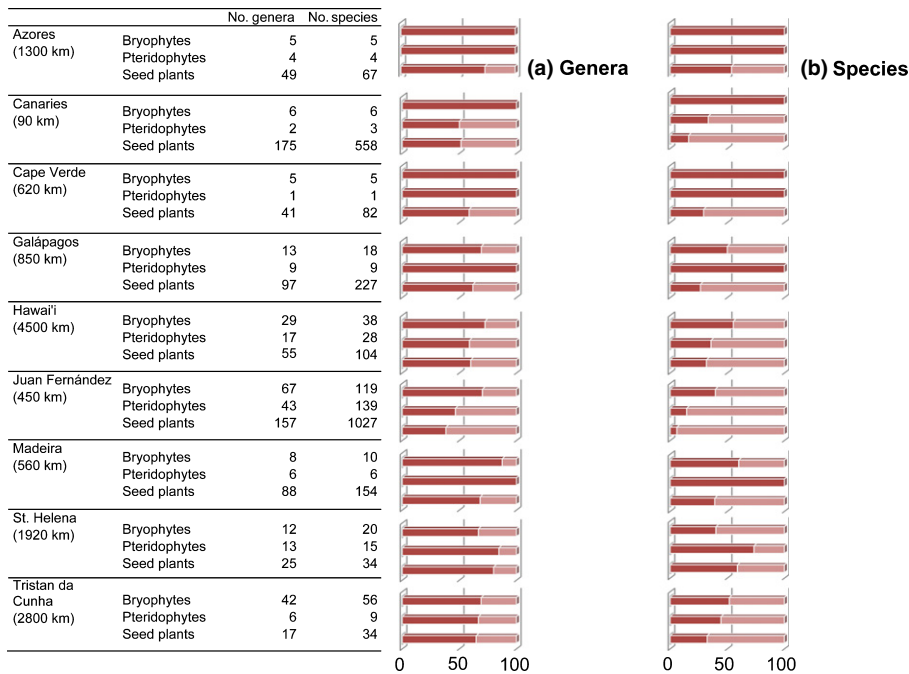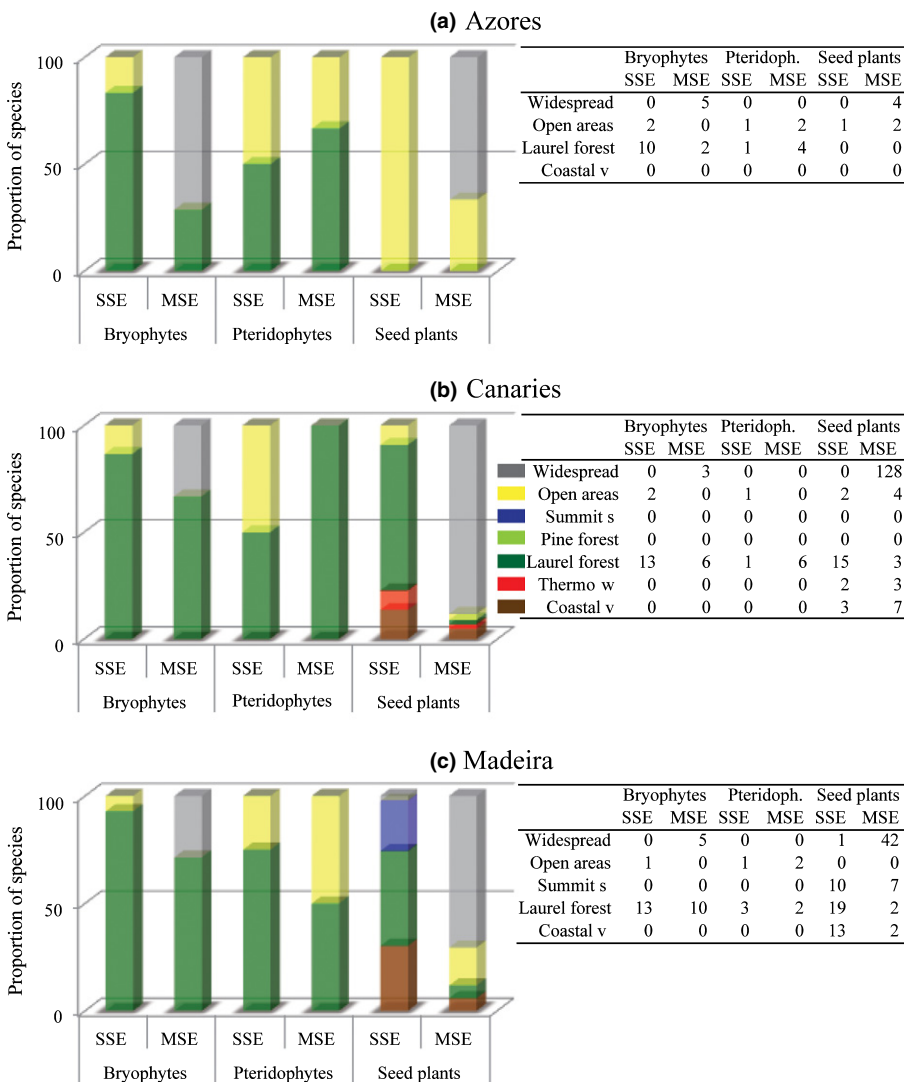|		No. genera	No. species
Azores (1300 km)	Bryophytes	5	5
	Pteridophytes	4	4
	Seed plants	49	67
Canaries (90 km)	Bryophytes	6	6
	Pteridophytes	2	3
	Seed plants	175	558
Cape Verde (620 km)	Bryophytes	5	5
	Pteridophytes	1	1
	Seed plants	41	82
Galápagos (850 km)	Bryophytes	13	18
	Pteridophytes	9	9
	Seed plants	97	227
Hawai'i (4500 km)	Bryophytes	29	38
	Pteridophytes	17	28
	Seed plants	55	104
Juan Fernández (450 km)	Bryophytes	67	119
	Pteridophytes	43	139
	Seed plants	157	1027
Madeira (560 km)	Bryophytes	8	10
	Pteridophytes	6	6
	Seed plants	88	154
St. Helena (1920 km)	Bryophytes	12	20
	Pteridophytes	13	15
	Seed plants	25	34
Tristan da Cunha (2800 km)	Bryophytes	42	56
	Pteridophytes	6	9
	Seed plants	17	34

(a) Genera   **(b) Species**

Fig. 2 (a) Proportion of genera holding endemics, and (b) the proportion of endemic species in the bryophyte, pteridophyte and seed plant floras of nine oceanic archipelagos. Patterns of anagenesis (number of single-species endemics (SSEs) per archipelago, red) and cladogenesis (number of multiple-species endemics (MSEs) per archipelago, pink) are distinguished. The actual numbers of genera and species for SSEs and MSEs are provided.

(a) Azores

	Bryophytes		Pteridoph.		Seed plants	
	SSE	MSE	SSE	MSE	SSE	MSE
Widespread	0	5	0	0	0	4
Open areas	2	0	1	2	1	2
Laurel forest	10	2	1	4	0	0
Coastal v	0	0	0	0	0	0

(b) Canaries

	Bryophytes		Pteridoph.		Seed plants	
	SSE	MSE	SSE	MSE	SSE	MSE
Widespread	0	3	0	0	0	128
Open areas	2	0	1	0	2	4
Summit s	0	0	0	0	0	0
Pine forest	0	0	0	0	0	0
Laurel forest	13	6	1	6	15	3
Thermo w	0	0	0	0	2	3
Coastal v	0	0	0	0	3	7

(c) Madeira

	Bryophytes		Pteridoph.		Seed plants	
	SSE	MSE	SSE	MSE	SSE	MSE
Widespread	0	5	0	0	1	42
Open areas	1	0	1	2	0	0
Summit s	0	0	0	0	10	7
Laurel forest	13	10	3	2	19	2
Coastal v	0	0	0	0	13	2

Fig. 3 Habitat partitioning by vegetation zones of single-species endemics (SSEs) per archipelago and multiple-species endemics (MSEs), with at least two endemic species, per archipelago in the bryophyte, pteridophyte and seed plant floras endemic to at least two Macaronesian archipelagos. Coastal v, coastal vegetation; Thermo w, thermophilous woodlands; Summit s, summit scrublands. The proportions and actual species numbers for the Azores (a), Canaries (b) and Madeira (c) are shown.

explained by wind connectivity than by geographical distance (Muñoz *et al.*, 2004). It is also consistent with the idea that, once airborne, spores travel randomly across various distances (Szövényi *et al.*, 2012). Although these hypotheses cannot be rejected, the idea that cladogenesis is impeded by intense gene flow is, however, weakened by mounting evidence indicating that many bryophyte species exhibit a moderate to strong geographical structure in their local patterns of genetic variation (Hutsemékers *et al.*, 2010, 2013; Korpelainen *et al.*, 2011, 2013; Wang *et al.*, 2012; Leonardía *et al.*, 2013; Patiño *et al.*, 2013b).

From partitioning the occurrence of bryophyte, pteridophyte and seed plant endemic species across the main vegetation zones in Macaronesia, it is apparent that, in contrast with seed plants (Domínguez Lozano *et al.*, 2010), the vast majority of endemic bryophyte and pteridophyte species are restricted to the subtropical evergreen laurel forest and failed to diversify in more open environments. Although bryophytes are physiologically plastic, they are ecologically constrained by their poikilohydric condition, which prevents them from thriving in dry environments (Proctor, 2009). Pteridophytes similarly favour shady and humid environments because of their drought strategy (Hietz, 2010; but see Anthelme *et al.*, 2011). Both groups further evolved the ability to photosynthesize in low light environments (Kawai *et al.*, 2003; Proctor, 2009), where they can avoid competitive exclusion by seed plants.

The failure of most laurel forest species and, by extension, of evergreen (sub)tropical forest biota to diversify could be explained by the stability of their habitat over their palaeoclimatic history (for a review, see Hughes *et al.*, 2013). Typically, rapidly changing environments exhibit more rapid diversification than stable ones (Pennington *et al.*, 2010; but see Kozak & Wiens, 2010). In pteridophytes, radiations have been reported in drought-adapted lineages of highly diversified open environments (Eiserhardt *et al.*, 2011) or coinciding with major environmental changes, such as the radiation of angiosperm-dominated vegetation (Schneider *et al.*, 2004; Schuettpelz & Pryer, 2009) or climate change (Janssen *et al.*, 2008). Although explosive speciation episodes have been reported in some tropical rainforest genera (Richardson *et al.*, 2001), early theories (Stebbins, 1974), supported by recent phylogenetic evidence (Angulo *et al.*, 2012; Särkinen *et al.*, 2012), point to gradual diversification patterns through time in stable tropical forest communities (Crisp *et al.*, 2009; Wiens *et al.*, 2010). In bryophytes and pteridophytes, although epiphytic communities provide a classical example of niche differentiation (Barkman, 1958), adaptive radiations may in fact not take place in a species-saturated tropical forest environment characterized by an extremely high epiphytic biomass (Freiberg & Freiberg, 2000). The strong niche conservatism reported in tropical biomes (Crisp *et al.*, 2009; Crisp & Cook, 2012) would further account for the failure of tropical species to colonize and diversify in habitats that are more prone to trigger radiations. In line with similar observations of steady speciation rates in tropical forest bryophytes (Wilson *et al.*, 2007), we therefore propose that the dominance of anagenesis in oceanic island bryophytes and pteridophytes is a result of a mixture of intrinsic factors, notably their strong preference for (sub)tropical forest environments, and extrinsic factors, that is, the long-term macroecological stability of these habitats and the associated strong phylogenetic niche conservatism of their floras. This hypothesis could be tested with phylogenetic comparative methods (Cooper *et al.*, 2010), given the increasing availability of phylogenies for whole groups at the scale of entire archipelagos (Schaefer *et al.*, 2011b).

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Supporting Information

Additional supporting information may be found in the online version of this article.

Fig. S1 Habitat partitioning by vegetation zones of single- and multiple-species endemics in the bryophyte, pteridophyte and seed plant floras endemic to a single Macaronesian archipelago, including the Azores, Canaries and Madeira.

Table S1 Literature sources used to document patterns of endemicity in the bryophyte, pteridophyte and seed plant floras of nine oceanic archipelagos

Table S2 Geographical features of the nine studied archipelagos

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