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## Research review

# Island disharmony revisited using orchids as a model group

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**Key words:** biotic interactions, disharmony, dispersal, environmental filtering, functional traits, orchids.

## Summary

One central concept in island biology is that island assemblages form subsets of the mainland species pool, being disproportionately rich or poor in certain taxonomic groups. This unbalanced composition, termed ‘disharmony’, is generally explained using a taxon-centred approach, linking the over- or under-representation of taxa to their colonisation abilities. However, islands may also harbour ‘functionally’ disharmonic flora, being disproportionately rich or poor in species with certain traits, which may offer greater insights into the processes driving island colonisation. Here, we use orchids as a model to illustrate key processes involved in the formation of functionally disharmonic island floras, including filtering effects (for example biotic interactions), and speciation. Our synthesis is based on a comprehensive orchid dataset of 27 637 species and combines both a literature review and simple exploratory analyses to show that orchids are significantly under-represented on islands relative to mainland regions and that insular orchids display shifts in functional traits, from the shortening of nectar spurs to facilitate ornithophily to changes in colour associated with generalist insect pollinators. We highlight that taxa are simply coarse proxies and that we need to consider species traits and interactions to gain a full understanding of the processes constraining plant assembly on islands.

## Introduction

Understanding the mechanisms shaping species assemblages remains one of the greatest challenges to the field of ecology. Islands, due to their discrete nature and evolutionary history have played a major role in unravelling these mechanisms, particularly with respect to the distribution of biodiversity, community assembly and evolution (Gillespie, 2004; Warren *et al.*, 2015). One fundamental aspect of island biology theory is that only a subset of species is able to disperse to, colonise and diversify on islands, resulting in an over- or under-representation of certain taxonomic groups relative to their mainland source pools (Carlquist, 1966; Whittaker & Fernández-Palacios, 2007). This biased representation, termed ‘disharmony’, has generally been related to variation in dispersibility, that is, good-dispersing taxa are expected to be over-represented while poor-dispersing taxa tend to be under-represented (Carlquist, 1966, 1974). Ferns, for example, are over-represented on islands, which is at least partly contingent on their microscopic spores that are easily dispersed by wind (Kreft *et al.*,

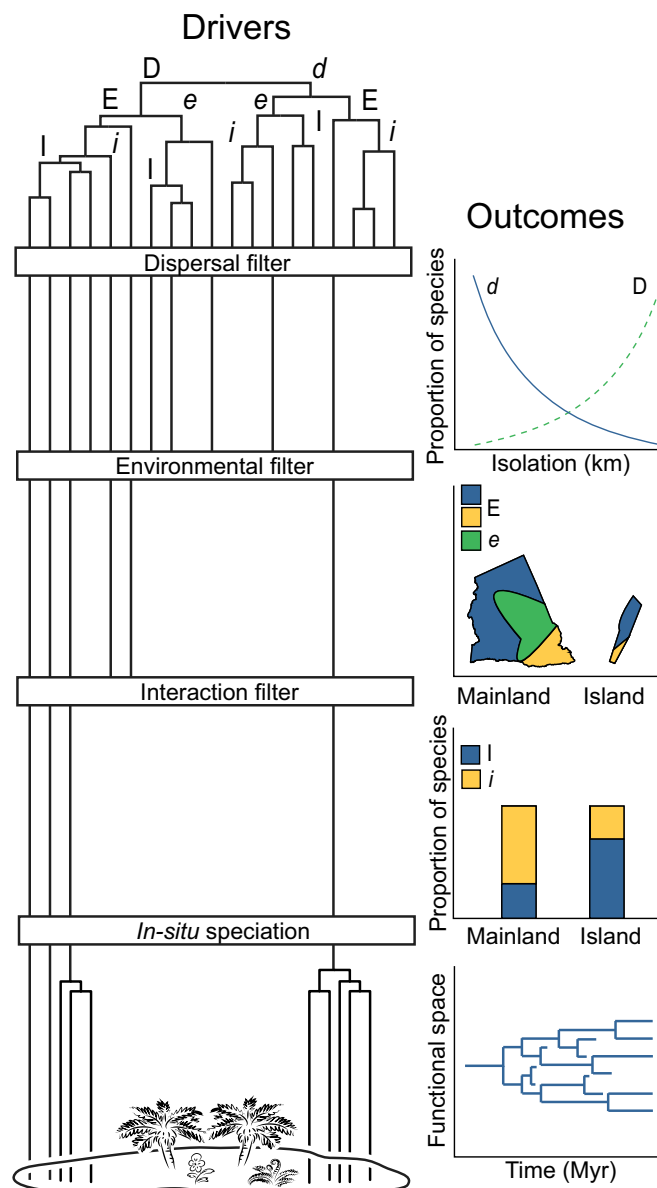
2010). Conversely, poorer dispersers such as nonvolant mammals are generally under-represented on oceanic islands, in large part due to their poor long-distance dispersal capabilities (Carlquist, 1966).

Although the concept of disharmony has a strong theoretical foundation, the general mechanisms responsible for the assembly of disharmonic biotas are commonly inferred from a taxonomic perspective, such as the over- or under-representation of specific genera or families that is then linked to taxon-specific variation in dispersibility. However, there is growing evidence that some plant families commonly characterised as being highly dispersive are under-represented on islands. Asteraceae, for example, are under-represented on the Azores (Heleno & Vargas, 2015), as are Poaceae on New Caledonia (Pillon *et al.*, 2010), and Orchidaceae on Hawai’i and Juan Fernández (Micheneau *et al.*, 2008a). Similarly, plant families that are traditionally viewed as being poor dispersers, such as Arecaceae (palms), have pronounced insular distributions, with island colonisation and subsequent speciation being an important driver of global palm diversity (Onstein *et al.*, 2017). This highlights one major limitation in taking a purely taxonomic

perspective – it is difficult to disentangle interacting processes such as dispersal, environmental filtering and speciation that may be constraining plant diversity on islands.

One way to overcome this limitation is to consider that islands are not only taxonomically disharmonic, but also functionally disharmonic, that is a subset of species with certain traits are disproportionally over- or under-represented. Because functional traits reflect ecological strategies that enable species to occupy a particular niche (Díaz *et al.*, 1998), functionally disharmonic biota may exhibit a suite of traits that reflects dispersal filtering effects, evolutionary responses to environmental conditions or to biotic interactions. Evolutionary shifts towards larger leaf and seed sizes on islands, for example, may be driven by competition between congeneric species (Kavanagh & Burns, 2014). Similarly, the abundance of adaptive floral morphologies and pollination traits such as self-compatibility may be driven both by the scarcity of compatible mates or the absence of pollinators (Grossenbacher *et al.*, 2017; Razanajatovo *et al.*, 2018). Taxa that do not rely heavily on biotic interactions should be favoured in island colonisation because a population may be founded on a single individual (Crawford *et al.*, 2011). Conversely, taxa that depend on specialist interactions should be less successful in island colonisation because populations require the colonisation of all symbionts to remain viable (Cameron *et al.*, 2006). For pollinator-dependent plants, pollination limitation may reduce reproductive output, leading to reproductive isolation (Barrett, 1996). Moreover, because islands generally support fewer pollinators, and pollinator assemblages differ relative to mainland regions, biotic interactions may act as a colonisation filter (Barrett, 1996; Pattemore & Anderson, 2013).

Deviations in insular species composition from mainland regions are not solely a function of dispersal and biotic interaction filtering but also of a species' ability to successfully establish a founder population under local environmental conditions (Carlquist, 1966). Such environmental filtering could be particularly strong for taxa dispersing to islands that differ considerably in climate from their mainland origin, or taxa that are unable to adjust to altered environmental conditions (Gaston *et al.*, 2003). For instance, islands with Mediterranean climate regimes may be disproportionately populated with taxa adapted to summer drought (for example Canary Islands, Whittaker & Fernández-Palacios, 2007), while islands with cooler climates may be disproportionately populated with taxa adapted to extended periods of frost (Körner *et al.*, 2016). Speciation within clades is also linked to environmental variables (for example island area, Losos & Ricklefs, 2009; environmental heterogeneity, Weigelt *et al.*, 2015), which may either promote or counteract the degree of functional disharmony. Herbaceous colonisers, for example, may diversify and fill the functional space typically occupied by trees on the mainland, a common trend in island plants dubbed 'derived insular woodiness' (Lens *et al.*, 2013). Therefore, several key ecological processes contribute to the formation of functionally disharmonic biotas, including dispersal, environmental and biotic interaction filtering and speciation. This highlights the importance of species traits to better understand the forces driving species colonisation and trait evolution on islands (Fig. 1).



**Fig. 1** Potential drivers (left) and outcomes (right) of island disharmony, modified after Weigelt *et al.* (2015). Uppercase letters indicate clades containing good dispersers (D) with adaptations to island environmental conditions (E), which are not reliant on biotic interactions (I). Lowercase letters indicate clades containing poor dispersers (*d*) with no adaptations to island conditions (*e*), and are heavily reliant on biotic interactions (*i*). Poor-dispersing taxa (*d*) should become increasingly rare on isolated islands while good dispersers (D) become disproportionately common. Conversely, species may disperse to an island, but are unable to colonise due to unfavourable environmental conditions. In this case, taxa 'preadapted' to a specific environment (E) may have a greater chance of colonisation if they encounter an environment similar to their mainland source. Similarly, taxa not dependent on biotic interactions (I) should be favoured in island colonisation over taxa with specialised interactions (*i*). Finally, taxa may colonise an island but fill the functional space that would otherwise be filled by other taxa on the mainland, therefore influencing the degree of disharmony through *in-situ* speciation. Ma, million yr ago.

Here, we revisit the classic concept of island disharmony with the goal of developing a more complete picture of the forces governing the unbalanced representation of plant taxa and traits on islands.

We use the megadiverse, cosmopolitan orchid family as a model group to illustrate key processes involved in the assembly of disharmonic island floras, including dispersal, environmental and biotic interaction filtering, and speciation. Our synthesis, on the one hand, outlines general patterns in the representation of orchids on islands using exploratory analyses, and, on the other hand, draws heavily from literature sources to show evidence of functional disharmony displayed by orchids on islands. We base our synthesis on a comprehensive orchid dataset obtained from our Global Inventory of Floras and Traits database, which includes distribution information on 27 637 orchid species spanning 1350 island and mainland regions (Weigelt *et al.*, 2019, see Supporting Information Methods S1 for further information, and Table S1 for the orchid dataset and corresponding bibliography).

In the absence of colonisation limitations brought about by biotic interactions, we expect orchids to be over-represented on islands relative to mainland regions and to follow a similar distribution pattern as ferns due to their similarity in propagule size and high dispersibility. We therefore compare orchids with ferns, which are known to be over-represented on islands, and do not require animal vectors for pollination or dispersal (Kreft *et al.*, 2010). Orchid colonisation may be particularly hindered by biotic interactions given that most orchids grow epiphytically and therefore require the initial colonisation of suitable host trees, are highly pollinator specific (average of 1–3 pollinators per orchid species, Tremblay, 1992; Ackerman & Roubik, 2012), and form a symbiotic relationship with a narrow range of mycorrhizal fungi (Dearnaley, 2007). In this case, we would expect to find that orchids are significantly under-represented on islands relative to mainland floras. Drawing from examples in the literature, we show that functional disharmony is possible even for highly dispersive organisms such as orchids, highlighting a strong role for biotic interactions in determining large-scale biogeographic patterns. We also identify future avenues of empirical research that may bring us closer to fully understanding the mechanisms underlying the disharmony and the assembly of insular floras in general.

## Long-distance dispersal and oddities in insular orchid distributions

Long-distance dispersal is a basic prerequisite for the successful colonisation, spatial distribution and gene flow of insular plant populations (Carlquist, 1974). Taxa with small propagules, such as ferns, are expected to be over-represented on islands (Kreft *et al.*, 2010), despite the fact that once colonisation has occurred it is a selective advantage to have larger propagules and reduced dispersibility (Kavanagh & Burns, 2014). Orchids have among the smallest seeds in the plant kingdom and are, therefore, expected to be proficient long-distance dispersers (Jacquemyn *et al.*, 2007; Mallet *et al.*, 2014). Despite this presumption, orchids are estimated to have undergone few long-distance dispersal events (Givnish *et al.*, 2016), suggesting that the mechanisms underpinning orchid distributions are more complex than previously thought. Indeed, centres of orchid diversity have been identified in island regions such as the south-west Pacific (Keppel *et al.*, 2016), and orchids were among the first pioneer species to colonise the

island of Krakatau following a volcanic eruption in 1883 (Docters van Leeuwen, 1936). However, is this representative of all islands?

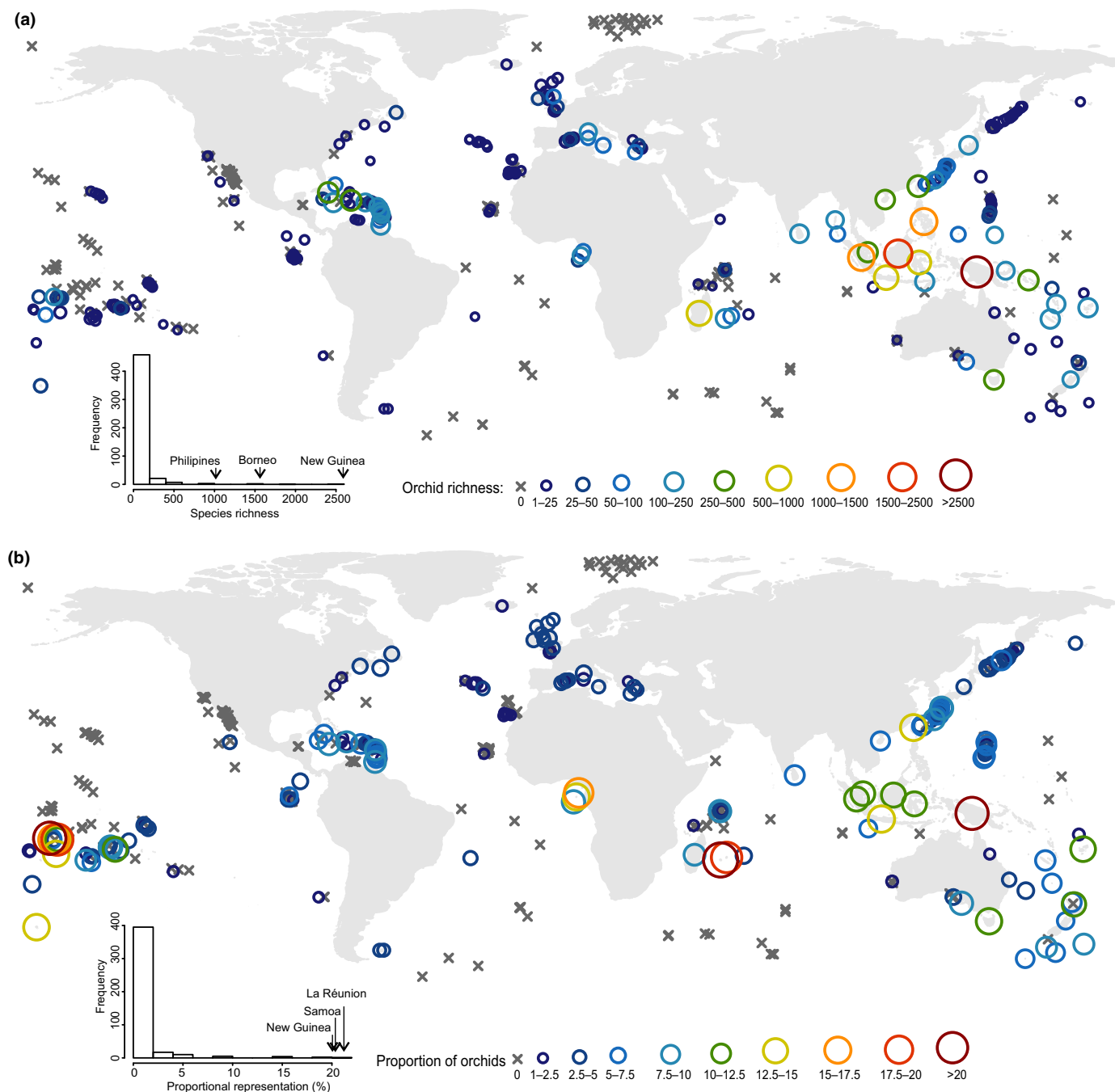
The continental islands of New Guinea (*c.* 2788 species), Sumatra (*c.* 1170 species), and Borneo (*c.* 1600 species) have exceptionally high numbers of orchids, with New Guinea alone accounting for 10% of the world's known species (Fig. 2a). While this suggests that continental islands harbour diverse orchid floras, we found that 39% of the continental islands included in our synthesis have no native orchids, and an additional 24% have < 10 species (see Methods S1 for details on the dataset and methodologies). A similar pattern emerges for oceanic islands, where 44% harbour no native orchids with only a small number of islands displaying high orchid richness. These few species-rich oceanic islands, perhaps unsurprisingly, are situated near major orchid source regions. La Réunion, for example, has the highest orchid richness of any oceanic island (215 species) followed by São Tomé (108 species), both of which are situated just 675 km and 270 km off the coasts of Madagascar and tropical Africa, respectively. After correcting for island area (by including area as a factor in our analysis), we found that orchid species richness on oceanic islands reaches just 10% of that on continental islands (GLM:  $z$ -value =  $-32.55$ ,  $P < 0.001$ ; Fig. 3a), although their proportional representation of the vascular flora is near identical (Mann–Whitney  $U$ -test:  $P = 0.17$ ; Fig. 3b). Additionally, while orchids represent 20% of the vascular flora of New Guinea, and over one-tenth of the flora of 13 additional islands, orchids account for < 1% of the vascular flora of 49% of islands, which is an oddity given their long-distance dispersal potential.

If orchids are disharmonic on islands, they should constitute a disproportionate fraction of the total vascular flora. Specifically, the mean proportional representation of orchids on islands should deviate significantly from that of mainland sites. We therefore took the mean mainland proportional richness of 3.4% as a null expectation (calculated as the mean proportional richness of orchids at 565 mainland regions), rather than the global proportion of orchids in the vascular flora (9%). In this respect, orchids are disharmonic on islands because they represent significantly less than 3.4% of the vascular flora (1.20%, Mann–Whitney  $U$ -test,  $P < 0.001$ ; Fig. 4a). Additionally, their under-representation in the flora did not change with increasing island isolation, suggesting that dispersal is not an important factor structuring orchid assemblages on islands (Fig. 5). A complementary analysis for ferns, conversely, shows that ferns are significantly over-represented on islands (8.6%, Mann–Whitney  $U$ -test,  $P < 0.001$ ; Fig. 4b), and significant increase in proportional representation with island isolation (GLM:  $z$ -value =  $11.85$ ,  $P < 0.001$ ), suggesting that constraints unrelated to dispersal acting on colonisation are much greater for orchids than for ferns.

## Functional disharmony

### Plant–pollinator interactions

Pollinator-mediated selection on plant traits is considered a driving force behind the diversification of flowering plants, including orchids (Givnish *et al.*, 2015). The convergence in plant traits to



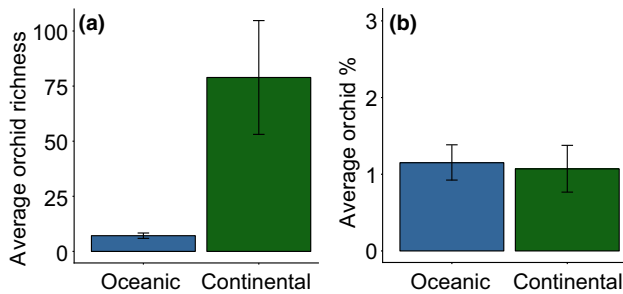
**Fig. 2** Global distribution of orchids on islands in terms of their species richness (a) and proportional representation (%) of the vascular flora (b). Data were obtained from GIFT ([gift.uni-goettingen.de](http://gift.uni-goettingen.de)) for 395 islands and island groups  $> 1 \text{ km}^2$ . A frequency distribution of richness values is also indicated bottom left.

attract specific pollinators is prevalent in *c.* one-third of orchids, for example to mimic rewarding signals (food deception; Cozzolino & Widmer, 2005) or mating signals (sexual deception; Dressler, 1981), while estimates of the number of pollinators per species suggest that most orchids are pollinated by a single species or a small guild of pollinators (Tremblay, 1992; Ackerman & Roubik, 2012). Additionally, low flower visitation rates and failed attempts to attach pollinia to pollinators are frequently observed, suggesting that orchids are often pollinator limited (Pellegrino *et al.*, 2005). Consequently, the local diversity and composition of pollinator

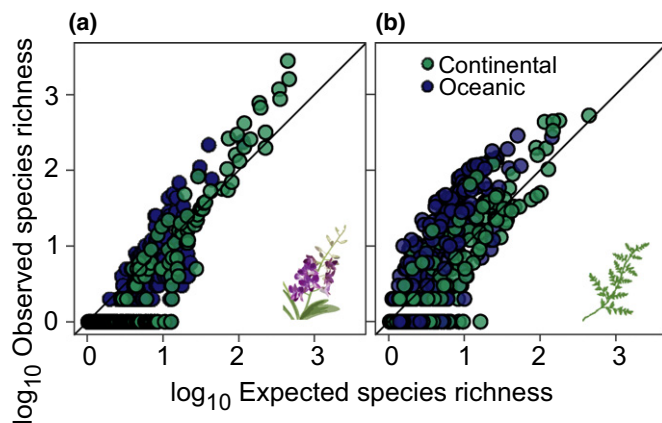
assemblages may act as a biotic interaction filter, which should be reflected in patterns of orchid occupancy on islands and their reproductive traits.

Pollinator composition may contribute to the disparity in orchid richness and proportional representation between some islands, such as La Réunion (215 orchid species, 23% of the flora) and Hawai'i (only three species, 0.5% of the flora). Despite similar estimates of native insects in both islands (5000 and 6500, respectively, Zimmerman, 1970; Rochat, 2009), pollinator assemblages differ. Notably, 79% of the endemic insects of Hawai'i are





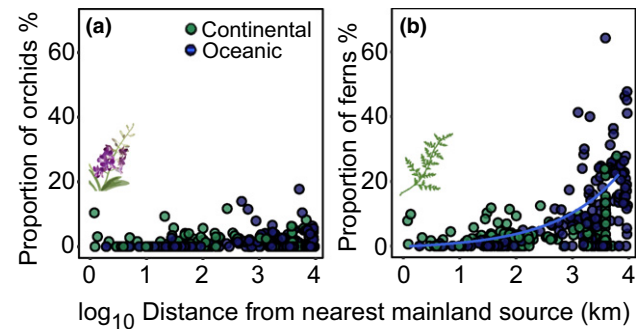
**Fig. 3** Average orchid species richness (a; oceanic =  $7.1 \pm 1.2$ , continental =  $78.9 \pm 25.8$ ; GLM:  $P < 0.001$ ) and proportional representation of the flora (b; oceanic =  $1.28 \pm 0.2\%$ , continental =  $1.05 \pm 0.3\%$ ; Mann–Whitney  $U$ -test:  $P = 0.17$ ). Error bars depict standard error. Note that although we accounted for area in the exploratory analyses, these figures illustrate only raw values.



**Fig. 4** Observed vs expected orchid (a) and fern (b) species richness on 395 islands split by geology. Points above the line indicate over-representation of species among islands, and points below the line indicate under-representation. Observed values are the true number of orchid and fern species on islands, and the expected values are the number of orchid and fern species we would expect on islands, using the average mainland proportion of orchids (3.4%) and ferns (4.0%) as a null expectation (see Supporting Information Methods S1). In this respect, orchids are significantly under-represented on islands (representing an average of just 1.20% of the flora, Mann–Whitney  $U$ -test:  $P < 0.001$ ), while ferns are over-represented (representing an average of 8.63% of the flora, Mann–Whitney  $U$ -test:  $P < 0.001$ ).

restricted to just 85 genera, and typical orchid pollinators are scarce (for example six species of hawkmoths; Barrett, 1996). La Réunion, conversely, has over twice as many hawkmoths (15 species; Attie *et al.*, 2010), and a diverse insect fauna that accounts for 80% of the island's animal species (Rochat, 2009). The absence of long-tongued bees and hawkmoths in New Zealand may impose similar interaction filters (Barrett, 1996), while the absence of orchid bees (tribe Euglossini) in Cuba may explain why neighbouring Jamaica has a similar number of orchids (Jamaica = 221 species vs Cuba = 316 species) despite being four times smaller in size ( $10\,990\text{ km}^2$  vs  $42\,430\text{ km}^2$ ).

Plants may overcome pollinator limitation on islands by selecting for floral traits that attract a wider variety of pollinators (Barrett, 1996) or nonstandard pollinators (for example lizards,



**Fig. 5** Proportional representation of orchids (a) and ferns (b) in relation to isolation on islands split by geology. All isolation values are logged ( $\log_{10}(x + 1)$ ). Poisson smoothed fit curve was fitted to show the significant relationship between oceanic island isolation and the increasing proportional representation of ferns (GLM:  $z$ -value = 11.85,  $P < 0.001$ ). By contrast, the proportional representation of orchids was not significantly related to isolation.

Olesen & Valido, 2003). An over-representation of inconspicuous, small, dull-coloured flowers, for example, is found on many oceanic or isolated continental islands such as Hawai'i or New Zealand and is related to pollinator assemblages composed of generalist flies and small moths (Fig. 6; Carlquist, 1966). Similar pollinator-mediated shifts in floral traits have been observed in the orchid flora of La Réunion (Jacquemyn *et al.*, 2005), New Zealand (Lehnebach & Robertson, 2004), and the Azores (Bateman *et al.*, 2013), in some cases demonstrating a remarkable shift in pollination syndrome from sphingophily (hawkmoth pollination) to ornithophily (bird pollination Micheneau *et al.*, 2006), or orthopterophily (pollination by crickets, Micheneau *et al.*, 2010). While biogeographical patterns in floral trait evolution are still poorly understood, trait selection relating to the generalisation of pollination systems are commonly observed on islands. The Izu Islands of Japan, for example, are depauperate in long-tongued Lepidoptera and bumblebees, which are important pollinators on the Japanese 'mainland'. Consequently, there is an absence of plant species typically associated with these pollinator groups, and shifts in reproductive traits to become more generalised have been observed (Inoue, 1993). Similar patterns have been found in Macaronesia



**Fig. 6** Examples of small, inconspicuous orchid flowers typical of island environments. The far-right image is *Goodyera macrophylla*, endemic to the island of Madeira (photograph credit: Miguel Sequeira) and all remaining images are of *Drymoanthus adversus*, an orchid endemic to New Zealand (photograph credit: Allan Ducker).

(Ojeda *et al.*, 2016), Antillean Islands (Martén-Rodríguez *et al.*, 2009), among others (for example New Zealand, Juan Fernandez, Hawai'i, Mascarenes) suggesting that a shift to generalised pollination syndromes is common among island floras (Olesen & Valido, 2003).

Self-compatibility is another trait associated with pollinator limitation, and becomes increasingly prevalent with increasing latitude, elevation and island isolation (Barrett, 1996; Jacquemyn *et al.*, 2005; Grossenbacher *et al.*, 2017). While up to 31% of all orchids are self-compatible (Catling, 1990), this proportion can reach up to 46% on oceanic islands (Micheneau *et al.*, 2008b). This suggests that self-compatible is not only an important trait in terms of a response to pollinator limitation on islands, but also an advantage for island colonisation in the first place. Understanding the mechanisms of autonomous self-pollination on islands might be particularly relevant for orchids. Mechanisms such as a reduction in rostellum tissue promotes contact between the pollinia and stigmatic fluid, therefore causing the pollen tubes to grow directly into the stigma (Peter & Johnson, 2009). Whether certain mechanisms of autonomous self-pollination could be generalised for insular orchids would be an interesting avenue for future empirical research.

### Plant–fungi interactions

Because of their minute seeds that lack a nutritive tissue, all orchids form a symbiosis with mycorrhizal fungi to meet their nutritional requirements during initial seedling development. The interaction between orchids and associated mycorrhizal fungi may influence their distribution, diversity and successful colonisation of vacant patches, including islands (Jacquemyn *et al.*, 2017). Because most orchids associate with only a narrow range of orchid mycorrhizal fungi (OMF), it is intuitive that OMF specificity should promote orchid rarity and limit orchid colonisation of islands. However, investigations into the effects of OMF specificity on orchid rarity and distributions have produced contrasting results (see review by Dearnaley, 2007), and whether orchids that associate with specific OMF strains are more limited in their distributions relative to orchids that associate with a wider range of OMF is still poorly understood (but see McCormick *et al.*, 2018).

On islands, varying degrees of orchid mycorrhizal specificity have been reported even between closely related species (for example Otero Tupac *et al.*, 2004). In the one extreme, an analysis of 77 orchid species on La Réunion found low mycorrhizal specialisation, and 95 *Rhizoctonia* Operational Taxonomic Units (OTUs) were isolated from orchid roots (Martos *et al.*, 2012). This is in stark contrast with Hawai'i, where only three fungal OTUs were isolated from roots of the endemic orchid *Anoetochilus sandvicensis* on four different islands (Hawai'i, Kaua'i, Maui, and O'ahu; Swift *et al.*, 2018). In this case, however, the effect of low fungal diversity was countered by their widespread and abundant distribution, suggesting that the presence of only a subset of appropriate OMF on an island would not limit orchid colonisation if they are widespread (Swift *et al.*, 2018).

Only few orchid genera (for example *Cyrtosia*, *Epipogium*, *Gastrodia*, *Wulfschlaegelia*), are fully myco-heterotrophic, meaning

that they acquire nutrients from mycorrhizal fungi throughout their entire life cycle (Dearnaley, 2007). Unlike photosynthetic orchids, which have been demonstrated in some cases to form a mutualistic mycorrhizal symbiosis with free-living saprophytic or pathogenic fungi, nonphotosynthetic orchids are parasitic exploiters of ectomycorrhizal fungi and display very high levels of fungal specificity (Bidartondo, 2005). This situation may explain why nonphotosynthetic orchids are rarely found on oceanic islands (Table 1), demonstrating again the importance of biotic interaction specificity on limiting plant colonisation. Moreover, whether or not orchids switch their fungal symbionts after island colonisation is unknown, although it has been inferred in *Platanthera pollostantha* of the Azorean archipelago (Bateman *et al.*, 2013). It also remains unknown to what extent the interaction between orchid–mycorrhizal fungi symbiosis and environmental conditions might limit orchid colonisation. Ecological specificity of OMF, for example, may impose an additional filter on island colonisation by orchids when the latter are unable to form a symbiosis under unfavourable environmental conditions (Phillips *et al.*, 2011).

### Plant–plant interactions

Of all orchids *c.* 69% are epiphytic and therefore require the initial colonisation of trees with suitable characteristics to colonise an island (Zotz, 2016). Although host-tree specificity is generally deemed low among epiphytic orchids (Wagner *et al.*, 2015), the

**Table 1** Fully myco-heterotrophic orchid genera and their distribution among mainland regions and islands (split between continental and oceanic).

Genus	No. species	No. occurrences		
		Mainland	Continental	Oceanic
<i>Aphyllorchis</i> Blume	21	39	32	2
<i>Auxopus</i> Schltr.	2	22	1	0
<i>Chamaegastrodia</i> Makino & F. Maek	3	14	2	0
<i>Corallorhiza</i> Hall	13	586	15	1
<i>Didymoplexis</i> Griff.	18	33	43	42
<i>Epipogium</i> J. Gmelin ex Borkh.	4	164	25	17
<i>Galeola</i> Lour.	6	52	13	1
<i>Gastrodia</i> R. Br.	67	130	75	15
<i>Hexaletris</i> Rafin.	11	113	0	0
<i>Neottia</i> Guett.	69	799	98	15
<i>Pachystoma</i> Blume	3	37	11	4
<i>Pogoniopsis</i> Reichb. f.	2	8	0	0
<i>Rhizanthella</i> R. Rogers	3	13	0	0
<i>Risleya</i> King & Pantl.	1	7	0	0
<i>Silvorchis</i> J.J. Sm.	1	0	1	0
<i>Stereosandra</i> Blume	1	6	10	4
<i>Uleiorchis</i> Hoehne	2	22	0	0
<i>Wulfschlaegelia</i> Reichb. f.	2	68	8	5
<i>Yoania</i> Maxim.	4	6	5	0
Total	233	2161	339	106
Proportional representation %	/	83%	13%	4%

Classification of genera follows Leake (1994).

intermittent water supply consistent with an arboreal lifestyle is a major constraint on epiphyte distributions (Zotz & Hietz, 2001). Epiphytic orchids are therefore largely restricted to tropical islands with a moist climate, such as New Guinea, Borneo, Sumatra and Sulawesi, where they comprise up to 80% of the orchid flora. Outside the wet tropics, however, the proportional representation of epiphytic orchids rapidly decreases with increasing latitude (Zotz, 2016).

The complex geological history and sheer size of continental islands in Southeast Asia have played a fundamental role in the evolution of epiphytism, particularly with respect to the formation of mountain ranges (Givnish *et al.*, 2016). These mountain ranges, which exceed 5000 m in elevation in New Guinea, not only allowed for the invasion of new environmental gradients, but also created barriers to dispersal that may have led to a substantial acceleration in orchid diversification (Givnish, 2010). Specifically, together with the partitioning of new aerial niches and the evolution of traits associated with the epiphytic habit (for example CAM photosynthesis, aerial roots), 'epiphytism' significantly accelerated diversification within the Orchidaceae (Givnish *et al.*, 2015). Therefore, traits particularly common among epiphytic taxa, related to water storage (for example pseudobulbs), water and nutrient uptake (for example velamen), or to reduction of water loss (for example CAM photosynthesis), are likely to be over-represented on islands with high proportions of epiphytic orchids.

## Functional disharmony and environmental constraints

Similar to the convergence in traits to select for specific pollinators, plant traits may also reflect ecological strategies to withstand particular environmental conditions (Diaz *et al.*, 1998), and an over- or under-representation of functional traits may reflect environmental filtering. For some island groups, such as New Caledonia or the Galápagos Islands, it is argued that environmental filtering, rather than dispersal, is a greater force limiting species colonisation (Isnard *et al.*, 2016; Carvajal-Endara *et al.*, 2017). This is in part because plant families associated with high dispersal ability only form a small portion of the flora, but also because climate similarity (that is the match of insular climate and the climate of the mainland source pool) is a better predictor of species composition than dispersal ability (Carvajal-Endara *et al.*, 2017).

The distributions of orchids differing in growth habit (epiphytic vs terrestrial), may be affected by different environmental factors. The aerial habit of epiphytes, for example, makes water availability a major limiting factor (Zotz & Hietz, 2001), while forest cover and light availability have been shown to be more important for terrestrial orchids (Zhang *et al.*, 2005; Huang *et al.*, 2008). Additionally, some studies have linked terrestrial orchid rarity to unfavourable soil conditions, and have demonstrated that orchid rarity is not necessarily a result of orchid–fungi specificity, but rather an indirect effect of soil properties (for example soil pH) inhibiting orchid–fungi interactions (for example Phillips *et al.*, 2011). For epiphytic orchids, certain bark substrates might also inhibit epiphytic orchid–fungi interactions, although epiphytic orchids seem to be less confounded by OMF relative to terrestrial orchids (Dearnaley, 2007).

## Speciation

While the biodiversity of young, less-isolated islands can be attributed to dispersal alone, biodiversity on older and more remote islands is often a result of *in situ* speciation, which may work to either promote or reduce the degree of island disharmony. For one, not all dispersal events will lead to successful colonisation, and only a few colonists will have the tendency to diversify, potentially accentuating the degree of island disharmony (Gillespie, 2007). Alternatively, colonisers may diversify but fill the functional space typically occupied by other taxa on the mainland, potentially reducing functional disharmony.

Despite their extraordinary diversity and high rates of diversification (Givnish *et al.*, 2015), orchids have only diversified on a handful of islands. In the Hawaiian flora, for example, orchids have not substantially diversified, while silverswords, bidens (both Asteraceae), mints (Lamiaceae), and palms (Arecaceae), among others, have diversified from a single ancestral colonist into a variety of species that now occupy a diverse range of habitats (Chapin *et al.*, 2004; Knope *et al.*, 2012). Islands on which orchids have diversified include large continental islands such as New Guinea (84% of the species are endemic) and Madagascar (83% endemic), which have the highest proportions of endemic orchids, as well as Borneo, Sulawesi, and the volcanic island La Réunion (*c.* 50% endemic). By contrast, Mauritius, which lies just 190 km east of La Réunion has just 9% endemic orchids, despite the fact that nearly half of the Mauritian flora are single-island endemics. Endemic orchids are even entirely missing on 79% of the 214 islands for which we have data on endemism. This generally low degree of endemism among orchids on islands suggests that orchids are dispersing to islands frequently due to their small seeds, yet are less frequently colonising or diversifying due to constraints by biotic interactions or alternatively orchids are colonising islands, yet do not form viable populations that significantly differ from their mainland source region, leading to overall lower levels of endemism. Orchid mycorrhizal fungi specificity may promote speciation both directly and indirectly, by influencing orchid distributions (indirectly) or reproductive isolation (directly), although the latter is difficult to quantify (Waterman & Bidartondo, 2008). Another possible avenue of orchid diversification is the evolution of deceit pollination, which has been linked to overall outcrossing success (Peakall & Beattie, 1996). The availability of appropriate OMF or pollinators on islands may therefore promote orchid diversification, and may explain the high proportion of endemics on nonisolated continental islands.

## Conclusion

The over- or under-representation of taxa, termed 'disharmony' (*sensu* Carlquist, 1966), represents a central concept of island biology as it embodies not only filtering by dispersal, but also the interplay between dispersal, environmental and biotic processes (Carlquist, 1966). However, to what degree these processes influence species diversity, endemism, and composition on island floras worldwide is still poorly understood. On the one hand, only a subset of species from the mainland species pool can undertake long-distance dispersal, and therefore good dispersers are expected



to be over-represented on islands. On the other hand, environmental filtering may exert greater pressure on taxa dispersing to islands that differ significantly in climate from their mainland origin, or taxa that are unable to adjust to altered environmental conditions. Furthermore, taxa with more specific biotic interactions, such as those that require a specific pollinator or seed disperser to reproduce, should be less successful in island colonisation because populations require the colonisation of all interacting species to remain viable. The disharmonic nature of orchid floras on both continental and oceanic islands contributes to this debate by highlighting that the ability to disperse to an island may not be as important as being able to establish, abiotic and biotic processes that are likely to interact with island characteristics (area, isolation, age). This situation may explain why continental islands can exhibit comparable levels of disharmony with oceanic islands. Finally, biotic interactions, which are usually not considered beyond the local scale as an important factor structuring species assemblages, may in fact play an important role in island colonisation.

## Future directions and perspectives

Despite the recent advances in mycorrhizal research, very little information is known about OMF insular distributions and to what extent they limit plant colonisation on islands (Jacquemyn *et al.*, 2017). Given that OMF are free-living organisms in the soil, it might be expected that edaphic conditions constrain OMF colonisation. By determining the diversity of orchid mycorrhizal fungi both in the soil and on orchid roots on islands, one could possibly tease apart this effect. Additionally, one could test whether orchids exhibit more generalised orchid–mycorrhizal fungi interactions on islands relative to the mainland, or whether they switch symbionts.

Similarly, it remains largely anecdotal whether pollinator composition or diversity is a useful predictor of plant distributions at large spatial scales (Wisz *et al.*, 2013), and the next step would be to synthesise plant–pollinator interactions on islands to determine whether the inclusion of biotic interactions are an important predictor of plant diversity on islands. Comparing islands with or without orchids in relation to pollinator assemblages, or estimating how environmentally different an island is relative to the nearest mainland, would then be a follow-up approach to determine whether biotic or environmental processes can explain orchid diversity on an island.

Exactly why orchids do not substantially diversify on islands relative to other plant families also warrants further investigation. Between the fact that islands and archipelagos are evolutionary arenas that foster speciation and that orchids have rapid diversification rates (Givnish, 2010), it is unusual that they exhibit a generally low degree of endemism on islands. Givnish *et al.* (2016) wrote of ‘the paradox of orchid dispersal’, because good-dispersing taxa are expected to have lower rates of diversification (due to the inability to form disjunct populations). However, our synthesis strongly suggests that dispersal is not the key. Rather, constraints acting on establishment, such as biotic interactions, are more limiting to orchid colonisation and diversification, at least on

islands. Therefore, we call for more empirical research on the role of filtering effects beyond dispersal as potential drivers of plant diversity at large spatial scales. Together, these insights can yield a road map to guide future research that will ultimately increase our mechanistic understanding of species assembly, including that of disharmony, trait evolution and biodiversity on islands.






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## Author contributions

AT and HK conceived the study, PW, CK and HK collated the orchid database, GZ collated the epiphyte database, AT performed all analyses with contributions from PW, CK and HK. AT wrote the manuscript, and all authors contributed substantially to revisions.

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## References

- Ackerman JD, Roubik DW. 2012. Can extinction risk help explain plant–pollinator specificity among euglossine bee pollinated plants? *Oikos* 121: 1821–1827.
- Attie M, Kitching IJ, Veslot J. 2010. Patterns of larval hostplant usage among hawkmoths (Lepidoptera, Sphingidae) from La Réunion, with a comparison of the Mascarenes with other regions of the world. *Revue d'Écologie* 65: 3–44.
- Barrett SC. 1996. The reproductive biology and genetics of island plants. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* 351: 725–733.
- Bateman RM, Rudall PJ, Moura M. 2013. Systematic revision of *Platanthera* in the Azorean archipelago: not one but three species, including arguably Europe's rarest orchid. *Peer J* 1: e218.
- Bidartondo MI. 2005. The evolutionary ecology of myco-heterotrophy. *New Phytologist* 167: 335–352.
- Cameron DD, Leake JR, Read DJ. 2006. Mutualistic mycorrhiza in orchids: evidence from plant–fungus carbon and nitrogen transfers in the green-leaved terrestrial orchid *Goodyera repens*. *New Phytologist* 171: 405–416.
- Carlquist S. 1966. The biota of long-distance dispersal. I. Principles of dispersal and evolution. *Quarterly Review of Biology* 41: 247–270.
- Carlquist S. 1974. *Island biology*. New York, NY, USA & London, UK: Columbia University Press.
- Carvajal-Endara S, Hendry AP, Emery NC, Davies TJ. 2017. Habitat filtering not dispersal limitation shapes oceanic island floras: species assembly of the Galápagos archipelago. *Ecology Letters* 20: 495–504.
- Catling P. 1990. Auto-pollination in the Orchidaceae. In: Arditti J ed. *Orchid biology, reviews and perspectives*. Portland, OR, USA: V. Timber Press, 121–158.
- Chapin MH, Wood KR, Perlman SP, Maunder M. 2004. A review of the conservation status of the endemic *Pritchardia* palms of Hawaii. *Oryx* 38: 273–281.

- Cozzolino S, Widmer A. 2005. Orchid diversity: an evolutionary consequence of deception? *Trends in Ecology & Evolution* 20: 487–494.
- Crawford DJ, Anderson GJ, Bernardello G. 2011. The reproductive biology of island plants. In: Brandvain D, Caujapé-Castells J, eds. *The biology of island floras*. Cambridge, UK: Cambridge University Press, 11–36.
- Dearnaley JD. 2007. Further advances in orchid mycorrhizal research. *Mycorrhiza* 17: 475–486.
- Díaz S, Cabido M, Casanoves F. 1998. Plant functional traits and environmental filters at a regional scale. *Journal of Vegetation Science* 9: 113–122.
- Docters van Leeuwen W. 1936. Krakatau: 1883–1933. *Annales du Jardin botanique de Buitenzorg* 46: 1–506.
- Dressler RL. 1981. *The orchids*. Cambridge, MA, UK: Harvard University Press.
- Gaston KJ, Jones AG, Hänel C, Chown SL. 2003. Rates of species introduction to a remote oceanic island. *Proceedings of the Royal Society of London. Series B, Biological Sciences* 270: 1091–1098.
- Gillespie R. 2004. Community assembly through adaptive radiation in Hawaiian spiders. *Science* 303: 356–359.
- Gillespie RG. 2007. Oceanic islands: models of diversity. In: Levin S, ed. *Encyclopedia of biodiversity*. Oxford, UK: Elsevier, 1–13.
- Givnish TJ. 2010. Ecology of plant speciation. *Taxon* 59: 1326–1366.
- Givnish TJ, Spalink D, Ames M, Lyon SP, Hunter SJ, Zuluaga A, Doucette A, Caro GG, McDaniel J, Clements MA. 2016. Orchid historical biogeography, diversification, Antarctica and the paradox of orchid dispersal. *Journal of Biogeography* 43: 1905–1916.
- Givnish TJ, Spalink D, Ames M, Lyon SP, Hunter SJ, Zuluaga A, Iles WJ, Clements MA, Arroyo MT, Leebens-Mack J. 2015. Orchid phylogenomics and multiple drivers of their extraordinary diversification. *Proceedings of the Royal Society of London. Series B, Biological Sciences* 282: 20151553.
- Grossenbacher DL, Bramwell Y, Auld JR, Burd M, Cheptou PO, Conner JK, Grant AG, Hovick SM, Pannell JR, Pauw A. 2017. Self-compatibility is over-represented on islands. *New Phytologist* 215: 469–478.
- Heleno R, Vargas P. 2015. How do islands become green? *Global Ecology and Biogeography* 24: 518–526.
- Huang B-Q, Yang X-Q, Yu F-H, Luo Y-B, Tai Y-D. 2008. Surprisingly high orchid diversity in travertine and forest areas in the Huanglong Valley, China, and implications for conservation. *Biodiversity and Conservation* 17: 2773.
- Inoue K. 1993. Evolution of mutualism in plant–pollinator interactions on islands. *Journal of Biosciences* 18: 525–536.
- Isnard S, L'huillier L, Rigault F, Jaffré T. 2016. How did the ultramafic soils shape the flora of the New Caledonian hotspot? *Plant and Soil* 403: 53–76.
- Jacquemyn H, Brys R, Vandepitte K, Honnay O, Roldán-Ruiz I, Wiegand T. 2007. A spatially explicit analysis of seedling recruitment in the terrestrial orchid *Orchis purpurea*. *New Phytologist* 176: 448–459.
- Jacquemyn H, Duffy KJ, Selosse MA. 2017. Biogeography of orchid mycorrhizas. In: Tedersoo L, ed. *Biogeography of mycorrhizal symbiosis*. Basel, Switzerland: Springer, 159–177.
- Jacquemyn H, Micheneau C, Roberts DL, Paillet T. 2005. Elevational gradients of species diversity, breeding system and floral traits of orchid species on Reunion Island. *Journal of Biogeography* 32: 1751–1761.
- Kavanagh PH, Burns KC. 2014. The repeated evolution of large seeds on islands. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 281: 20140675.
- Keppel G, Gillespie TW, Ormerod P, Fricker GA. 2016. Habitat diversity predicts orchid diversity in the tropical south-west Pacific. *Journal of Biogeography* 43: 2332–2342.
- Knope ML, Morden CW, Funk VA, Fukami T. 2012. Area and the rapid radiation of Hawaiian *Bidens* (Asteraceae). *Journal of Biogeography* 39: 1206–1216.
- Körner C, Basler D, Hoch G, Kollas C, Lenz A, Randin CF, Vitasse Y, Zimmermann NE. 2016. Where, why and how? Explaining the low-temperature range limits of temperate tree species. *Journal of Ecology* 104: 1076–1088.
- Kreft H, Jetz W, Mutke J, Barthlott W. 2010. Contrasting environmental and regional effects on global pteridophyte and seed plant diversity. *Ecography* 33: 408–419.
- Leake JR. 1994. The biology of myco-heterotrophic ('saprophytic') plants. *New Phytologist* 127: 171–216.
- Lehnebach CA, Robertson AW. 2004. Pollination ecology of four epiphytic orchids of New Zealand. *Annals of Botany* 93: 773–781.
- Lens F, Davin N, Smets E, del Arco M. 2013. Insular woodiness on the Canary Islands: a remarkable case of convergent evolution. *International Journal of Plant Sciences* 174: 992–1013.
- Losos JB, Ricklefs RE. 2009. Adaptation and diversification on islands. *Nature* 457: 830–836.
- Mallet B, Martos F, Blambert L, Paillet T, Humeau L. 2014. Evidence for isolation-by-habitat among populations of an epiphytic orchid species on a small oceanic island. *PLoS ONE* 9: e87469.
- Martén-Rodríguez S, Almarales-Castro A, Fenster CB. 2009. Evaluation of pollination syndromes in Antillean Gesneriaceae: evidence for bat, hummingbird and generalized flowers. *Journal of Ecology* 97: 348–359.
- Martos F, Munoz F, Paillet T, Kottke I, Gonneau C, Selosse M-A. 2012. The role of epiphytism in architecture and evolutionary constraint within mycorrhizal networks of tropical orchids. *Molecular Ecology* 21: 5098–5109.
- McCormick MK, Whigham DF, Canchani-Viruet A. 2018. Mycorrhizal fungi affect orchid distribution and population dynamics. *New Phytologist* 219: 1207–1215.
- Micheneau C, Carlswald BS, Fay MF, Bytebier B, Paillet T, Chase MW. 2008a. Phylogenetics and biogeography of Mascarene angraecoid orchids (Vandaeae, Orchidaceae). *Molecular Phylogenetics and Evolution* 46: 908–922.
- Micheneau C, Fournel J, Gauvin-Bialecki A, Paillet T. 2008b. Auto-pollination in a long-spurred endemic orchid (*Jumellea stenophylla*) on Reunion Island (Mascarene Archipelago, Indian Ocean). *Plant Systematics and Evolution* 272: 11–22.
- Micheneau C, Fournel J, Paillet T. 2006. Bird pollination in an angraecoid orchid on Reunion Island (Mascarene Archipelago, Indian Ocean). *Annals of Botany* 97: 965–974.
- Micheneau C, Fournel J, Warren BH, Hugel S, Gauvin-Bialecki A, Paillet T, Strasberg D, Chase MW. 2010. Orthoptera, a new order of pollinator. *Annals of Botany* 105: 355–364.
- Ojeda DI, Valido A, de Castro AG, Ortega-Olivencia A, Fuertes-Aguilar J, Carvalho JA, Santos-Guerra A. 2016. Pollinator shifts drive petal epidermal evolution on the Macaronesian Islands bird-flowered species. *Biology Letters* 12: 20160022.
- Olesen JM, Valido A. 2003. Lizards as pollinators and seed dispersers: an island phenomenon. *Trends in Ecology & Evolution* 18: 177–181.
- Onstein RE, Baker WJ, Couvreur TL, Faurby S, Svenning J-C, Kissling WD. 2017. Frugivory-related traits promote speciation of tropical palms. *Nature Ecology & Evolution* 1: 1903–1911.
- Otero Tupac J, Ackerman JD, Bayman P. 2004. Differences in mycorrhizal preferences between two tropical orchids. *Molecular Ecology* 13: 2393–2404.
- Pattemore DE, Anderson SH. 2013. Severe pollen limitation in populations of the New Zealand shrub *Alseuosmia macrophylla* (Alseuosmiaceae) can be attributed to the loss of pollinating bird species. *Austral Ecology* 38: 95–102.
- Peakall R, Beattie AJ. 1996. Ecological and genetic consequences of pollination by sexual deception in the orchid *Caladenia tentaculata*. *Evolution* 50: 2207–2220.
- Pellegrino G, Gargano D, Noce ME, Musacchio A. 2005. Reproductive biology and pollinator limitation in a deceptive orchid, *Serapias vomeracea* (Orchidaceae). *Plant Species Biology* 20: 33–39.
- Peter CI, Johnson SD. 2009. Autonomous self-pollination and pseudo-fruit set in South African species of *Eulophia* (Orchidaceae). *South African Journal of Botany* 75: 791–797.
- Phillips RD, Barrett MD, Dixon KW, Hopper SD. 2011. Do mycorrhizal symbioses cause rarity in orchids? *Journal of Ecology* 99: 858–869.
- Pillon Y, Munzinger J, Amir H, Lebrun M. 2010. Ultramafic soils and species sorting in the flora of New Caledonia. *Journal of Ecology* 98: 1108–1116.
- Razanajatovo M, van Kleunen M, Kreft H, Dawson W, Essl F, Pergl J, Pyšek P, Winter M, Weigelt P. 2018. Autofertility and self-compatibility moderately benefit island colonisation of plants. *Global Ecology and Biogeography* 28: 341–352.
- Rochat J. 2009. *Terrestrial invertebrate biodiversity of Reunion Island*. [WWW document] URL [http://www.regionreunion.com/fr/spip/IMG/pdf/insectarium\\_in\\_english.pdf](http://www.regionreunion.com/fr/spip/IMG/pdf/insectarium_in_english.pdf) [accessed 2 March 2018].
- Swift S, Munroe S, Im C, Tipton L, Hynson N. 2018. Remote tropical island colonisation does not preclude symbiotic specialists: new evidence of mycorrhizal specificity across the geographic distribution of the Hawaiian endemic orchid *Anoectochilus sandwicensis*. *Annals of Botany* 123: 657–666.
- Tremblay RL. 1992. Trends in the pollination ecology of the Orchidaceae: evolution and systematics. *Canadian Journal of Botany* 70: 642–650.

- Wagner K, Mendieta-Leiva G, Zotz G. 2015. Host specificity in vascular epiphytes: a review of methodology, empirical evidence and potential mechanisms. *AoB Plants* 7: plu092.
- Warren BH, Simberloff D, Ricklefs RE, Aguilée R, Condamine FL, Gravel D, Morlon H, Mouquet N, Rosindell J, Casquet J *et al.* 2015. Islands as model systems in ecology and evolution: prospects fifty years after MacArthur–Wilson. *Ecology Letters* 18: 200–217.
- Waterman J, Bidartondo MI. 2008. Deception above, deception below: linking pollination and mycorrhizal biology of orchids. *Journal of Experimental Botany* 59: 1085–1096.
- Weigelt P, Kissling WD, Kisel Y, Fritz SA, Karger DN, Kessler M, Lehtonen S, Svenning J-C, Kreft H. 2015. Global patterns and drivers of phylogenetic structure in island floras. *Scientific Reports* 5: 12213.
- Weigelt P, König C, Kreft H. 2019. GIFT – a Global Inventory of Floras and Traits for macroecology and biogeography. *BioRxiv*, doi:10.1101/535005.
- Whittaker RJ, Fernández-Palacios JM. 2007. *Island biogeography: ecology, evolution, and conservation*. Oxford, UK: Oxford University Press.
- Wisz MS, Pottier J, Kissling WD, Pellissier L, Lenoir J, Damgaard CF, Dormann CF, Forchhammer MC, Grytnes JA, Guisan A. 2013. The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modelling. *Biological Reviews* 88: 15–30.
- Zhang S, Hu H, Zhou Z, Xu K, Yan N, Li S. 2005. Photosynthesis in relation to reproductive success of *Cypripedium flavum*. *Annals of Botany* 96: 43–49.
- Zimmerman EC. 1970. Adaptive radiation in Hawaii with special reference to insects. *Biotropica* 2: 32–38.
- Zotz G. 2016. *Plants on plants – the biology of vascular epiphytes*. Basel, Switzerland: Springer.
- Zotz G, Hietz P. 2001. The physiological ecology of vascular epiphytes: current knowledge, open questions. *Journal of Experimental Botany* 52: 2067–2078.

## Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

**Methods S1** Detailed methodologies and information concerning the Global Inventory of Floras and Traits dataset and quantification of orchid disharmony.

**Table S1** Information on the number of native and endemic orchids on 395 islands and their corresponding reference, from which the dataset was generated.

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