

# ECOGRAPHY

## Research

### Functional traits are key to understanding orchid diversity on islands

Amanda Taylor, Gunnar Keppel, Patrick Weigelt, Gerhard Zotz and Holger Kreft

A. Taylor (<https://orcid.org/0000-0002-0420-2203>) ✉ ([amanda.taylor@uni-goettingen.de](mailto:amanda.taylor@uni-goettingen.de)), G. Keppel (<https://orcid.org/0000-0001-7092-6149>), P. Weigelt (<https://orcid.org/0000-0002-2485-3708>) and H. Kreft (<https://orcid.org/0000-0003-4471-8236>), Dept of Biodiversity, Macroecology and Biogeography, Faculty for Forest Sciences and Forest Ecology, Univ. of Goettingen, Göttingen, Germany. GK also at: UniSA STEM and Future Industries Inst., Univ. of South Australia, Adelaide, Australia. – G. Zotz (<https://orcid.org/0000-0002-6823-2268>), Inst. of Biology and Environmental Sciences, Univ. of Oldenburg, Oldenburg, Germany. HK also at: Centre of Biodiversity and Sustainable Land Use (CBL), Univ. of Goettingen, Göttingen, Germany.

#### Ecography

44: 703–714, 2021

doi: 10.1111/ecog.05410

Subject Editor: John-Arvid Grytnes

Editor-in-Chief:

Jens-Christian Svenning

Accepted 23 December 2020



The extraordinary diversity of orchids has captivated scientists for more than a century, yet their complex spatial patterns at large scales remain poorly resolved. On islands, orchid diversity patterns are especially puzzling. While some islands are centres of orchid diversity, orchids are underrepresented on most islands. To disentangle such complex patterns, key functional differences among orchids must be considered – a distinction seldom made in biogeographical analyses. Using a global dataset of 454 islands, we tested prominent hypotheses in island biogeography, while simultaneously making the distinction between epiphytes and two terrestrial life forms (geophytes and non-geophytes). Orchid diversity was unevenly distributed across islands and life forms. Epiphytic orchid diversity strongly increased with temperature, illustrating the near confinement of epiphytes to the tropics. Geophytes became proportionally more important with increasing seasonality, highlighting their ability to withstand harsh climatic conditions. Epiphytes and non-geophytes both displayed responses (e.g. negative relationship with seasonality) related to their dependence on consistently favourable conditions, possibly because of the absence of subterranean storage organs. This highlights that the factors explaining orchid diversity differ strongly with, and are related to, life form. We suggest that key functional differences within and across plant families be considered in future studies to better understand drivers of complex diversity patterns.

Keywords: endemism, functional traits, life form, Orchidaceae, species richness

#### Introduction

Orchids are a highly diverse, cosmopolitan plant family (~28 000 species, Givnish et al. 2016), and their complex biotic interactions and attractive floral morphology have fascinated scientists for over 150 years (Darwin 1859). Numerous studies have linked the extraordinary diversity of orchids to their specialized interactions with pollinators and obligate mycorrhizal fungi (Cozzolino and Widmer 2005, Otero and Flanagan 2006), but also to epiphytism and associated traits such as Crassulacean acid metabolism



[www.ecography.org](http://www.ecography.org)

© 2020 The Authors. Ecography published by John Wiley & Sons Ltd on behalf of Nordic Society Oikos  
This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

(CAM) (Gravendeel et al. 2004, Givnish et al. 2015). As well as being highly diverse, orchids as a family are cosmopolitan in their distribution, which is often linked to their ‘dust-sized’ seeds that are produced in huge quantities and can disperse thousands of kilometres by wind currents (Jersáková and Malinová 2007). Consequently, orchids are believed to be proficient long-distance dispersers, which has been invoked to explain their rapid colonization of newly formed islands (e.g. Krakatau, Partomihardjo 2003) and isolated archipelagos (e.g. Hawaiian Islands, Carlquist 1967).

Regional studies focusing on selected archipelagos or islands suggest that orchids can reach high levels of species diversity on islands (Jacquemyn et al. 2005, Ackerman et al. 2007, Micheneau et al. 2008, Keppel et al. 2016), which is not congruent with patterns observed at the global scale. Specifically, while some islands constitute global centres of orchid diversity, most islands harbour few to no orchids (Taylor et al. 2019, König et al. 2020). Although part of this variation is potentially linked to differences in island geological history, spatial arrangement, size, isolation and climate, i.e. the processes by which islands gain biota differ substantially among islands (Neill and Trewick 2008, Weigelt et al. 2013, Ali 2017), another source of variation could be related to orchid functional traits. Orchids have a remarkable diversity in functional traits, rooting either in the ground (as terrestrial geophytes or non-geophytes), or growing on the branches of a host tree (epiphytic) – a distinction that has not been accounted for in previous regional to global scale studies, yet might be key to explaining the complex spatial patterns of orchids on islands.

Because plant functional traits are tightly linked to the immediate environment (Dwyer et al. 2015, Blonder et al. 2018), the global distribution of orchid life forms may be influenced by different factors relating to key functional characteristics (Ordonez and Svenning 2015, Blonder et al. 2018, Zanne et al. 2018). Most epiphytic orchids are characterized by thick, succulent leaves and aerial roots that are covered by a layer of dead cells (velamen radicum), which can rapidly absorb water (Zotz and Winkler 2013). A considerable proportion of epiphytic orchids have water-storing pseudobulbs (Göbel and Zotz 2020), while others use CAM photosynthesis to conserve water (Barbante et al. 2012, Yang et al. 2016). These functional traits are considered to aid the survival of epiphytes in forest canopies where water availability is a major limiting factor (Zotz and Hietz 2001, Laube and Zotz 2003). Conversely, geophytes possess traits associated with carbohydrate storage, such as bulbs, corms or tubers, which enables their survival during prolonged winters or summer droughts (Raunkiaer 1934, Ellenberg 1988). This strategy is particularly favoured in seasonal Mediterranean and temperate climates, where environmental cues induce a period of plant dormancy during unfavourable climatic conditions, minimizing the risk of mortality during the hot, dry summers (Ofir and Kigel 2003) and winter frost (Shefferson et al. 2005), respectively. Two other terrestrial life forms exhibited by orchids are chamaephytes (e.g. *Dendrobium vannouhuysii*, WCSP 2018) and hemicryptophytes (e.g. *Neottia ovata*,

WCSP 2018), which have buds that are positioned just aboveground that enables plants to withstand the coldest winter months under the protection of snow cover (termed hereafter ‘non-geophytes’ for simplicity, Mueller-Dombois and Ellenberg 1974). Thus, because each life form has a unique set of traits that represent different ecological strategies, it is crucial to understand the ecological constraints acting on each life form separately in order to disentangle the complex and poorly understood spatial patterns of orchids on islands.

Here, we present a comprehensive global analysis of 454 islands, relating patterns of orchid species richness and endemism to geographical (island area, geologic type, geographical isolation, age, elevational range, topographic heterogeneity), climatic (cloud cover, precipitation, temperature, seasonality) and biological (forest cover) characteristics of islands. We analyse diversity patterns for all orchids and separately for epiphytes, geophytes and non-geophytes. Specifically, we address the following questions: 1) what are the global drivers of orchid species richness and endemism on islands? 2) Can the diversity of epiphytes, geophytes and non-geophytes be predicted by the same variables? We expected epiphytic orchid diversity, which is generally presumed to be constrained by water availability (Zotz and Hietz 2001), to be best predicted by variables such as annual precipitation and cloud cover. Conversely, because geophytes possess subterranean organs to survive climate extremities, we expected orchid geophytes to be well-represented in highly seasonal climates (i.e. islands with Mediterranean climates or islands at high latitudes with a pronounced winter, Howard et al. 2019). Although non-geophytes lack subterranean storage organs, they should be less affected by cooler temperatures than epiphytic orchids and therefore should occur on cooler, less seasonal islands than epiphytic orchids.

## Material and methods

### Orchid distributions and life forms

Orchid distribution data was extracted from the Global Inventory of Floras and Traits database (GIFT ver. 1.0, <<https://gift.uni-goettingen.de>>), which contains checklist information for over 315 000 plant species – including 27 640 orchid species (Weigelt et al. 2020). Checklists range from global-scale key resources, e.g. World Checklist of Selected Plant Families (WCSP 2014), to regional checklists, e.g. western Pacific (Keppel et al. 2016) plus numerous single island and archipelago checklists. For detailed information about the conceptual framework of GIFT including checklist standardization procedures see Weigelt et al. (2020).

We followed strict island selection criteria with the aim of producing a harmonised and standardised dataset with islands representative of different climates, geology and locality. Floristic information was first extracted for 1027 islands and archipelagos for which complete orchid checklist information was available. We wished to focus on single islands

instead of the archipelagos they are nested in. In cases where checklists were only available at the archipelago level, we considered the ratio between the geographical extent of the largest constituent island and the entire geographical extent of the terrestrial landmass of the archipelago as a measure of the proportion of total archipelago landmass constituted by the main island. Large islands with small satellite islands receive a geographical extent ratio close to 1 (e.g. Cuba, Hispaniola, Taiwan, Tasmania, Sumatra and more), while archipelagos composed of multiple islands spread over a large geographical area receive smaller ratios (e.g. New Caledonia, ratio: 0.27). We used a geographical–extent ratio threshold of 0.60, which ensured to exclude archipelagos for which the species list was unlikely to be representative of the largest island from the analyses while retaining units mostly consisting of one large main island. Very small islands ( $< 1 \text{ km}^2$ ) were also excluded because the resolution (30 arc-seconds, i.e.  $\sim 1 \text{ km}^2$ ) of the environmental data was insufficient to produce reliable values. The final dataset consisted of 454 islands and island units for which complete checklists of native orchids were available, and 358 islands for which endemic orchid information could be derived. We defined an endemic orchid as one found only on a specific island or island unit. The references used to compile this dataset can be found in Supporting information.

For each orchid species, we assigned life form (epiphytic, geophyte or non-geophyte) information based on a comprehensive species list for epiphytes (Zotz 2016) and the WCSP (2018) for terrestrial orchids. Following Mueller-Dombois and Ellenberg (1974), we differentiated between two terrestrial life forms; ‘geophytes’ as orchids that possess below-ground storage organs and ‘non-geophytes’ as terrestrial orchids without below-ground storage organs, which included hemicryptophytes and chamaephytes. Based on these definitions, the orchid family is composed of 69% epiphytic (Zotz 2016), 21% geophyte and 3% non-geophyte species (WCSP 2018). We did not consider lithophytic or holomycotrophic orchids due to their rarity on islands ( $n < 30$  species each), and also omitted climbers because 96% of all climbing species in our dataset belonged to the genus *Vanilla*, and thus were not representative of orchids in general. All species names (i.e. nomenclature) were standardised to The Plant List ver. 1.1 prior to extraction from the GIFT database (see Weigelt et al. (2020) for the full standardisation procedure).

### Selection of environmental variables

We selected 12 environmental variables based on the outcome of previous global-scale plant analyses and with consideration of the three orchid life forms. Because large, less-isolated continental islands have been shown to harbour great orchid diversity in previous studies (Givnish et al. 2016, Taylor et al. 2019) we included the classical biogeographic variables island area ( $\text{km}^2$ ), geology (continental, fragment, oceanic), the surrounding landmass proportion of an island (SLMP, a measure of isolation that accounts for stepping stone islands and

irregular coastlines, Weigelt and Kreft 2013), and elevational range (m, Danielson and Gesch 2011), all of which have been consistently shown to be important predictors of plant diversity on islands (MacArthur and Wilson 1967, Kreft et al. 2008). We defined continental islands as islands located on the continental shelf (e.g. New Guinea), fragments as continental islands separated from the mainland through plate tectonics (e.g. Cuba), and oceanic islands as either volcanic islands or sea-floor islands uplifted through plate tectonics (e.g. Niue), following Whittaker and Fernández-Palacios (2007). By this definition, we considered the islands of New Caledonia as ‘oceanic’, since the archipelago was at one point fully submerged, thus gaining biota in the fashion of an oceanic island (Grandcolas et al. 2008). Another important island biogeographic variable is geological age (Ma), which should be particularly important for predicting the number of endemic orchids on oceanic islands. Assuming that islands are dynamic systems, thus changing in area and species numbers through island ontogeny, we employed the general dynamic model of island biogeography, which predicts a unimodal relationship between geological age and species richness/endemism (Whittaker et al. 2008). Finally, we selected topographic heterogeneity (calculated here as the terrain ruggedness index, TRI, Danielson and Gesch 2011), which has been shown to influence orchid diversity patterns across different spatial scales (Keppel et al. 2016, Tsiftsis 2020). For further detailed information on the assignment of geology, calculation of island area and other biogeographic metrics see Weigelt et al. (2020).

In addition to the six biogeographical variables, we selected six climatic factors hypothesised to constrain the distribution of epiphytes, geophytes and non-geophytes. Based on the assumption that water availability is a strong limiting factor for epiphytes (Zotz and Hietz 2001, Kreft et al. 2004), we selected mean annual precipitation (mm) and mean annual cloud cover (% mean cloud cover) (both derived from the CHELSA database, Karger et al. 2017). We also selected percent forest cover (%), Tuanmu and Jetz 2014), given that epiphytic orchids rely on trees for structural support. To capture seasonality, which we expected to affect the diversity of geophytes, we selected two metrics; cloud cover concentration seasonality (cloud cover seasonality, Wilson and Jetz 2016) and precipitation seasonality (coefficient of variation) (CHELSA database, Karger et al. 2017). Temperature seasonality strongly covaried with mean annual temperature ( $^{\circ}\text{C}$ ) (CHELSA database, Karger et al. 2017) and we opted to remove the former and retain the latter variable. Mean annual temperature should best capture the diversity of the orchids assigned as non-geophytes (hemicryptophytes, chamaephytes), which we expected to increase in diversity with decreasing temperature. Temperature should also be an important predictor for epiphytic orchids due to their mainly tropical affinities (Givnish et al. 2015). All predictor values were extracted at a resolution of 30 arc-seconds, except TRI, which was based on digital elevation data at a resolution of 15 arc-seconds.

## Statistical analyses

To determine the most appropriate model structure for our dataset (multiple regression versus mixed effects models), we first tested for the presence of spatial autocorrelation using the Moran I statistic (Dormann et al. 2007). Since residuals from a simple multiple linear regression model showed significant levels of spatial autocorrelation (Moran I statistic = 0.28;  $p \leq 0.001$ ), we included archipelago and botanical continent as random effects. Another test established that the inclusion of random effects removed any spatial autocorrelation in our dataset (Moran I statistic = 0.02;  $p = 0.84$ ), and therefore we considered linear mixed effects models an appropriate framework for our analyses (Bunnefeld and Phillimore 2012). In this regard, the inclusion of archipelago as a random effect would account for the unique geologic and biogeographic histories of the different archipelagos (Patiño et al. 2013). We also tested for zero inflation in our models, given the large number of islands devoid of orchids (144, 32% islands). Following Zuur (2012), we found no evidence for over-dispersion in model residuals ( $\text{chisq}/\text{rdf} \leq 5$ ,  $p = 1.00$ ).

Our final models included the response variables 1) native species richness, 2) endemic species richness, 3) epiphyte richness, 4) geophyte richness, 5) non-geophyte richness, 5) proportion epiphytes, 6) proportion geophytes and 7) proportion non-geophytes. The proportion variables refer to the proportion of the species richness constituted by a particular life form compared to the total richness of orchid species. For all models, island area ( $\text{km}^2$ ), geology, SLMP, elevational range (m), TRI, mean annual temperature ( $^{\circ}\text{C}$ , hereafter temperature), mean annual precipitation (mm, hereafter precipitation), mean annual cloud cover (%), hereafter cloud cover), cloud cover seasonality concentration (hereafter cloud seasonality), precipitation seasonality (coefficient of variation) and forest cover (%) were treated as fixed effects, while archipelago and botanical continent were retained as random effects. In a complimentary analysis for 248 oceanic islands, we included island geologic age (Ma) as an additional fixed effect in the model. Following the general dynamic model (GDM) of oceanic island biogeography, we included a quadratic term for age ( $\text{age} + \text{age}^2$ ) (Whittaker et al. 2008). We also explored possible interactions between the geology of an island and island area and SLMP, given that continental and fragment islands are usually larger and less isolated compared to oceanic islands. In addition, we tested for an interaction between precipitation seasonality and temperature to potentially capture the variation in life form diversity among highly seasonal warm islands versus non-seasonal cool islands versus non-seasonal warm islands. Island area, SLMP, elevational range, TRI, forest cover, as well as all species richness response variables were  $\log_{10}(x+1)$  transformed to reduce skewed distributions.

We selected minimum adequate models using the Akaike information criterion corrected for small sample sizes (AICc) and delta  $\Delta\text{AIC}$  weights, which determine between-model similarity (Burnham and Anderson 2003). AIC weights were summed across models to quantify the relative importance

of each variable (Burnham and Anderson 2003). Models exhibiting  $\Delta\text{AIC}$  values of 2 or less were considered to be the most adequate. In addition, we report the variation explained by both the random effects (conditional  $r^2$ ) and fixed effects (marginal  $r^2$ ) of each model using the pseudo- $r^2$  value, following (Nakagawa and Schielzeth 2013). All statistical analyses were conducted in R (3.5.1, <www.r-project.org>), using the packages ‘lme4’ (Bates et al. 2014), ‘jtools’ (Long 2019a), ‘interactions’ (Long 2019b) and ‘MuMIn’ (Barton 2009).

## Results

### Global distribution of native and endemic orchid diversity

In our global analysis of 454 islands, orchids were distributed as far south as Macquarie Island ( $55^{\circ}\text{S}$ ) and as far north as Iceland ( $65^{\circ}\text{N}$ ), peaking in species richness and endemism in tropical Asia (e.g. New Guinea, Borneo, Fig. 1A–B), followed by Madagascar, which had the second highest proportion of endemic orchids after New Guinea (83% and 84% endemic species, respectively). Despite a great latitudinal spread, orchids were entirely absent from 144 out of 454 islands (32%), while 289 of the 358 islands with endemic species data (81%) had no endemic orchids. Oceanic islands had, on average, significantly fewer native and endemic orchids compared to continental and fragment islands (Supporting information) and gained comparatively fewer species with increasing island area (Fig. 2, Supporting information).

Orchid species richness was best predicted by island area ( $z = 0.41 \pm 0.05$ ,  $p \leq 0.001$ ) and mean cloud cover ( $z = 0.40 \pm 0.04$ ,  $p \leq 0.001$ ), but also showed strong positive relationships with increasing temperature, forest cover and elevational range (Fig. 2, 3). The positive effects of increasing island area, temperature and precipitation were more pronounced for endemic orchids relative to all native orchids. Both the number of endemic and native orchids increased with SLMP (surrounding landmass proportion) on oceanic islands only, but the number of endemic orchids decreased overall with increasing SLMP (Fig. 2, 3, Supporting information). Fixed effects alone explained 68% and 53% (marginal  $r^2$ ) of the orchid diversity and endemism model variance, respectively, which increased to 88% and 82% with the inclusion of random effects (conditional  $r^2$ ). In our complimentary analyses that included oceanic island age as a fixed effect, we found that both the linear and quadratic term were significant, indicating that orchid species richness and endemism on oceanic islands follow a unimodal pattern in congruence with island ontogeny (Fig. 2, 3).

### Diversity among life forms

The different functional groups varied in their responses to predictor variables, with island area and geology being the only consistent significant predictors of all three life forms (Fig. 2, 4). Epiphytic orchids were predominantly found in



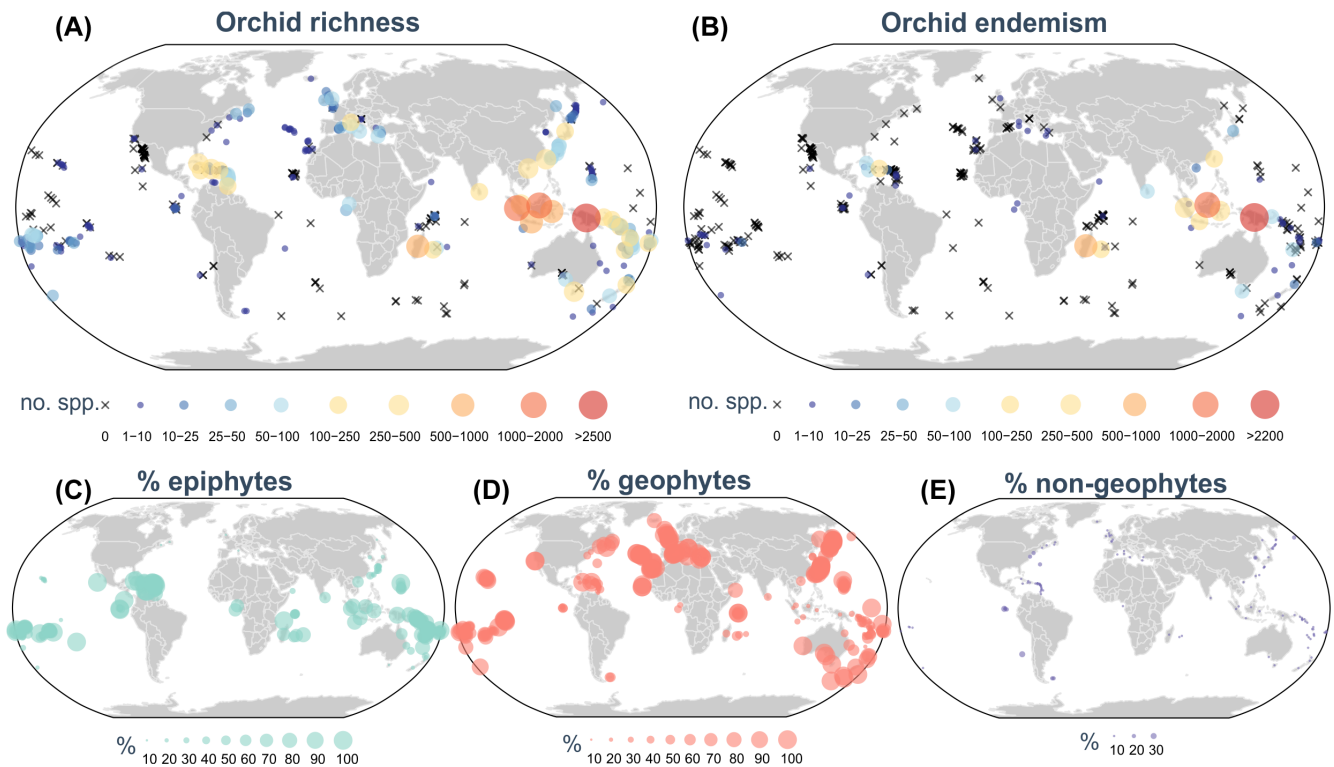


Figure 1. Species richness of native orchids on 454 islands (A) and endemic orchids on 358 islands (B), and the proportional representation % of the following orchid life forms: epiphytes (C), geophytes (D) and non-geophytes (E). Points are scaled according to the number of species (A) and (B) or by the proportional representation of each orchid life form (C–E). no. spp. = number of species.

the tropics (Fig. 1C), and on oceanic islands, with almost half of all oceanic islands (48%) having at least 1 epiphyte species. Although epiphytic orchids occurred on just 27% of all continental islands, they contributed substantially to the diversity of orchids on the most orchid-rich islands, representing 81, 79 and 78% of the orchids of the large tropical islands New Guinea, Borneo and Sumatra, respectively. This contrasts with geophytes, which were better represented on fragment islands, contributing, on average, 62% to the orchid flora of this island geology. Non-geophytes (chamaephytes/hemicryptophytes) were overall poorly represented on islands, reaching their greatest proportional representation in the oceanic Juan Fernandez Islands (30% of the orchid flora), yet represented on average just 2% of the flora on continental islands, 1% on oceanic islands and 0.4% on fragment islands.

For epiphytic orchids, temperature had the strongest effect on both richness ( $z=0.62 \pm 0.07$ ,  $p \leq 0.001$ , Fig. 4) and proportional representation ( $z=0.48 \pm 0.07$ ,  $p \leq 0.001$ , Fig. 5), while island area was more important for both terrestrial life forms. Precipitation and forest cover only predicted the diversity of non-geophytes and geophytes, respectively. Despite forest cover not being an important predictor of epiphyte diversity, the proportion of epiphytes significantly increased with increasing forest cover ( $z=0.24 \pm 0.04$ ,  $p \leq 0.001$ ). Epiphytes and non-geophytes showed similar positive responses to elevational range and a negative response to increasing cloud seasonality. Likewise, epiphytes and geophytes displayed shared increases in diversity with increasing

cloud cover and temperature (Fig. 4). Conversely, the proportional representation of geophytes increased with increasing cloud seasonality and decreased with increasing temperature along with terrestrial non-geophytes. The diversity of non-geophytes significantly decreased with increasing cloud seasonality and their proportional representation decreased with increasing precipitation seasonality on warmer islands (Fig. 5F). Finally, significant interactions were observed between the number and proportion of life forms for island geology, geology:area and geology:SLMP (Supporting information). Fixed effects alone explained more variation in the species richness models of epiphytes (59%), geophytes (66%) and non-geophytes (52%) than in the proportional representation models (epiphytes: 39%, geophytes: 25%, terrestrial non-geophytes: 17%). With the inclusion of random effects, however, variation explained increased to 86% in both the epiphyte and geophyte richness models, 66% in the non-geophyte model, and 57, 63 and 43% for the models explaining the proportional representation of epiphytes, geophytes and non-geophytes, respectively.

## Discussion

Our study identifies several global centres of orchid richness and endemism on islands (Fig. 1), with the most speciose islands located in Malesia (e.g. New Guinea), western Indian Ocean (e.g. Madagascar), Pacific Ocean (e.g. Terra Grande,

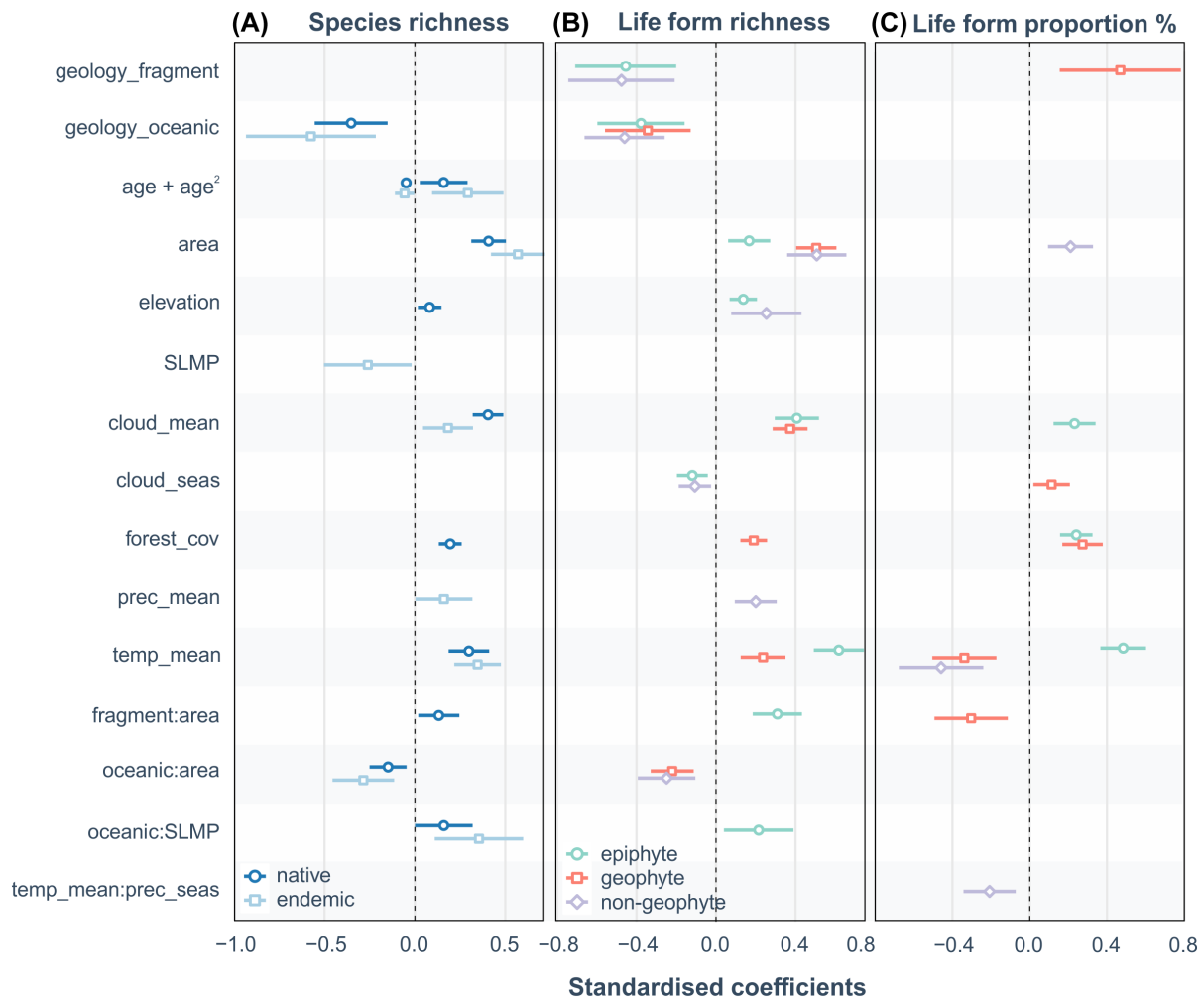


Figure 2. Standardized coefficient plots (z-scores) showing the relative importance of biogeographic [geology, age + age<sup>2</sup> (Ma) = island age + quadratic term, area (km<sup>2</sup>), elevation = elevational range (m), SLMP = surrounding landmass proportion] and bioclimatic [cloud\_mean = mean annual cloud cover (%), cloud\_seas = cloud cover seasonality metric, forest\_cov = forest cover (%), prec\_mean = mean annual precipitation (mm), temp\_mean = mean annual temperature (°C)] fixed effects on (A) the total number of native and endemic orchids; and (B) the number and (C) proportional representation of the orchid life forms (epiphyte, geophyte, non-geophytes). Also shown are 95% confidence intervals. Note that the coefficients for age + age<sup>2</sup> were obtained using a subset of 264 oceanic islands for which the age of the island was known. Only significant effects ( $p \leq 0.05$ ) are shown. The result of geology\_fragment and geology\_oceanic is in reference to geology\_continental.

New Caledonia) and the Caribbean (e.g. Hispaniola), corroborating previous studies (Jacquemyn et al. 2005, Ackerman et al. 2007, Micheneau et al. 2008, Keppel et al. 2016, Traxmandlová et al. 2018, Taylor et al. 2019). However, we also highlight a number of orchid diversity ‘cold’ spots, including islands that lack orchids entirely (32% of islands) or have no endemic species (81% of islands), a pattern that cannot be understood by considering species richness alone. Differences among life forms, however, had considerable impacts on the distribution and diversity of orchids. We found that key predictors of orchid diversity varied markedly with life form, which could be related to different ecological strategies associated with environmental and biogeographical limitations of different species. Functional traits can therefore be of extraordinary importance when investigating species

distribution and diversity patterns (Pollock et al. 2012, Blonder et al. 2018) and should be considered more widely in future biogeographic investigations.

### Global distribution of native and endemic orchid diversity

Numerous studies have contributed to our understanding of orchid diversity at the local scale (Barthlott et al. 2001, Jacquemyn et al. 2005, 2015), yet we are only beginning to understand drivers of orchid diversity at the regional (Ackerman et al. 2007, Keppel et al. 2016, Traxmandlová et al. 2018, Tsiftsis et al. 2019, Crain and Fernández 2020) to global scale (Traxmandlová et al. 2018, Taylor et al. 2019). Here, we found that orchid species richness and endemism

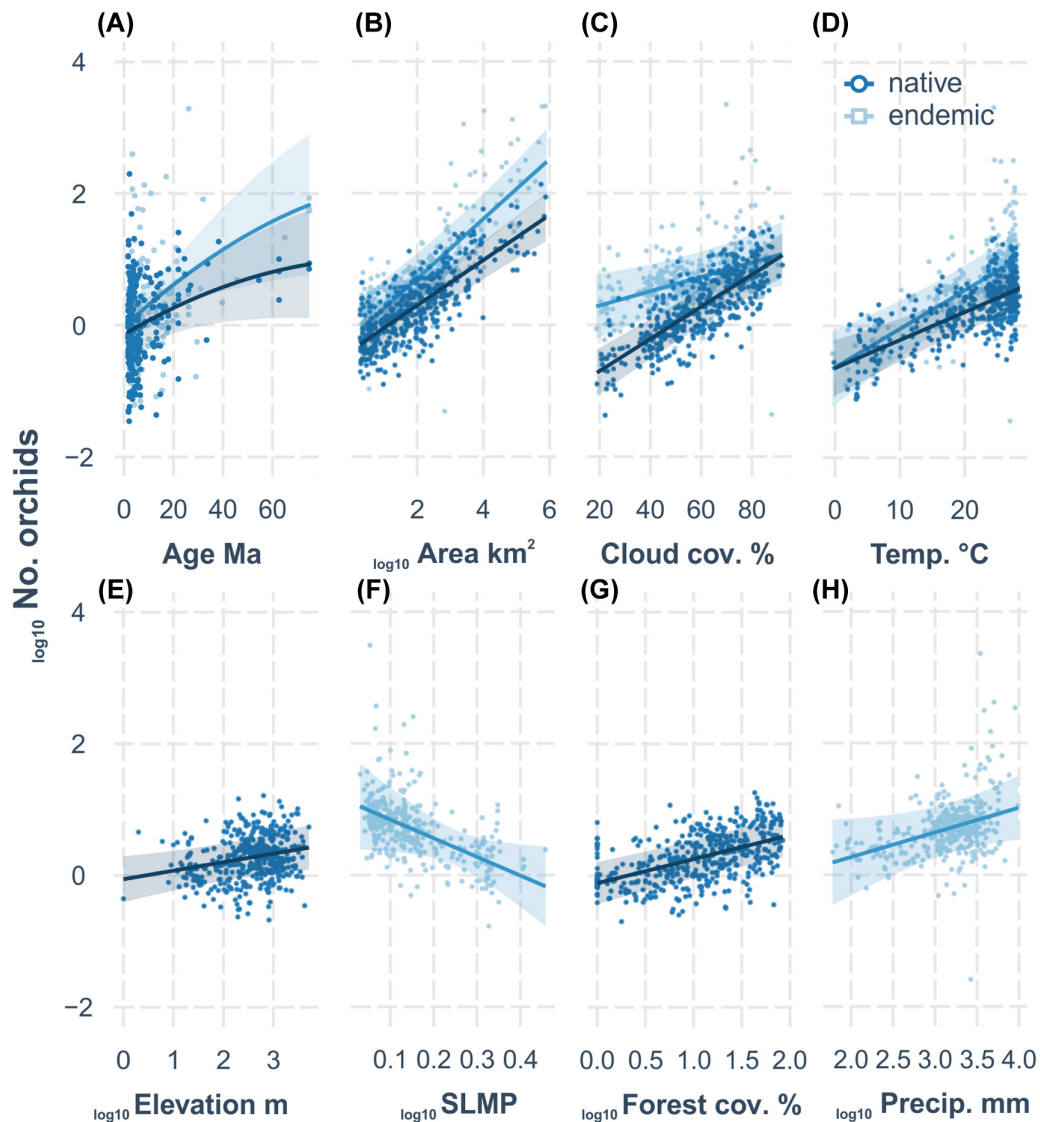


Figure 3. Partial residual plots showing the effects of island age (Ma) for oceanic islands only (A),  $\log_{10}$  area ( $\text{km}^2$ ) (B), cloud cover (%) (C), mean annual temperature ( $^{\circ}\text{C}$ ) (D),  $\log_{10}$  elevational range (m) (E),  $\log_{10}$  surrounding landmass proportion, SLMP (F),  $\log_{10}$  forest cover (%) (G) and  $\log_{10}$  mean annual precipitation (mm) (H) on the total number of  $\log_{10}$  native (dark blue) and  $\log_{10}$  endemic (light blue) orchids on 454 and 358 islands, respectively. Points are partial residuals; solid and shaded lines are model predicted slopes and their respective 95% confidence limits. Note that the relationship between oceanic island age and the number of orchids is quadratic ( $\text{age} + \text{age}^2$ ). Only significant effects ( $p \leq 0.05$ ) are shown.

differ vastly among islands worldwide, and are closely linked to island area, geology, cloud cover and temperature.

The importance of island area as a predictor of species richness and endemism on islands is well established (MacArthur and Wilson, 1967, Kreft et al. 2008, Triantis et al. 2012). Larger islands may offer a greater target area for dispersing propagules (MacArthur and Wilson 1967, Whitehead and Jones 1969), can host more individuals, and have a greater diversity of habitats (Schrader et al. 2019), promoting speciation and reducing extinctions (MacArthur and Wilson 1967, Kisel and Barraclough 2010). These processes explain the high incidence of endemic orchids on large, complex islands, such as continental New Guinea (84% endemic) and

continental fragment Madagascar (83% endemic), and why oceanic islands, which are generally smaller, have comparatively few native and endemic orchids. Second only to area in importance was cloud cover. Cloud cover may influence several key ecological processes that limit plant diversity, such as influencing the length of growing seasons and daily solar radiation (Graham et al. 2003). For orchids, particularly epiphytic orchids, which reach peak diversity in cloud forests, cloud cover may reflect a tempering effect and constant moisture supply.

The positive effect of SLMP (surrounding landmass proportion) on orchid species richness and endemism on oceanic islands and the overall negative effect of SLMP (the inverse of

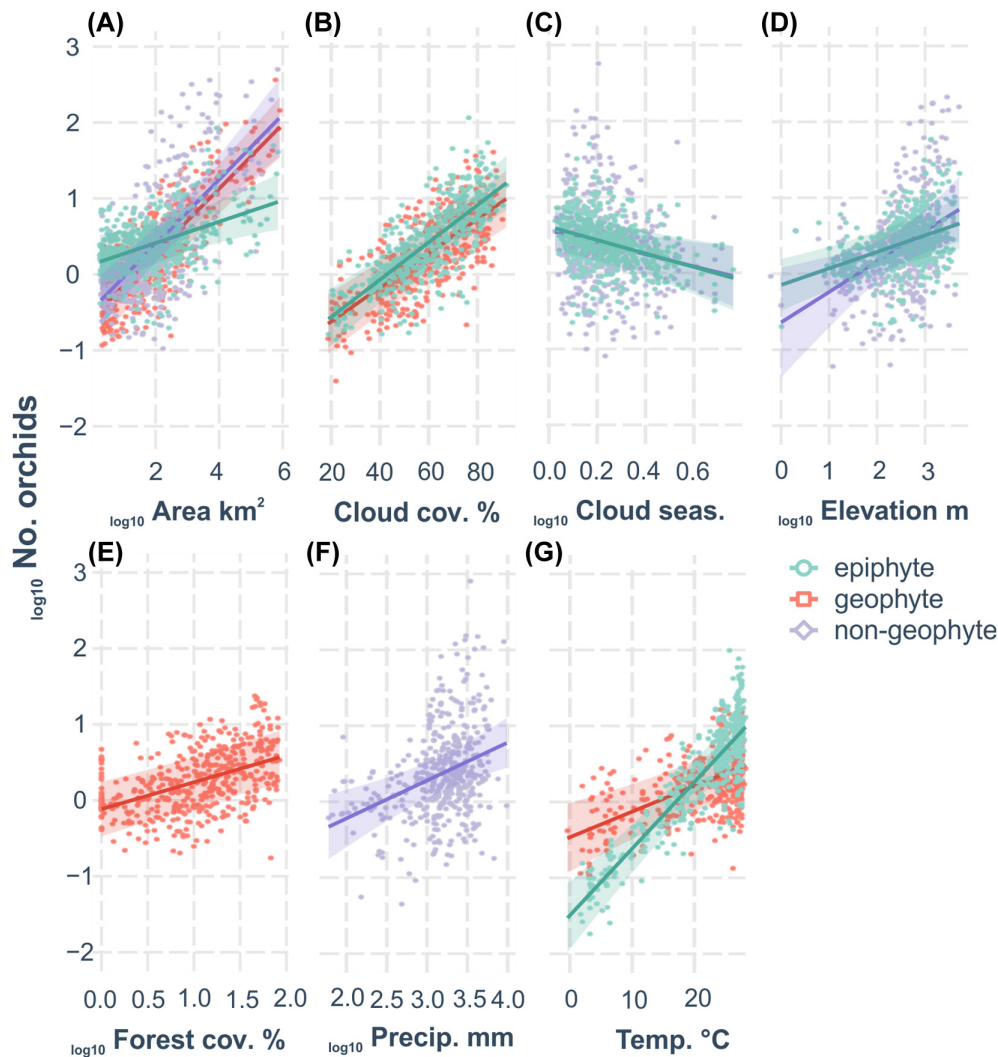


Figure 4. Partial residual plots showing the effects of log<sub>10</sub> island area (km<sup>2</sup>) (A), cloud cover (%) (B), log<sub>10</sub> cloud seasonality (C), log<sub>10</sub> elevational range (m) (D), log<sub>10</sub> forest cover (%) (E), log<sub>10</sub> mean annual precipitation (mm) (F) and mean annual temperature (°C) (G) on the total log<sub>10</sub> number of epiphytic (green), geophyte (orange) and non-geophyte (purple) orchids on 454 islands. Points are model partial residuals; solid and shaded lines are model predicted slopes and their respective 95% confidence limits. Only significant effects ( $p \leq 0.05$ ) are shown.

isolation) on endemic orchids demonstrates the importance of isolation in the assembly of insular floras (Weigelt et al. 2015). On the one hand, oceanic islands are the most isolated in the world and colonization is difficult, even for adept long-distance dispersers like orchids (Arditti and Ghani 2000). On the other hand, isolation may foster speciation by reducing gene flow between islands and source regions, likely contributing to the overall negative effect of SLMP on the number of endemic orchids.

Finally, we found a unimodal relationship between orchid species richness and island age, which is in line with predictions by the general dynamic model (GDM) of oceanic island biogeography (Whittaker et al. 2008). Orchids were on average either entirely absent or present in low numbers on both recently emerged (e.g. Chirpoi Island of the Kuril Islands – 0.0012 Ma, 7 orchid species) and older oceanic

islands (e.g. Palmyra – 75 Ma, 0 orchid species). Moreover, we found that the number of endemic orchids peaked later compared to native orchids, which could be attributed to the fact that endemic species amass over greater time periods (Steinbauer et al. 2012, Cabral et al. 2019). It is important to note, however, that fixed effects alone only explained 53% of the variation in the number of endemic orchids on islands, which increased to 82% with the inclusion of archipelago as a random effect, suggesting that idiosyncratic archipelago attributes (e.g. geological history and isolation) play a pivotal role in the accumulation of endemic orchids.

#### Diversity among life forms

The three orchid life forms displayed important differences in diversity patterns among islands, yet shared similarities



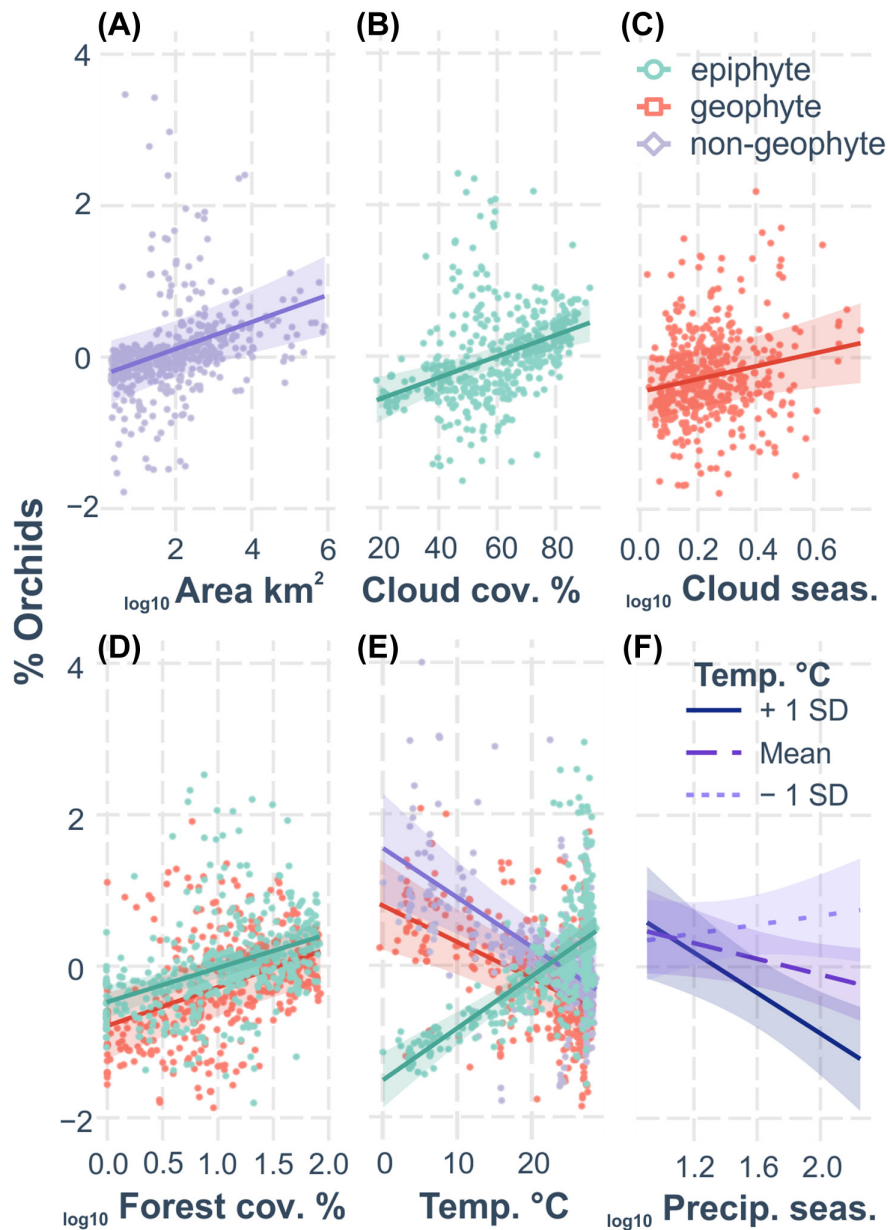


Figure 5. Partial residual plots showing the effects of log<sub>10</sub> island area (km<sup>2</sup>) (A), cloud cover (%) (B), log<sub>10</sub> cloud seasonality (C), log<sub>10</sub> forest cover (%) (D) and temperature (°C) (E) on the proportional representation of epiphytic (green), geophyte (orange) and non-geophytes (purple) orchids on 454 islands. Panel (F) displays the interaction between precipitation seasonality and temperature on the proportional representation of non-geophytes. It shows that on islands with warmer temperatures (+1 SD of mean), non-geophytes decrease in their proportional representation with increasing precipitation seasonality. Points are model partial residuals; solid and shaded lines are model predicted slopes and their respective 95% confidence limits. Only significant effects ( $p \leq 0.05$ ) are shown.

in key island biogeographic properties, i.e. being positively related to island area and being most diverse on continental islands (Fig. 4). Temperature explained the greatest proportion of variation for epiphytic orchids, reflecting the tropical restriction of epiphytism in most orchid groups (Kreft et al. 2008, Zotz 2016). Epiphytic orchids form an important component of wet, tropical forest ecosystems, where they can account for more than two thirds of total epiphyte diversity (Zotz 2005). Frost, in particular, is thought to be a key

constraint on the distribution of epiphytes (Kessler 2002, Zotz 2005), which may explain why only three epiphytic orchids occurred on islands with average temperatures of < 10°C, and none on islands with average temperatures of < 5°C. Although geophyte diversity also increased with increasing temperature, both terrestrial life forms decreased in their proportional representation, reflecting the shift in the relative contribution of epiphytic orchids in the tropics to terrestrial orchids in progressively cooler latitudes.

Both life forms without subterranean storage organs, epiphytes and non-geophytes, displayed similar negative responses to the precipitation metric cloud seasonality. Seasonal changes in precipitation may negatively affect plants by reducing growth rates and increasing rates of desiccation leading to mortality (Goldsmith et al. 2013). Because epiphytes do not root in the ground and have an aerial root system, water limitation is considered a major constraint on epiphyte distributions (Zotz and Hietz 2001). The risk of desiccation for orchid geophytes, however, may be offset due to their ability to undergo prolonged dormancy states underground during unfavourable environmental conditions (Tatarenko and Kondo 2003). The relevance of desiccation risk for orchids is further illustrated by the significant effect of the interaction between temperature and precipitation seasonality on the diversity of non-geophytes, which decreased in diversity with increasing seasonality on islands with high temperatures, but not on islands with cooler temperatures (Fig. 5F).

Because epiphytic orchids rely on host trees for structural support, we expected that forest cover would be an important predictor of epiphytic orchid diversity. While this was not observed in the richness model, forest cover was an important predictor of the proportional representation of epiphytic orchids. The higher susceptibility of forest trees to low temperatures and precipitation may also contribute to the correlation between the diversity of epiphytic orchids with both temperature and cloud cover. Similarly, the high diversity of epiphytic orchids in tropical montane cloud forests (Cardelús et al. 2006), which may occur at relatively low elevations on oceanic islands (Keppel and Thomas 2009), may explain the positive effect of elevation on epiphytic orchid diversity. Indeed, non-geophytes also showed a positive relationship with elevation and precipitation, further illustrating their preference for non-seasonal, wet climates.

## Conclusion

Our study revealed various biogeographic and bioclimatic factors that influence orchid species richness and endemism across different geological types and among three orchid life forms. We found that considering plant life forms clarified some perplexing results in orchid diversity patterns on islands and enabled a better understanding of the processes driving these diversity patterns. We therefore suggest that future studies include key functional differences to tease apart complex relationships, which may not be captured by considering species richness alone. Determining additional factors that may better predict the number of endemic orchids on islands should be made a priority. In the specific case of orchids and other groups with many epiphytes like aroids and bromeliads, one might also consider the distance to tropical source regions (review by Zotz 2005), or ecological factors such as the distribution of mycorrhizal fungi in the soil/on trees to reach a more complete understanding of the mechanisms underpinning orchid diversity patterns.

## Data availability statement

All data used for analyses are provided as Supporting information.

*Acknowledgements* – We would also like to thank the subject editor and two reviewers for constructive feedback on our manuscript.

*Funding* – GK was partially supported by an Alexander von Humboldt foundation fellowship. HK acknowledges funding by the German Research Foundation in the framework of the DynaCom project.

## Author contributions

**Amanda Taylor:** Conceptualization (equal); Data curation (equal); Formal analysis (lead); Investigation (lead); Methodology (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal). **Gunnar Keppel:** Conceptualization (equal); Data curation (equal); Formal analysis (supporting); Funding acquisition (supporting); Investigation (supporting); Methodology (supporting); Writing – original draft (supporting); Writing – review and editing (equal). **Patrick Weigelt:** Conceptualization (equal); Data curation (equal); Formal analysis (supporting); Investigation (supporting); Methodology (supporting); Writing – review and editing (equal). **Gerhard Zotz:** Conceptualization (supporting); Data curation (equal); Investigation (supporting); Writing – review and editing (equal). **Holger Kreft:** Conceptualization (equal); Data curation (supporting); Formal analysis (supporting); Funding acquisition (supporting); Investigation (supporting); Methodology (supporting); Writing – review and editing (equal).

## References

- Ackerman, J. D. et al. 2007. Orchids of the West Indies: predictability of diversity and endemism. – *J. Biogeogr.* 34: 779–786.
- Ali, J. R. 2017. Islands as biological substrates: classification of the biological assemblage components and the physical island types. – *J. Biogeogr.* 44: 984–994.
- Arditti, J. and Ghani, A. K. A. 2000. Tansley review No. 110. Numerical and physical properties of orchid seeds and their biological implications. – *New Phytol.* 145: 367–421.
- Barbante, G. et al. 2012. Crassulacean acid metabolism in epiphytic orchids: current knowledge, future perspectives. – In: Han (ed.), *Applied photosynthesis*. InTech, Rijeka, pp. 81–104.
- Barthlott, W. et al. 2001. Diversity and abundance of vascular epiphytes: a comparison of secondary vegetation and primary montane rain forest in the Venezuelan Andes. – *Plant Ecol.* 152: 145–156.
- Barton, K. 2009. MuMIn: multi-model inference. R package ver. 0.12.0. – <<http://r-forge.r-project.org/projects/mumin/>>.
- Bates, D. et al. 2014. lme4: linear mixed-effects models using Eigen and S4. R package ver. 1: 1–23. – <<https://cran.r-project.org/web/packages/lme4/index.html>>.

- Blonder, B. et al. 2018. Microenvironment and functional–trait context dependence predict alpine plant community dynamics. – *J. Ecol.* 106: 1323–1337.
- Bunnefeld, N. and Phillimore, A. B. 2012. Island, archipelago and taxon effects: mixed models as a means of dealing with the imperfect design of nature’s experiments. – *Ecography* 35: 15–22.
- Burnham, K. P. and Anderson, D. R. 2003. Model selection and multimodel inference: a practical information–theoretic approach. – Springer.
- Cabral, J. S. et al. 2019. Assessing predicted isolation effects from the general dynamic model of island biogeography with an eco–evolutionary model for plants. – *J. Biogeogr.* 46: 1569–1581.
- Cardelús, C. L. et al. 2006. Vascular epiphyte distribution patterns: explaining the mid–elevation richness peak. – *J. Ecol.* 94: 144–156.
- Carlquist, S. 1967. The biota of long–distance dispersal. V. Plant dispersal to Pacific Islands. – *Bull. Torrey Bot. Club* 94: 129–162.
- Cozzolino, S. and Widmer, A. 2005. Orchid diversity: an evolutionary consequence of deception? – *Trends Ecol. Evol.* 20: 487–494.
- Crain, B. J. and Fernández, M. 2020. Biogeographical analyses to facilitate targeted conservation of orchid diversity hotspots in Costa Rica. – *Divers. Distrib.* 26: 853–866.
- Danielson, J. J. and Gesch, D. B. 2011. Global multi–resolution terrain elevation data 2010 (GMTED2010). – U.S. Geological Survey Open–File Report 2011–1073, 26 p.
- Darwin, C. 1859. On the origin of species by means of natural selection. – Routledge, London.
- Dormann, C. F. et al. 2007. Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. – *Ecography* 30: 609–628.
- Dwyer, J. M. et al. 2015. Climate moderates release from nutrient limitation in natural annual plant communities. – *Global Ecol. Biogeogr.* 24: 549–561.
- Ellenberg, H. H. 1988. Vegetation ecology of central Europe. – Cambridge Univ. Press.
- Givnish, T. J. et al. 2015. Orchid phylogenomics and multiple drivers of their extraordinary diversification. – *Proc. R. Soc. B* 282: 20151553.
- Givnish, T. J. et al. 2016. Orchid historical biogeography, diversification, Antarctica and the paradox of orchid dispersal. – *J. Biogeogr.* 43: 1905–1916.
- Göbel, C. Y. et al. 2020. What is a pseudobulb? Toward a quantitative definition. – *Int. J. Plant Sci.* 181: 686–696.
- Goldsmith, G. R. et al. 2013. The incidence and implications of clouds for cloud forest plant water relations. – *Ecol. Lett.* 16: 307–314.
- Graham, E. A. et al. 2003. Cloud cover limits net CO<sub>2</sub> uptake and growth of a rainforest tree during tropical rainy seasons. – *Proc. Natl Acad. Sci. USA* 100: 572–576.
- Grandcolas, P. et al. 2008. New Caledonia: a very old Darwinian island? – *Phil. Trans. R. Soc. B* 363: 3309–3317.
- Gravendeel, B. et al. 2004. Epiphytism and pollinator specialization: drivers for orchid diversity? – *Phil. Trans. R. Soc. B* 359: 1523–1535.
- Howard C. C. et al. 2019. The monocotyledonous underground: global climatic and phylogenetic patterns of geophyte diversity. – *Am. J. Bot.* 106: 850–63.
- Jacquemyn, H. et al. 2005. Elevational gradients of species diversity, breeding system and floral traits of orchid species on Reunion Island. – *J. Biogeogr.* 32: 1751–1761.
- Jacquemyn, H. et al. 2015. Mycorrhizal diversity, seed germination and long–term changes in population size across nine populations of the terrestrial orchid *Neottia ovata*. – *Mol. Ecol.* 24: 3269–3280.
- Jersáková, J. and Malinová, T. 2007. Spatial aspects of seed dispersal and seedling recruitment in orchids. – *New Phytol.* 176: 237–241.
- Karger, D. N. et al. 2017. Climatologies at high resolution for the earth’s land surface areas. – *Sci. Data* 4: 170122.
- Keppel, G. and Thomas, N. T. 2009. Composition and structure of the cloud forest on Mt. Delaco, Gau, Fiji. – *S Pacific J. Nat. Appl. Sci.* 27: 28–34.
- Keppel, G. et al. 2016. Habitat diversity predicts orchid diversity in the tropical south–west Pacific. – *J. Biogeogr.* 43: 2332–2342.
- Kessler, M. 2002. Species richness and ecophysiological types among Bolivian bromeliad communities. – *Biodivers. Conserv.* 11: 987–1010.
- Kisel, Y. and Barraclough, T. G. 2010. Speciation has a spatial scale that depends on levels of gene flow. – *Am. Nat.* 175: 316–334.
- Kreft, H. et al. 2008. Global diversity of island floras from a macroecological perspective. – *Ecol. Lett.* 11: 116–127.
- Kreft, H. et al. 2004. Diversity and biogeography of vascular epiphytes in Western Amazonia, Yasuni, Ecuador. – *J. Biogeogr.* 31: 1463–1476.
- König, C. et al. 2020. Source pools and disharmony of the world’s island floras. – *Ecography* 44: 44–55.
- Laube, S. and Zotz, G. 2003. Which abiotic factors limit vegetative growth in a vascular epiphyte? – *Funct. Ecol.* 17: 598–604.
- Long, J. A. 2019a. jtools: analysis and presentation of social scientific data. R package ver., 2.0.1. – <<https://cran.r-project.org/web/packages/jtools/index.html>>.
- Long, J. A. 2019b. Interactions: comprehensive, user–friendly toolkit for probing interactions. R package ver., 1.1.0. – <<https://cran.r-project.org/web/packages/interactions/index.html>>.
- MacArthur, R. H. and Wilson, E. O. 1967. The theory of island biogeography. – Princeton Univ. Press.
- Micheneau, C. et al. 2008. Phylogenetics and biogeography of Mascarene angraecoid orchids (Vandaeae, Orchidaceae). – *Mol. Phylogenet. Evol.* 46: 908–922.
- Mueller–Dombois, D. and Ellenberg, H. 1974. Aims and methods of vegetation ecology. – Wiley.
- Nakagawa, S. and Schielzeth, H. 2013. A general and simple method for obtaining R<sup>2</sup> from generalized linear mixed–effects models. – *Methods Ecol. Evol.* 4: 133–142.
- Neall, V. E. and Trewick, S. A. 2008. The age and origin of the Pacific islands: a geological overview. – *Phil. Trans. R. Soc. B* 363: 3293–3308.
- Ofir, M. and Kigel, J. 2003. Variation in onset of summer dormancy and flowering capacity along an aridity gradient in *Poa bulbosa* L., a geophytic perennial grass. – *Ann. Bot.* 91: 391–400.
- Ordóñez, A. and Svenning, J–C. 2015. Geographic patterns in functional diversity deficits are linked to glacial–interglacial climate stability and accessibility. – *Global Ecol. Biogeogr.* 24: 826–837.
- Otero, J. T. and Flanagan, N. S. 2006. Orchid diversity – beyond deception. – *Trends Ecol. Evol.* 21: 64–65.

- Partomihardjo, T. 2003. Colonisation of orchids on the Krakatau Islands. – *Telopea* 10: 299–310.
- Patiño, J. et al. 2013. Baker's law and the island syndromes in bryophytes. – *J. Ecol.* 101: 1245–1255.
- Pollock, L. J. et al. 2012. The role of functional traits in species distributions revealed through a hierarchical model. – *Ecography* 35: 716–725.
- Raunkiaer, C. 1934. The life forms of plants and statistical plant geography. – Oxford Univ. Press.
- Schrader, J. et al. 2019. Plants on small islands revisited: the effects of spatial scale and habitat quality on the species–area relationship. – *Ecography* 42: 1405–1414.
- Shefferson, R. P. et al. 2005. Adult whole-plant dormancy induced by stress in long-lived orchids. – *Ecology* 86: 3099–3104.
- Steinbauer, M. J. et al. 2012. Increase of island endemism with altitude–speciation processes on oceanic islands. – *Ecography* 35: 23–32.
- Tatarenko, I. V. and Kondo, K. 2003. Seasonal development of annual shoots in some terrestrial orchids from Russia and Japan. – *Plant Species Biol.* 18: 43–55.
- Taylor, A. et al. 2019. Island disharmony revisited using orchids as a model group. – *New Phytol.* 223: 597–606.
- Traxmandlová, I. et al. 2018. Determinants of orchid species diversity in world islands. – *New Phytol.* 217: 12–15.
- Triantis, K. A. et al. 2012. The island species–area relationship, biology and statistics. – *J. Biogeogr.* 39: 215–231.
- Tsiftsis, S. 2020. The complex effect of heterogeneity and isolation in determining alpha and beta orchid diversity on islands in the Aegean archipelago. – *Syst. Biodivers.* 18: 281–294.
- Tsiftsis, S. et al. 2019. Role of way of life, latitude, elevation and climate on the richness and distribution of orchid species. – *Biodivers. Conserv.* 28: 75–96.
- Tuanmu, M.-N. and Jetz, W. 2014. A global 1-km consensus land-cover product for biodiversity and ecosystem modelling. – *Global Ecol. Biogeogr.* 23: 1031–1045.
- WCSP. 2014. World checklist of selected plant families. – <<http://apps.kew.org/wcsp/home.do>>, accessed 1 December 2014.
- WCSP. 2018. World checklist of selected plant families. – <<http://apps.kew.org/wcsp/home.do>>, accessed 1 April 2018.
- Weigelt, P. and Kreft, H. 2013. Quantifying island isolation—insights from global patterns of insular plant species richness. – *Ecography* 36: 417–429.
- Weigelt, P. et al. 2013. Bioclimatic and physical characterization of the world's islands. – *Proc. Natl Acad. Sci. USA* 110: 15307–15312.
- Weigelt, P. et al. 2015. Global patterns and drivers of phylogenetic structure in island floras. – *Sci. Rep.* 5: 12213.
- Weigelt, P. et al. 2020. GIFT – a Global Inventory of Floras and Traits for macroecology and biogeography. – *J. Biogeogr.* 47: 16–43.
- Whitehead, D. R. and Jones, C. E. 1969. Small islands and the equilibrium theory of insular biogeography. – *Evolution* 23: 171–179.
- Whittaker, R. J. and Fernández-Palacios, J. M. 2007. Island biogeography; ecology, evolution and conservation. – Oxford Univ. Press.
- Whittaker, R. J. et al. 2008. A general dynamic theory of oceanic island biogeography. – *J. Biogeogr.* 35: 977–994.
- Wilson, A. M. and Jetz, W. 2016. Remotely sensed high-resolution global cloud dynamics for predicting ecosystem and biodiversity distributions. – *PLoS Biol.* 14: e1002415.
- Yang, S.-J. et al. 2016. Two strategies by epiphytic orchids for maintaining water balance: thick cuticles in leaves and water storage in pseudobulbs. – *AoB Plants* 8: plw046.
- Zanne, A. E. et al. 2018. Functional biogeography of angiosperms: life at the extremes. – *New Phytol.* 218: 1697–1709.
- Zotz, G. 2005. Vascular epiphytes in the temperate zones – a review. – *Plant Ecol.* 176: 173–183.
- Zotz, G. 2016. Plants on plants – the biology of vascular epiphytes. – Springer.
- Zotz, G. and Hietz, P. 2001. The physiological ecology of vascular epiphytes: current knowledge, open questions. – *J. Exp. Bot.* 52: 2067–2078.
- Zotz, G. and Winkler, U. 2013. Aerial roots of epiphytic orchids. The velamen radicum and its role in water and nutrient uptake. – *Oecologia* 171: 733–741.
- Zuur, A. F. 2012. A beginner's guide to generalized additive models with R. – Highland Statistics Limited, Newburgh, NY, USA.