

The influence of geometric constraints on the colonisation, speciation and range expansion of orchids

David L. Roberts^{1,2} & Neil A. Brummitt^{1,3}

¹Royal Botanic Gardens, Kew, Richmond, Surrey, TW9 3AB, U.K.

²d.roberts@rbgkew.org.uk

³n.brummitt@rbgkew.org.uk

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Abstract

Variation in species richness along a gradient is a well-known phenomenon and many attempts have been made to correlate this with various environmental factors. Recently, however, the potential influence of non-biological factors has also been highlighted. Species distributions might be constrained by hard geographical boundaries, such as the ocean surrounding an island, since ranges cannot extend either below the sea or above the highest point on the island. This means a greater probability of overlapping elevational ranges, and also therefore species richness, towards middle elevations. This has been termed the ‘mid-domain effect’ (MDE). The colonisation and speciation of island floras has fascinated biologists since the days of Wallace and Darwin, since their isolation restricts the number of possible hypotheses to explain evolutionary events. In this study, species richness of orchids (Orchidaceae) was studied along the elevational gradient both of the Mascarene Islands and of the islands of the Gulf of Guinea. Here we show how geometric constraints can effect speciation, future colonisation and range expansion of these insular orchids.

Introduction

The colonisation and speciation of island floras and faunas, in particular the study of isolated oceanic island archipelagos, has fascinated biologists since the days of Wallace and Darwin. As Stuessy and Ono (1998) recently stated,

“Oceanic island archipelagos are profoundly interesting ecosystems in which to ask questions about evolutionary patterns and processes. Their isolation from other land masses restricts numbers of plausible hypotheses that can be advanced to explain evolutionary events, often resulting in stronger scientific inferences. Island archipelagos may rightly be considered one of the best places on earth to understand origins and elaborations of biological diversity.”

Variation in species richness along a gradient is a well-known phenomenon, and many attempts have been made to correlate this with environmental factors such as temperature, rainfall, productivity, etc, either singly or in concert (Rosenzweig, 1992, 1995; Rosenzweig and Abramsky, 1993; Rahbek, 1997, and references therein; Kaspari *et al.*, 2000). More recently, however, non-environmental factors have been highlighted (Colwell and Hurtt, 1994; Colwell and Lees, 2000).

One of the simplest, one-dimensional gradients is that of elevation. It is widely recognised that species richness patterns can be unimodal, peaking at mid-elevations (Rahbek, 1995, 1997; Heaney, 2001; Kessler, 2001; Md. Nor, 2001; Rickart, 2001; Sánchez-Cordero, 2001). If the mid-point of a species’ range occurs at the mid-elevation level, then the species has a greater potential to occupy more of the domain, as it can extend to the very top and bottom of the island. If the mid-point of a species’ range occurs near the top or the bottom of the elevational range, however, that species can

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extend only a little way either up or down in elevation. Widespread species are therefore constrained to having mid-points near the centre of the elevational gradient, whereas species with a small elevational range could be found anywhere over the elevational gradient. The greater the proportion of widespread species in a flora, the greater the likelihood that species richness will peak towards the middle of the domain, simply because the number of overlapping species ranges will be greatest at mid-elevations: localised species can be found anywhere over the domain, but widespread species are much more likely to be found at mid-elevations (Colwell and Lees, 2000). This phenomenon is termed the ‘mid-domain effect’ (MDE).

The concept was originally noted as a possible artefact in studies of species richness across environmental gradients (Colwell and Hurtt, 1994), and has yet to gain widespread acceptance as a possible explanation for species richness patterns. Although never proposed as being the sole or even the principal explanation for species richness patterns, the MDE has quickly generated a storm of protest (Bokma and Mönkkönen, 2000; Koleff and Gaston, 2001, Diniz-Filho *et al.*, 2002,). The existence of the MDE can be assessed through randomisation simulations, placing empirical species ranges at random within a defined geographical domain and comparing the species richness patterns shown by this null model with those shown by the empirical data, which is the approach followed here. Few MDE studies to date have focused on flowering plants (but see Grytnes and Vetaas, 2002; Bachman *et al.*, in press) and curiously only two MDE studies have been conducted into species richness patterns on tropical islands (Lees *et al.*, 1999; Bachman *et al.*, in press). Following the pioneering work of MacArthur and Wilson (1967), much of the recent research into island biogeography has largely been centred on Hawaii (Myers, 1991; Cowie, 1995; Pax *et al.*, 1997), the Galapagos Islands (Wight and Simovich, 1985; Peck and Kukalovapeck, 1990; Yeakley and Weishampel, 2000) and the Canary Islands (Francisco-Ortega *et al.*, 1996; Kim *et al.*, 1996; Emerson *et al.*, 2000), with comparatively little interest being shown in the Mascarene and Gulf of Guinea Islands until quite recently.

In this paper, we investigate patterns of orchid species richness on two such archipelagos associated with the African continent, those of the Mascarene Islands and the Gulf of Guinea Islands, using the elevational gradient from sea level to the tops of these islands. We assess patterns of endemism across these archipelagos, investigate possible causes for the observed patterns of species richness with elevation, and suggest a possible scenario for the development of the Mascarene Islands orchid flora.

Methods

Study location

The Mascarene Islands, situated in the western Indian Ocean, are of volcanic origin and have never been connected to one another, or to any other landmass. The three main islands are Mauritius, La Réunion and Rodrigues, with La Réunion (55°30'E, 21°05'S) 150 km south-west of Mauritius (57°30'E, 20°20'S), Rodrigues (63°30'E, 19°40'S) 574 km east of Mauritius and Mauritius itself some 900 km east of its nearest landmass, Madagascar. La Réunion is the largest island in the region at 2,512 km², as well as the highest, rising to 3,069 m (Table 1) (Strahm, 1996a).

Table 1: Age and elevation of the Mascarene Islands

Island	Elevation (m)	Age (myo)
La Réunion	3069	2.1
Mauritius	828	7.8
Rodrigues	393	≥7.8

Data

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A preliminary enumeration of the Mascarene Islands' orchid flora, along with the collation of altitudinal data for 203 species from La Réunion, was compiled based on herbarium material (BM, CGE, E, G, K, MAU, P and REU), complemented with an extensive review of relevant literature and 16 months field study within the region from 1998 to 2000 (Roberts, 2001). This enumeration was then augmented with distributions outside of the Mascarene Islands for the non-endemic species, largely taken from Du Puy *et al.* (1999).

Following enumeration of the orchid flora, the percentage endemism at the species level was calculated for each of the three islands, and the Mascarene Islands as a whole, along with endemism for the broader regions of Madagascar and the Mascarene Islands together and the Mascarene Islands with the Indian Ocean as a whole. Then, for La Réunion, the number of species occurring at every 100 m altitude was determined for each of the following floristic components: (a) species endemic to La Réunion, (b) species shared only with Madagascar, (c) species shared with Mauritius and (d) total orchid flora (sum of a, b and c).

Analytical methods

An MDE null distribution was calculated for each floral component of La Réunion using the RangeModel software (Colwell, 2000). We used Model 4, which selects (with replacement) ranges from the empirical range-size frequency distribution (RSFD) and randomly places them in the domain (the elevation gradient). Model 5, which uses empirical midpoints and random range-sizes, was not used because the null model is too closely constrained by the empirical data (Koleff and Gaston, 2001). The purely theoretical Models 1-3 were also not used because of the implicit biological assumptions they make regarding RSFD's. The model was iterated 1000 times for each floristic component and the mean value for each altitudinal band taken as the null distribution; to account for possible artefacts in the null distribution from using too few or too many bins, bin sizes (\approx number of altitudinal bands) of 10, 15, 30 and 60 were used for each floristic component. The strength of the relationship between the observed species richness *versus* the richness values from the MDE null distribution was tested using a simple linear regression, on the assumption that the closer the slope (as shown by the r^2 value) is to the maximum value of 1, the more closely the MDE null model estimates the number of observed taxa along that elevational gradient (Bachman *et al.*, in press).

Preliminary study into the Gulf of Guinea Islands

As a comparison, this same protocol for studying MDE patterns was then applied to similar data on the orchid floras of the Gulf of Guinea islands São Tomé and Príncipe (Table 2), from the enumeration of on Stévant and de Oliveira (2000), using the floral components (a) endemic, (b) non-endemic and (c) total.

Table 2: Age and elevation of the Gulf of Guinea islands

Island	Elevation (m)	Age (myo)
Bioko	3308	Unknown (Dan Barfod, pers. com.)
Príncipe	935	31.0
São Tomé	2024	13.0
Annobon	654	4.8

Results

Levels of endemism

The Mascarene Islands orchid flora contains 219 species, with 68.0% endemic to the whole region (Table 3). Levels of endemism within the region vary, the lowest being found in Mauritius with 11.0%, followed by 14.3% for Rodrigues and up to 48.8% for La Réunion. 87.2% of species are

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endemic to the greater Madagascar – Mascarene region, and only 5.9% are also found outside the Western Indian Ocean as a whole.

Table 3: Distribution of endemism in the Mascarene Islands orchid flora

Islands	No. Species	No. Endemics	Endemism (%)
Mauritius	100	11	11.0
La Réunion	203	99	48.8
Rodrigues	7	1	14.3
Mascarene Islands	219	149	68.0
Madagascar – Mascarene Is.	219	191	87.2
Indian Ocean – Mascarene Is.	219	206	94.1

The orchid flora of the Gulf of Guinea islands is almost as rich as that of the Mascarene Islands with 207 species; however only 26.1% are endemic to the archipelago (Table 4). Levels of endemism within the region are also lower than those seen in the Mascarene Islands, ranging from a low on Príncipe of only 10.9% to a high of 20.0% for São Tomé.

Table 4: Distribution of endemism in the Gulf of Guinea orchid flora

Islands	No. Species	No. Endemics	%age Endemism
Annobon	22	3	13.6
São Tomé	100	20	20.0
Príncipe	64	7	10.9
Bioko	119	18	15.1
Annobon – Príncipe	133	35	26.3
Annobon – Bioko	207	54	26.1

Species richness gradients

Figure 1 shows numbers of species of orchids across the elevational gradient of La Réunion, with the orchid flora divided into three floral components (endemics; those shared with Mauritius; those shared with Madagascar; and the total orchid flora). Although the greatest number of species are found at 1000 m, there is a clear variation in altitudinal distribution of the La Réunion orchid flora. The Mauritian component peaks in species richness at a lower altitudinal level (600 m) than the Malagasy component, and then tails off towards the maximum elevation; the Malagasy component peaks at 1000 m, in common with the total orchid flora; while the endemics peak much higher than the Mauritian component at 1200 m.

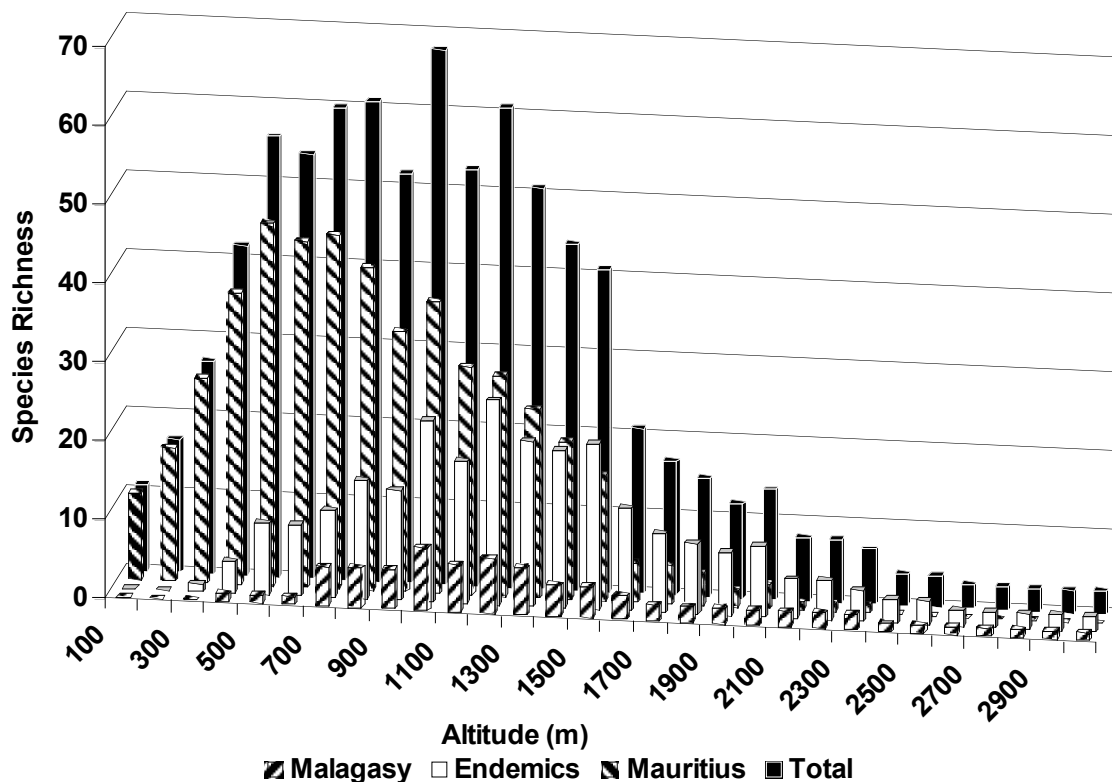


Figure 1: Altitudinal distribution of the orchid flora of La Réunion

MDE studies

The r^2 values given in Table 5 below show the relationship between the observed orchid species richness along the altitudinal gradient of La Réunion and the MDE null model predictions. The MDE was found to explain only a quarter of the variance in the total observed richness patterns ($r^2 = 0.25 - 0.29$). The amount that the MDE explained in the various floral components varied from only one-twentieth of the variance in the Mauritian component ($r^2 = 0.05 - 0.06$) to around two-thirds for the endemic component ($r^2 = 0.61 - 0.64$).

Table 5: Results of simple linear regression between observed species richness patterns and MDE null model predictions for La Réunion

No. of Bins (Size of Alt. Band)	Endemics	Malagasy	Mauritius	Total
	r^2 values			
60 (50 m)	0.61	0.32	0.05	0.25
30 (100 m)	0.63	0.32	0.06	0.28
15 (200 m)	0.63	0.35	0.05	0.27
10 (300 m)	0.64	0.38	0.06	0.29
Alt. max. of origin	3069 m	2876 m	828 m	3069 m

r^2 values for the relationship between orchid species richness and the MDE null model along the altitudinal gradient of the Gulf of Guinea islands are shown in Table 6 and 7. MDE was found to explain around two-thirds of the variance in the total observed richness patterns for São Tomé ($r^2 = 0.60 - 0.65$) and Príncipe ($r^2 = 0.58 - 0.76$). The amount that the MDE explained in the various floral components varied little for both islands compared with that shown for La Réunion. No pattern consistent with varying bin size could be found for São Tomé, whereas the r^2 value of the total floral component of Príncipe was greatest, and that of the endemics the lowest.

Table 6: Results of simple linear regression between observed species richness patterns and MDE null model predictions for São Tomé

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No. of Bins (Size of Alt. Band)	Endemics	Non-Endemics r^2 values	Total
60 (33.7 m)	0.45	0.57	0.64
30 (67.5 m)	0.57	0.57	0.65
15 (135 m)	0.70	0.54	0.63
10 (202.4 m)	0.68	0.51	0.60

Table 7: Results of simple linear regression between observed species richness patterns and MDE null model predictions for Príncipe

No. of Bins (Size of Alt. Band)	Endemics	Non-Endemics r^2 values	Total
60 (15.6 m)	0.47	0.57	0.58
30 (31.2 m)	0.48	0.59	0.60
15 (62.3 m)	0.52	0.56	0.58
10 (93.5 m)	0.73	0.74	0.76

Discussion

Data quality, area effects and interpolation

There are several potential drawbacks to this study:

Firstly, due to considerable habitat destruction and subsequent degradation of the Mascarene Islands (Strahm, 1989, 1996b), we will never know the total natural Holocene orchid flora of the archipelago. The vegetation of Rodrigues was totally destroyed before the first scientific survey was conducted in 1874 and much of the coastal and lowland vegetation of the other islands has been seriously degraded (Strahm, 1989). This may have had a marked impact on orchid diversity at lower altitudes where much habitat destruction occurs. A similar situation has occurred in the Gulf of Guinea islands; however, our poor understanding of the original floras of São Tomé and Príncipe is further exacerbated by our current lack of knowledge of the floras of the other islands, Annobon and Bioko.

Secondly, the use of herbarium specimen records may provide spurious results. For example, pre-twentieth century herbarium records, important for estimating species elevational ranges before extensive habitat clearance had taken place, are less likely to have accurate elevation records due to imprecision of maps and inadequate measuring equipment (Bachman *et al.*, in press). This study, however, uses the best available data and is built directly on current taxonomic expertise, and much of the data for the La Réunion analysis are derived directly from individual herbarium records and for the Gulf of Guinea islands on the recent taxonomic account of Stévant and de Oliveira (2000).

Thirdly, this study has not accounted for the effects of different amounts of available land-area at different elevational bands. The relationship between area and number of species is well known with species richness increasing as the area increases, following the power-law model of Arrhenius (1921). Since in small oceanic islands the area of lowland greatly exceeds the area of highland, species richness might be expected to decline with elevation simply because the amount of available land-area does so, irrespective of any effects of altitude *per se*. Accounting for this variation in land-area with elevation can effect the patterns of observed richness along an elevational gradient (Rahbek, 1997; Sanders, 2002; Bachman *et al.*, in press).

Fourthly, observations of the occurrence of a species are made in space and time. The problem is to use these observations to estimate the boundary of the range of the species. Of course, even when interest focuses on the one-dimensional range of a species, the observations themselves will be

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made in two dimensions. These two-dimensional locations are then converted into one-dimensional observations by retaining only their projections along the orientation of interest (e.g. elevation). The true boundary of a one-dimensional range is typically estimated by the pair of most extreme locations at which the species is observed. For example, when interest centres on altitudinal range, the upper boundary is estimated as the highest altitudinal location at which the species is observed and the lowest boundary is estimated as the lowest altitudinal location at which the species is observed. In reality these are rarely the extremes of the range, it is just where that taxon has been observed. As a result this can give rise to unimodal peaks in species richness along gradients since the range of a taxon may be poorly known at its geographical extremes. It has been suggested that this interpolation results in an overestimation of species richness towards the centre of the gradient (Grytnes and Vetaas, 2001). However, this interpolation is merely a pragmatic solution to an intractable analytical problem (Bachman *et al.*, in press) typical of most studies of species richness along environmental gradients.

The mid-domain effect in the Mascarene and Gulf of Guinea Island orchid floras

Currently, there is still great scepticism surrounding the importance of the mid-domain effect. So far only a handful of vascular plant studies have considered the MDE and even fewer have been based on taxa from tropical islands. However, results now suggest the existence of the MDE across a wide range of taxa and areas (Colwell and Hurtt, 1994; Lyons and Willig, 1997; Pineda and Caswell, 1998; Willig and Lyons, 1998; Colwell and Lees, 2000; Jetz and Rahbek, 2001; Grytnes and Vetaas, 2002; Sanders, 2002; Bachman *et al.*, in press). The relationship between orchid richness and MDE along an altitudinal gradient for the various floral components of La Réunion shows an interesting pattern (Table 5). The MDE was found to explain the greatest variance in the endemics ($r^2 = 0.61 - 0.64$). This is not surprising since they have evolved within the geometric constraints imposed by the elevation of the island. The next highest was the Malagasy component ($r^2 = 0.32 - 0.38$); this may be because Madagascar rises to 2876 m, compared with La Réunion which rises to 3069 m. The Mauritian component on La Réunion had the weakest relationship with the MDE null model predictions ($r^2 = 0.05 - 0.06$) since Mauritius rises to only 828 m. This suggests that geometric constraints influence variation in species richness across the elevational gradient, and might effect speciation, future colonisation and range expansion as outlined in the scenario given below for the Mascarene Islands.

In contrast no such pattern could be seen in the results of the Gulf of Guinea Islands. This is likely to be due to their close proximity to the African mainland, leading to multiple colonisation events extending into recent times, and therefore a confused pattern with no clear picture emerging. The effect of proximity to major landmasses can be seen in the endemism data for the region; Annobon – Príncipe contains 26.3% endemism where as Annobon – Bioko has 26.1%. This lack of difference is even more pronounced if you consider that Bioko may have been connected to the mainland during to the last glacial period. In contrast, the levels of endemism found in the Mascarene Islands suggest that there is little movement outside the region but considerable movement within, since 68.0% of the regions orchid flora is endemic.

The observed differences between the results for the Mascarene Islands and the Gulf of Guinea islands are not simply due to differences in the underlying range-size frequency distributions between the two archipelagos. If a flora was to be made up of numerous species with narrow ranges with few wide ranging species this should produce a smaller mid-domain effect, since these narrow-ranged species could be found anywhere within the domain, and species richness would thus be more even. Floras with a greater proportion of large-ranged species should show a greater mid-domain effect, since large-ranged species are more likely to be constrained to the middle of the domain. However, when comparing the range-size frequency distributions of La Réunion and São Tomé we find the opposite pattern (Fig. 2): La Réunion has a greater proportion of narrow-ranged species, yet still has a stronger mid-domain effect than does São Tomé.

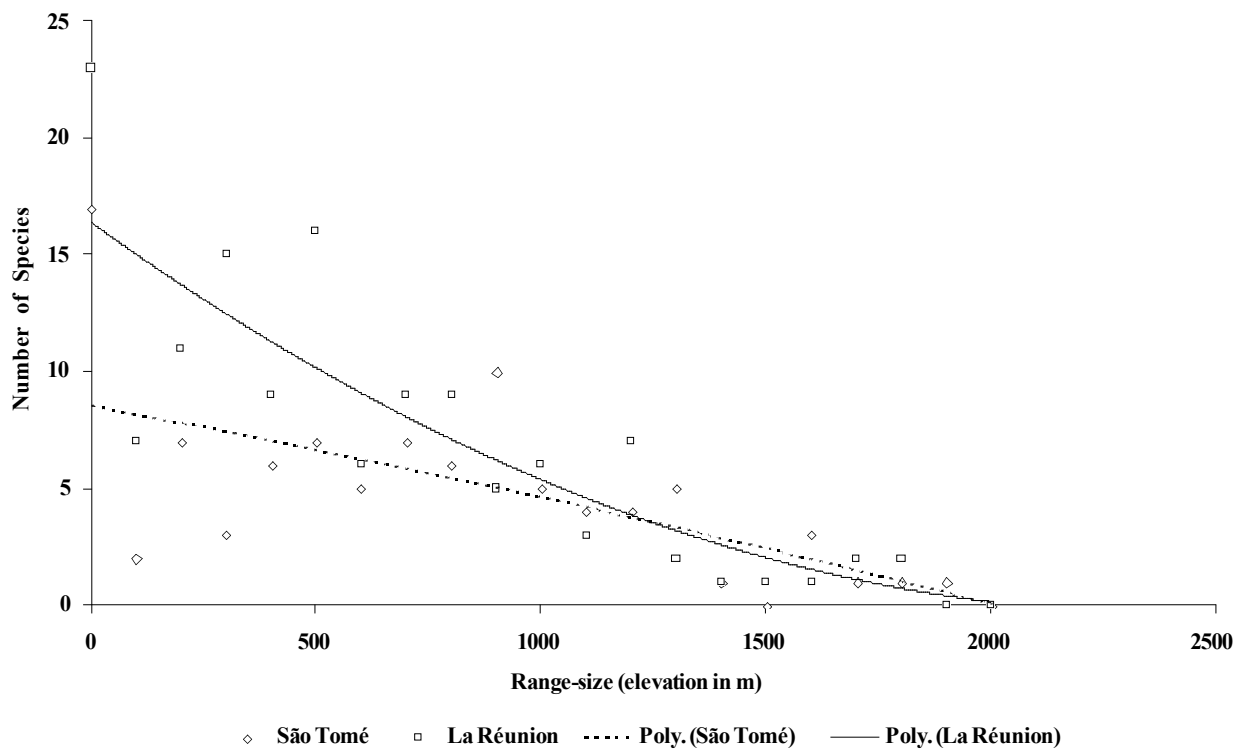


Figure 2: Range size frequency distribution of the orchid floras of La Réunion and São Tomé

Origin of the orchid flora of the Mascarene Islands

The following scenario, consistent with the differing ages and elevational profiles of the different islands, and thus the geometric constraints, of each island, is proposed for the genesis of the Mascarene archipelago's orchid flora:

1. After the formation of Mauritius approximately 7.8 my ago orchids of several different lineages from Madagascar colonised the island, followed by speciation.
2. Endemism would have been much higher on Mauritius at that time, as would be expected from such an isolated oceanic island orchid flora soon after successful colonisation and radiation.
3. La Réunion, formed 2.1 my ago, was rapidly colonised from Mauritius, thus reducing the level of endemism on Mauritius.
4. This rapid colonisation from Mauritius occurred mainly at low altitudinal levels on La Réunion, reflecting the geometric constraints imposed by the island on which the orchids had evolved.
5. Speciation on La Réunion of the acquired Mauritian orchids, along with colonisation of additional species from Madagascar, occurred. With the greater altitudinal range of La Réunion, newly-evolved species expanded their ranges into higher elevational bands than could the existing Mauritian component.
6. Few, if any, species could spread back to Mauritius from La Réunion due to the lack of high altitude sites and the presence of a well established orchid flora, and thus the Mauritian component in the orchid flora of La Réunion remains small.

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The volcanic archipelagos of the African continent seem to have been largely forgotten but offer an excellent opportunity to study patterns of species richness. Although there is still great scepticism surrounding the existence of the mid-domain effect, it offers an exciting new area of research in the study of such patterns. Together with species-area relationships, the mid-domain effect can have a profound effect on species richness along a gradient, and should be considered in all studies of environmental determinants of species richness. Here we suggest, for the first time, that the study of the mid-domain effect can also help explain evolutionary patterns, through the effect of past geometric constraints on evolutionary processes.

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