FORUM

The ghost of competition past in the phylogeny of island endemic plants

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Summary

1 Large endemic plant taxa found on oceanic archipelagos are frequently monophyletic, indicating that they originate from a single colonization event.

2 Colonization is a two-stage process requiring both dispersal and establishment to be successful. Accordingly, once-only colonization may be explained either by dispersal barriers limiting colonization, or by the first successful colonization of an island inhibiting the establishment of later arrivals through niche pre-emption and interspecific competition.

3 Using the endemic flora of the Canaries and Macaronesia as a test case, I argue that barriers to dispersal are low and that niche pre-emption is therefore the more likely explanation for the monophyly of large endemic groups in these islands.

Key-words: Canary Islands, colonization, endemism, interspecific competition, Macaronesia, niche pre-emption, phylogeny, plants, speciation

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Introduction

Oceanic island floras are typically rich in endemic species and these offer some of the clearest known examples of adaptive radiation (Givnish & Sytsma 1997). High rates of endemism are due to the biological isolation of such islands, which are usually colonized by only a very restricted number of continental species that then evolve and sometimes speciate in spectacular fashion. It is common, for example, for herbaceous colonists to speciate into a wide variety of growth forms, including shrubs and trees, and for species to radiate into new habitat types (Carlquist 1974; Givnish 1998). According to the ecological theory of adaptive radiation, competition plays two distinct roles in the process (Schluter 2000). Intraspecific competition for resources provides a 'push' that impels species towards ecological diversification, while the absence of interspecific competition in uncolonized environments constitutes ecological opportunities that 'pull' species into those new environments. As habitat and niche space is filled by new species, interspecific competition will increase, ecological opportunities will decline and radiation may cease. This is one way in which the signature of a changing competitive environment may be impressed upon the phylogeny of island endemics.

In a well-known and now classic paper, Connell (1980) expressed scepticism about the evidence for the involvement of interspecific competition in coevolution and community structure and said that he would no longer be persuaded by the invoking of 'the ghost of competition past' to explain community patterns. In the more than two decades since those challenging words were written the experimental evidence for strong interspecific competition, at least in plant communities, has become overwhelming (e.g. Goldberg & Barton 1992; Gurevitch *et al*. 1992) and the application of null models has revealed that some communities do appear to be structured by interspecific competition (e.g. Silvertown *et al*. 1999; Gotelli & McCabe 2002). More recently still, molecular phylogenies have clarified the evolutionary history and relationships of plant communities, especially those confined to islands. It is therefore time to re-consider whether the ghost of competition past could be more than a figment of the imagination.

Molecular phylogenies now exist for a significant number of plant groups that are endemic to Hawai'i (Wagner & Funk 1995), the Galapagos (Schilling & Paner 2002), the Juan Fernández Islands (Sang *et al*. 1994) and the Canary Islands (e.g. Francisco-Ortega *et al*. 1996), and these show that most are monophyletic and evolved from a single colonization of the archipelago where they are found. Though gene trees based upon a single locus must be interpreted with caution, especially in the case of nuclear genes that are subject to

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recombination when different lineages hybridize, there is concordant evidence of monophyly from sequences of both nuclear and chloroplast genes (e.g. Barber *et al.* 2002).

Successful colonization is a two-stage process requiring first dispersal and then establishment. Two alternative hypotheses to explain why endemic island groups are monophyletic are that: (i) dispersal barriers limit colonization and make repeated colonization very unlikely, or (ii) dispersal barriers are low enough to permit repeated colonization, but the first successful colonization inhibits the establishment of later arrivals by interspecific competition and niche pre-emption. Isolation and competitive exclusion are not mutually exclusive, but I shall argue that restricted dispersal (hypothesis 1) is very unlikely to explain the monophyletic origins of large endemic plant genera, at least in one important case, and that hypothesis 2 is actually more likely to be correct, implying that the signature of a ghost of competition past is present in the phylogeny of island endemic plants. I base my evidence on the flora of the Canary Islands and the region of Macaronesia to which they belong because, for the reasons explained below, this provides a good test case.

Dispersal limitation

The monophyly of endemic groups on archipelagos such as Hawai'i or the Galapagos, which are a thousand kilometres or more from the nearest continental landmass, is to be expected because their remoteness makes multiple arrivals by progenitors a rare event. Hypothesis 1 is therefore difficult to reject in these cases, even if hypothesis 2 may be partly correct. However, monophyly in the Canary Islands is much more surprising because the island of Fuerteventura, at the eastern end of this archipelago, is only 100 km from the coast of Africa, which, moreover, would have been nearer still in the Quaternary when sea levels were lower. At 21 million years old, Fuerteventura is also much older than, for example, any island in the Hawai'ian archipelago. There would therefore appear to have been plenty of time for most plant taxa that were able to cross the 100 km distance from North Africa to the Canaries to have done so more than once. Indeed, this is one reason why the endemics of the Canary Islands were until recently thought to be mainly relics of a Tertiary flora now extinct in their continental source regions. While it is likely that certain Canary Island species such as *Dracaena draco* are palaeoendemics, this is not true of the genera that are richest in endemic species, including *Aeonium* (Mes & Hart 1996; Mort *et al.* 2002), *Argyranthemum* (Francisco-Ortega *et al.* 1996), *Crambe* (Francisco-Ortega *et al.* 2002), *Echium* (Bohle *et al.* 1996), *Sideritis* (Barber *et al.* 2000, 2002), *Sonchus* (Kim *et al.* 1996) and *Tolpis* (Moore *et al.* 2002, Park *et al.* 2001) (Table 1). Molecular phylogenies now show that all of these genera radiated in Macaronesia and that their Canary Island representatives originated from a single colonization of the archipelago.

The example of the colonization of the Canaries by the endemic subspecies of olive *Olea europaea* ssp. *cerasiformis* illustrates the more general case that applies to other endemics in the archipelago. The Canary Islands are volcanic in origin and their geological ages decrease approximately from east to west (Carracedo 2001). Hess *et al.* (2000) used ITS-1 sequences, RAPDs and ISSR markers to reconstruct the colonization of the Canaries by *O. europaea* ssp. *cerasiformis*. They discovered that all populations originated from a single colonization of the oldest island, Fuerteventura (*c.* 21 million years old), and that the olive then island-hopped westwards along the archipelago to Gran Canaria (*c.* 14 million years old), Tenerife (*c.* 7 million years old) and La Gomera (*c.* 12 million years old), finally reaching La Palma (*c.* 2 million years old). No reliable molecular clock is available by which the successive colonization events may be dated, but the known geological ages of the islands and the sequence in which they were colonized allows us to place limits on the earliest and latest dates by which the olive reached each island and from this evidence we can create two alternative scenarios that bracket all the possibilities.

In scenario 1, I assume that each island was colonized soon after formation and thus the olive reached Fuerteventura about 21 million years ago, Gran Canaria 7 million years later and Tenerife 7 million years after that. It so happens that the distances separating each of these three islands from their particular source population, including the distance from Fuerteventura to Morocco, where the ancestor of the Canary olive appears to have lived, are about the same (*c.* 100 km) and therefore the barriers to dispersal between each of these island populations and their source are approximately equal. Thus, there should have been three equivalent colonization events by olives in the first 14 million years of Canary Island history. At this rate, allowing for the fact that fractional colonization events are meaningless, we should expect olives to have colonized Fuerteventura a total of four or so times in its 21 million year history, Gran Canaria up to three times in 14 million years and Tenerife once or twice. In fact, the populations on these islands are monophyletic, showing that each was successfully colonized only once. The actual, combined colonization rate for all three islands was therefore between three-eights and three-tenths of that expected under scenario 1. Hypothesis 1 is inconsistent with this difference between observed and expected rates.

In scenario 2, I assume that each island was colonized only recently, i.e. within the lifetime of La Palma (the youngest island where it is found). Because La Palma island is only 2 million years old, scenario 2 faces the problem of how to account for a sudden burst of colonization success in the last 2 million years, the olive having failed to colonize the older islands, that are also nearer Morocco, for over 10 million years previously. This too is inconsistent with hypothesis 1. Of course, the two scenarios described are extremes and

Table 1 Genera and clades of Macaronesian endemic plants for which the number of ancestral colonizations of Macaronesia can be inferred from molecular phylogenies. Cases are ranked by the number of endemic species in the group. Colonizations by non-endemics have been excluded

	Family	Genus or clade of genera	Number of endemic species	Number of colonizations	Reference
1	Crassulaceae	*Aeonium*, *Aichryson*, *Greenovia* *Monanthes* clade	63	1	Mes & T'Hart (1996), Mort *et al.* (2002)
2	Boraginaceae	*Echium*	37	1	Bohle *et al.* (1996)
3	Asteraceae	*Sonchus* & 5 related genera	34	1	Kim *et al.* (1996)
4	Lamiaceae	*Sideritis*	24	1	Barber *et al.* (2000, 2002)
5	Asteraceae	*Argyranthemum*	23	1	Francisco-Ortega *et al.* (1996)
6	Fabaceae	*Teline*	12	2	Percy & Cronk (2002)
7	Asteraceae	*Pericallis*	15	1	Panero *et al.* (1999)
8	Asteraceae	*Cheirolophus*	14	1	Susanna *et al.* (1999)
9	Brassicaceae	*Crambe*	14	1	Francisco-Ortega *et al.* (2002)
10	Asteraceae	*Tolpis*	11	1	Park *et al.* (2001), Moore *et al.* (2002)
11	Asteraceae	*Gonospermum*, *Lugoa*, *Tanacetum*	8	1	Francisco-Ortega *et al.* (2001a)
12	Rosaceae	*Bencomia* alliance	8	1	Helfgott *et al.* (2000)
13	Asteraceae	*Asteriscus*	5	1	Francisco-Ortega *et al.* (1999, 2001b)
14	Euphorbiaceae	*Euphorbia* subsect. *Pachycladae*	5	3	Molero *et al.* (2002)
15	Solanaceae	*Solanum*	4	2	Bohs & Olmstead (2001)
16	Araliaceae	*Hedera*	3	3	Vargas *et al.* (1999)
17	Fabaceae	*Adenocarpus*	3	1	Percy & Cronk (2002)
18	Agavaceae	*Dracaena*	2	2	Marrero *et al.* (1998)
19	Aquifoliaceae	*Ilex*	2	2	Cuenod *et al.* (2000)
20	Asteraceae	*Pulicaria*	2	2	Francisco-Ortega *et al.* (2001b)
21	Colchicaceae	*Androcymbium*	2	1	Caujape-Castells *et al.* (1999)
22	Fabaceae	*Genista*	2	1	Percy & Cronk (2002)
23	Malvaceae	*Lavatera*	2	2	Fuertes-Aguilar *et al.* (2002)
24	Saxifragaceae	*Saxifraga*	2	1	Vargas *et al.* (1999)
25	Asteraceae	*Allagopappus*	1	1	Francisco-Ortega *et al.* (2001c)
26	Asteraceae	*Viera*	1	1	Francisco-Ortega *et al.* (2001c)
27	Asteraceae	*Schizogyne*	1	1	Francisco-Ortega *et al.* (2001c)
28	Gentianaceae	*Ixanthus viscosus*	1	1	Thiv *et al.* (1999)
29	Oleaceae	*Olea europaea* ssp. *cerasiformis*	1	2	Hess *et al.* (2000), Medail *et al.* (2001)

some intermediate schedule of events is more likely, but intermediate scenarios simply suffer from combinations of the problems that afflict the extremes and are just as incompatible with hypothesis 1. I admit that these back-of-the-envelope calculations are crude and that source populations must have varied in size through time, that dispersal opportunities were probably not constant (and would vary between species), that some islands such as Tenerife have a complex history and structure and even that distances between islands and their sources may be greater now than in the past. However, the discrepancies between observed and expected colonization rates are so large that one would have to make more assumptions than I have done in making these calculations to reject my conclusion. It is more parsimonious to reject hypothesis 1 as an explanation of the monophyly of so many large Canarian endemic genera.

The final piece of evidence that suggests that dispersal barriers have not played a significant role in preventing the repeated colonization of the Canaries is the simple observation that 60% of the native flora is not endemic (Santos 2001), indicating that there have been at least 730 independent colonization events by these species during the history of the archipelago. In addition, palaeoendemics, which form an imprecisely known fraction of the remainder of the native flora, will also have colonized independently.

An absence of dispersal limitation may solve another puzzle in the Canarian endemic flora. In a review of allozyme diversity in populations of 69 Canarian endemic species, Francisco-Ortega *et al.* (2000) discovered that their mean total genetic diversity (or mean expected heterozygosity, H_T) was twice that found in populations of island endemics on other oceanic archipelagos. This difference could not be explained by mating system, population size or the greater antiquity of populations in the Canaries and Francisco-Ortega *et al.* (2000) suggested that it might reflect multiple arrivals of plants in the early phase of island colonization, before radiations took place. If it is correct that the initial colonization events were repeated, it is all the more strange that later colonization events appear to have failed to establish new lineages. This too suggests that niche pre-emption by early colonists may have inhibited the success of later ones.

Niche pre-emption

If dispersal is unlikely to be a significant barrier to plant colonization of the Canary Islands then, by default, a barrier to establishment may explain the apparent failure of species to colonize repeatedly (hypothesis 2). It is difficult to test this hypothesis directly, but there is circumstantial evidence in its favour. The phylogeography of *Argyranthemum* elucidated by Francisco-Ortega *et al*. (1996) shows that species in this endemic genus have often dispersed successfully between islands, but generally remained within the habitat types in which they originated. The apparent ease with which *Argyranthemum* species have been able to disperse to new islands contradicts hypothesis 1, while the rarity with which they invade novel habitats where these are already occupied by other species in the genus supports hypothesis 2. Similar vagility of species among the Canary islands is revealed in the phylogeography of the genera *Aeonium* (Mort *et al*. 2002), *Crambe* (Francisco-Ortega *et al*. 2002), *Sideritis* (Barber *et al*. 2000) and *Sonchus* (Kim *et al*. 1996), although these genera show more frequent evolutionary shifts between habitats than occurred in *Argyranthemum*.

The species-richness of endemics as a whole in the Canaries correlates better with island height than with island area because taller islands support more habitat types than lower ones (Hobohm 2000). This pattern also implies the primacy of establishment (hypothesis 2) over dispersal (hypothesis 1) in controlling the colonization process, as opportunities for establishment in competition-free environments are greater on islands with more habitat types, whereas, if colonization were dispersal limited, species richness would be determined by the area that an island presents as a 'target'.

My last piece of evidence is less circumstantial, but more tentative. If hypothesis 2 is correct, then endemic groups with many species in them should be more effective at excluding repeat colonizations by relatives than groups represented by fewer species, because larger groups should pre-empt more of the niche or habitat space available for colonization. If such pre-emption occurs, there should be an inverse relationship between the size (species-richness) of a group and the number of colonization events it represents. I have listed all the published cases I can find where the number of colonizations in Macaronesian plant groups can be estimated from a phylogeny (Table 1). Of the 40 independent colonization events in this sample, precisely half were unique and not repeated, whereas the other half involved repeated colonization by members of the same genus or clade. The 20 unique colonizations radiated to produce a total of 269 species, while the same number of repeated colonizations produced only 38 species between them: monophyletic groups are on average bigger by a factor of seven. To look at the data another way: there are 13 groups that contain more than five species and, of these, all but one are monophyletic and hence colonized Macaronesia only once. The remaining smaller

groups divide equally (8 : 8) between those containing one and those containing more than one colonization event. The probability of obtaining this difference in colonization between large and small groups by chance is $P = 0.0178$ (Fisher's exact test, one-tailed).

There are two alternative interpretations of the inverse relationship between number of colonizations and group size, depending upon which is cause and which effect. Whether profuse speciation inhibits repeat colonization, as hypothesis 2 would predict, or whether repeat colonization inhibits speciation is not clear from the data, though the former seems more likely for two reasons. The first is a theoretical consideration: the presence of numerous species is likely to be a more effective barrier to establishment by subsequent colonizers than small numbers of multiple colonizations are to speciation. Secondly, data show that the Asteraceae, a group with good powers of dispersal, is disproportionately represented among monophyletic endemic groups in Macaronesia, as elsewhere (Francisco-Ortega *et al*. 2001b). I would therefore argue that these observations support hypothesis 2, though this conclusion can only be considered tentative because the sample on which it is based is incomplete.

A test that might be applied to hypothesis 2 is to determine whether speciation rates declined over time in a density-dependent manner as habitats were filled by adaptive radiation. This test would require a reliable molecular clock, which is not at present available for plants. Finally, I predict that as more data on the phylogeny of Macaronesian endemics are collected, the patterns that support hypothesis 2 will become stronger rather than weaker. It may yet be too early to call in Ghostbusters, but there seems to be a distinct odour of competition in the phylogeny of Macaronesian endemics.

Acknowledgements

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