

The ghost of hybridization past: niche pre-emption is not the only explanation of apparent monophyly in island endemics

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Summary

1 Published molecular phylogenies show that many plant groups in the Canary Islands are monophyletic despite the fact that the short distance between the islands and Africa should have led to many independent colonization events.

2 Low establishment rates of later migrants owing to niche pre-emption by earlier, already established, colonists could explain these patterns. The apparent monophyly is, however, also compatible with multiple colonizations, with later colonizers making only limited contributions to the total gene pool (and therefore being undetected in the molecular phylogeny) or being wiped out by stochastic processes.

3 Experimental evidence for niche pre-emption and species-specific interactions in plants is weak, with survival and establishment of a newly immigrant species depending on the overall composition of the community, rather than on the presence of a particular ‘ecologically similar’ species.

4 Although niche pre-emption might have contributed to the observed patterns of monophyly, we do not think that phylogeographical data from Macaronesia can be taken as evidence for its action in the geological past.

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Over the past few years, extensive data have been collected from many islands on the molecular phylogeny of their endemic plant groups. Various independent studies allow us to address novel and challenging issues; in particular, to determine group monophyly in a much more accurate fashion. In a recent paper, Silvertown (2004) reviewed molecular data on endemic plant assemblages in Macaronesia, with emphasis on the Canary Islands and Madeira, and used available molecular evidence to show that many of the groups of island endemics in these archipelagoes have arisen from a single colonization event. Although these islands are volcanic in origin and have never been connected to a continent, they are quite close to the mainland (Fuerteventura, the Canary Island closest to Africa, now lies only *c.* 100 km from the coast and was actually much closer

in certain periods of the Quaternary). The dispersal barrier is thus not nearly as strong as for really remote islands in the Pacific (e.g. Hawai’i). Molecular evidence of multiple (and numerous) colonizations in some Macaronesian groups (e.g. Genisteeae: Percy & Cronk 2002) is consistent with this relatively weak barrier, as is the high genetic variation of Macaronesian endemics relative to the Pacific angiosperms (Francisco-Ortega *et al.* 2000), and the pattern of interisland distribution seen in many assemblages (e.g. *Argyranthemum*, *Crambe*, *Echium*, *Pericallis*, *Pinus*, *Sonchus*, *Tolpis*, *Teline*). Therefore, it is likely that colonization events should occur relatively frequently in Macaronesia and large monophyletic groups should consequently be rare.

However, published molecular phylogenies do show many monophyletic groups and thus indicate a low number of colonization events. Silvertown (2004) proposes that this apparent paradox can be resolved by considering colonization as a two-stage process requiring both dispersal and establishment to be successful. Thus, if dispersal rates are likely to be higher than indi-

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Editors’ note: Further contributions on this topic are currently in press, and correspondence is now closed.

cated by the molecular evidence, apparent monophyly should be associated with low establishment rates. He suggests that low establishment rates in such islands may be due to niche pre-emption by earlier, already established, colonists that prevent survival of later arrivals, and that the observed pattern of monophyly thus serves as evidence for niche pre-emption operating in the past.

Although this hypothesis is plausible, it requires a more thorough examination. If monophyly is used as evidence for niche pre-emption, it is not sufficient that niche pre-emption is likely or possible; it is necessary for it to be (by far) the most likely explanation of the pattern of monophyly and to explain most of the variation in it. This strict requirement means not only that niche pre-emption must be a plausible explanation, given other (neontological) evidence for its action, but also that possible alternative hypotheses should be much less likely. If these conditions are not fulfilled, niche pre-emption might still have contributed to the patterns that we see, but the patterns can hardly be used as evidence for its action.

In order for niche pre-emption to be a plausible explanation for the pattern of monophyly in the Macaronesian islands, it is necessary that two criteria are met: competition should have a strong species-specific component, i.e. ecologically more similar species should compete more strongly, and there should be correlation between a phylogenetic (taxonomic) relationship and ecological similarity. Only in such cases would an already established population of an earlier migrant prevent establishment of a later migrant from the same group. The survival probability of second and subsequent species of the same group would then be much lower than that of the first migrant, driving later arrivals to extinction and leading to the prevalence of monophyly in the molecular data.

Apart from the fact that a phylogenetic relationship does not necessarily confer an ecological relationship (see Barber *et al.* 2000; Francisco-Ortega *et al.* 2002 for examples from the Canarian flora), a major difficulty with the niche pre-emption hypothesis stems from the fact that there is very little experimental evidence that competitive interactions in plants have a strong species-specific component (Bengtsson *et al.* 1994; Freckleton & Watkinson 2001). Most experimental data show that sheer plant size is the best predictor of competitive success in comparative experiments (e.g. Dietz *et al.* 1998; Keddy *et al.* 2000, 2002; Freckleton & Watkinson 2001). The species-specific component of interactions becomes stronger only if plants are of similar sizes and even then the evidence is not particularly conclusive (Johansson & Keddy 1991; Wilson 1999). Furthermore, intraspecific competition in plants is generally not stronger than or different from interspecific competition (Goldberg & Barton 1992). Moreover, in most field situations the role of species-specific interactions is low owing to the sessile habit of plants. Plants compete with their immediate neighbours, and this leads to diffuse competition prevailing over pairwise interactions

(McLellan *et al.* 1997; Uriarte *et al.* 2004). Survival and establishment of a newly immigrant species thus depends on the overall composition of the community, rather than on the presence of a particular 'ecologically similar' species. Presence (or local density) of the naturalized species is therefore of little importance; it is the overall plant density that makes the difference and determines the ultimate success of the immigrant. Therefore, a naturalized species does not necessarily have any advantage over a random immigrant.

Niche pre-emption theory is also difficult to reconcile with the patterns of interisland colonizations of Macaronesian plants. Phylogenetically very similar species have been documented to occur together wherever particular habitats are found, e.g. *Aeonium* (Mort *et al.* 2002), *Crambe* (Francisco-Ortega *et al.* 2002), *Pericallis* (Panero *et al.* 1999) or *Sideritis* (Barber *et al.* 2000). Although such species alliances were often the result of a single arrival from the continent, subsequent radiation and repeated colonizations occurred within the archipelago. Two or more closely related taxa would be unlikely to coexist in the same environment over a long period of time if niche pre-emption were a predominant factor involved.

When considering alternative explanations for the apparent rarity of colonization events, we propose that hybridization and introgression between the migrant and already established population of a closely related species should be considered. Although mentioned briefly, this possibility is not explored by Silvertown (2004).

In many extant groups of the Canarian flora, hybrids are both common and often fertile (e.g. *Argyranthemum*, *Carlina*, *Echium*, *Micromeria*) (Francisco-Ortega *et al.* 2000; J. Suda *et al.* personal observations). Several cases of hybridization between endemic and alien continental species have also been reported, as in the genera *Arbutus*, *Phoenix*, *Senecio* and *Teline* (Francisco-Ortega *et al.* 2000; Percy & Cronk 2002). Further indirect evidence for hybridization may be provided by the incongruity between chloroplast (with maternal inheritance) and nuclear (with bi-parental inheritance) phylogenies or between phylogenetic trees based on molecular markers and on morphology, as observed, for example, in *Aeonium*, *Argyranthemum* and *Sideritis* (Francisco-Ortega *et al.* 1997; Barber *et al.* 2000; Mort *et al.* 2002). Although such patterns can, in theory, also reflect hybridization events prior to colonization of the archipelago, it is highly unlikely in these endemic clades. It should also be noted that the common barrier for plant hybridization, i.e. different numbers of chromosomes in the potential parents, is not present in many groups in the Canary Islands owing to chromosomal stasis during insular speciation of angiosperms (Stuessy & Crawford 1998).

In summary, both direct and indirect evidence indicates that hybridization between related taxa is rather common and has played an important role in the evolutionary history of Macaronesian plants. Therefore, it

is plausible that a later migrant arriving on an island where there is an established population of a related species may hybridize, and eventually disappear as a result of repeated backcrossing of the hybrids with already established species. Although this would not necessarily lead to a fast and complete disappearance of its genes from the population (although it can), there are several arguments why traces of later migrants hybridizing with the established populations would not be shown in a molecular study.

1. If hybridization occurs between an already established species and a new arrival, later immigrants will make only a very small contribution to the total gene pool. The alleles it introduces are thus likely to disappear from the population in a few generations owing to stochastic processes. As island populations are often rather small, genetic drift is likely to play a strong role and lead to fixation of alleles, both of nuclear (Mendelian-inherited) and of chloroplast markers (Hartl & Clark 1997). This is even more likely when unidirectional introgression exists between two independently colonizing lineages, in which case a phylogenetic signal falsely suggesting a single colonization may be easily produced, especially when only one molecular marker is used. Thus, evidence for hybridization in the past would be likely to be recovered only if a large array of unlinked loci were examined. However, most of the studies cited by Silvertown (2004) utilized only a single marker, and none of them investigated more than four loci. An example of the different colonization scenarios proposed reflecting the number of molecular markers used (together with the number of populations involved) can be seen in the *Asteriscus* alliance: two introductions were suggested on the basis of nuclear ITS 1+2 phylogeny (Francisco-Ortega *et al.* 1999), whereas at least four colonization events were required to explain the phylogeny based on combined chloroplast *ndhF* gene and nuclear ETS (Goertzen *et al.* 2002). Similar inconsistency in monophyly/polyphyly evidence is known from the genus *Teline* (compare the results of Käss & Wink 1995 with those of Percy & Cronk 2002).

2. Even if the alleles do not disappear, they are likely to be maintained in low frequencies (reflecting their initially small contribution to the total allele frequency). Most of the studies referred to in Silvertown (2004) are based on only a few insular individuals (from 1(!) to 52, with an average number of 16) in which rare alleles are unlikely to show up.

3. Monophyly within the archipelago can only be reliably demonstrated when not only have all closely related taxa been included, but sufficient sampling has also been undertaken on potential migrants present on the mainland (to cover the genetic variation existing in the source area). If sampling of continental congeneric species is limited, one should treat any conclusions of monophyly with caution, particularly when large intra-archipelago genetic divergences are involved (as in various Macaronesian groups; see above and Emerson 2002). Quite a few studies showing monophyly used

rather limited reference data from non-island populations/groups (e.g. in *Tolpis*, Moore *et al.* 2002 or the *Aeonium* clade, Mes & Hart 1996). Importantly, studies that have included thorough sampling of continental congeners have often revealed multiple colonizations (*Ilex*, Cuenoud *et al.* 2000; *Hedera*, Varcárcel *et al.* 2003; *Asteriscus* alliance, Goertzen *et al.* 2002). Of the molecular papers cited by Silvertown (2004), those that showed single colonization sampled an average of 24 non-Macaronesian taxa, in contrast to 33 taxa in studies demonstrating multiple introductions. Indications of single colonization may also be less reliable when group monophyly is supported by very low bootstrap values (as in the *Gonospermum* alliance, Francisco-Ortega *et al.* 2000) or when several contrasting, equally parsimonious phylogenies are obtained (e.g. in *Tolpis*, Moore *et al.* 2002). Moreover, it should be noted that monophyly itself does not exclude the possibility of several dispersal events occurring prior to, or in the early stages of, the radiation of insular endemics (Francisco-Ortega *et al.* 2000).

It should also be noted that still other compatible scenarios can be outlined. For example, low migration rates of later arrivals, which might be due to rapidly changing environments on young islands, could lead to patterns of monophyly. The consequent establishment of colonization barriers might lead to later migrants no longer being able to find suitable habitats.

In summary, the competitive exclusion/niche pre-emption hypothesis of Silvertown (2004) is not the only explanation for the apparent monophyly in Macaronesian endemics: there are other explanations that do not contradict the available evidence and are not necessarily less likely. Niche pre-emption might have contributed to the observed patterns of monophyly, but can hardly be taken as the only cause. Indeed, independent experimental evidence for species-specific competition and niche pre-emption is weak and their effects in ecological experiments are generally minor. Therefore, niche pre-emption is not the most plausible hypothesis, and we think that the phylogeographical data from Macaronesia cannot be taken as evidence for its action in the geological past.

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