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FORUM

Breeding system, branching processes, hybrid swarm theory, and the humped-back diversity relationship as additional explanations for apparent monophyly in the Macaronesian island flora

N. ELIZABETH SAUNDERS and DAVID J. GIBSON
Department of Plant Biology, Southern Illinois University, Carbondale, IL 62901–6509, USA

Summary

1 Niche pre-emption and competitive exclusion is unsatisfactory as a sole explanation for the apparent paradox of a large number of monophyletic taxa in the Macaronesian island flora.
2 Undetected hybridizations have been proposed as an additional plausible explanation. In addition, hybrid swarm theory predicts that hybridizations between invading species would promote adaptive radiation.
3 We suggest that branching processes and coalescence offer yet another plausible explanation allowing for multiple colonizations of closely related taxa, which, because of their later local extinction or hybridization, would lead to apparent monophyly in the molecular record.
4 The cause of such widespread radiation of a few taxa has not been explained, but may involve intermediate conditions of disturbance or productivity. This proposition has, to date, only been tested in a microbial model system, but it offers a reasonable explanation for the patterns observed in the Macaronesian flora, and perhaps in other island floras worldwide.

Key-words: adaptive radiation, branching processes, coalescent theory, hybrid swarm theory, Macaronesia, monophyly, microbial model systems, niche pre-emption, phylogeny

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In his Forum article (The ghost of competition past in the phylogeny of island endemic plants), Silvertown (2004a) proposes two hypotheses to explain why many/most Macaronesian endemic groups are monophyletic: either new recruits cannot get to islands easily (clearly not the case for Macaronesia), or interspecific competition or niche pre-emption prevents later recruits of closely related species from establishing. We welcome this approach as it provides an ecological explanation for an observed evolutionary pattern. Nevertheless, at the heart of Silvertown's hypothesis is the idea that each monophyletic lineage currently present on the Macaronesian Islands arrived in a single colonizing event shortly after the islands' genesis. He proposes that, by primacy of establishment, the initial colonizers were able to shut out closely related species (intrageneric taxa) through the mechanisms of competitive exclusion and niche pre-emption. Without the assumption of a single colonizing event to account for each monophyletic lineage, the mechanisms of competitive exclusion and niche pre-emption are without merit.

Herben *et al*. (2005) (HSM thereafter) offer past hybridization of closely related colonists as a plausible explanation, additional to the niche pre-emption hypothesis offered by Silvertown (2004a). Here we offer additional observations on HSM's argument, which we find convincing, and on other points related to breeding system, branching processes and coalescent theory, hybrid swarm theory and the ecological constraints on adaptive radiation. Together, these persuade us that niche pre-emption may be a likely explanation, but is certainly not the only one, for the patterns observed by Silvertown (2004a).

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Correspondence: David J. Gibson (e-mail dgibson@plant.siu.edu).

Breeding system may be an important factor in the colonization of islands and subsequent radiation. Selfing species and species producing many-seeded fruits may hold a colonizing advantage (Sakai *et al.* 2001). As breeding system can vary widely within a genus, not all congeners are expected to have an equal probability of colonization, which might explain some instances of island monophyly. However, successful colonization does not always translate into successful establishment or radiation on islands. Changes in breeding system have been associated with radiation into novel habitats and, in such cases, may become strongly associated with a single habitat type (e.g. *Schidea* and *Alsinidendron* in the Hawaiian flora) (Weller *et al.* 1995). If the strong correlation between breeding system evolution and habitat loyalty, as seen for *Schidea* and *Alsinidendron*, holds true, then this may explain Silvertown's point that species tend to island-hop into identical habitat types. However, as congeners may in fact have more immediate and direct life-history limitations, such as breeding system, that influence colonization, persistence and radiation, it is, at best, tenuous to assign such advantage to the realm of competitive exclusion

As recently observed by Silvertown (2004b), niche separation between species is a probable causative mechanism that can be invoked to allow ecologists to understand local species diversity and coexistence better. However, as Silvertown (2004b) notes, much is unknown, and the actual importance of niche separation in plant communities is unclear. Indeed, the relative importance of intra vs. interspecific niche separation has been virtually ignored (although see Davies *et al.* 1998). For niche pre-emption to be of paramount importance in the Macaronesian flora, intrageneric niche separation needs to be of greater importance than intergeneric niche separation. This possibility has also been inadequately investigated. Moreover, recent work with yeast has shown the relationship between the abundance of taxa and phylogenetic relatedness to vary depending upon environmental conditions (Anderson *et al.* 2004).

Silvertown (2004a) uses the tips of the phylogenetic trees (i.e. what is observed today) to make assumptions about the past, an approach that Silvertown and others have cautioned against (Rees 1995; Silvertown & Dodd 1997). He assumes that monophyletic taxa on the Canary Islands have always been monophyletic. Indeed, his hypothesis (i.e. that monophyly is maintained by competitive exclusion and niche pre-emption) demands it. There are a number of problems with this argument. It is possible that the monophyly inferred from molecular analysis is an artifact of historical branching processes, that is, current presumed monophyly can be explained by a recent coalescence. In such a case, the apparent monophyly is not pre-emptive (i.e. one lineage did not out-compete another but the pattern is an artifact of unequal reproduction among lineages). In such a case, the extant taxa would be historically paraphyletic, i.e at the time of colonization

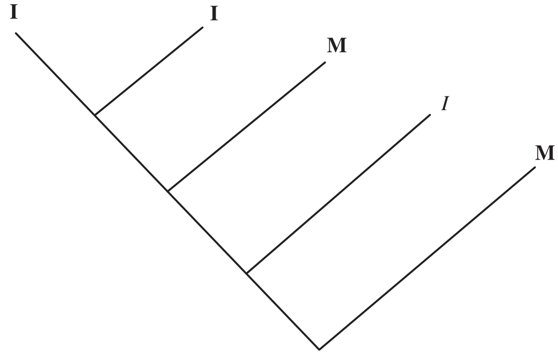

Fig. 1 Branching processes applied to a phylogenetic tree. A hypothetical phylogenetic tree is shown in which two colonizations of an island occurred but extant island taxa are derived from a single mainland lineage. Extant taxa represented by boldface extinct taxa in italics. In this scenario, paraphyly is masked and monophyly incorrectly inferred. I = island; M = mainland. Adapted from Avise (2004).

they would not have been not monophyletic as presumed (Fig. 1). The use of extant taxa allows no inferences to be made about the occurrence or longevity of extinct taxa. Of course, in the absence of a fossil record these arguments are merely speculation, but no more or less plausible than niche pre-emption or hybridization as explanations for the patterns of taxa observed on Macaronesia. As mentioned by HSM, poor sampling of either island or continental species may also mask paraphyletic lineages. Finally, although phylogenies based upon molecular analysis can be used to support hypotheses regarding phylogenetic relationships, they seldom provide evidence strong enough for falsifying alternative hypotheses. Rather, phylogenies are used as a framework for guiding future studies.

An issue not addressed by either Silvertown (2004a) or HSM is the question of what allowed a few genera within the Macaronesian flora to radiate to such a large extent. The Macaronesia flora is not unusual. Similar patterns of wide radiation of presumed monophyletic taxa occur in Hawaii (Sakai *et al.* 2002), where distance is a much greater barrier to colonization than in Macaronesia. In studies of invasive species, Ellstrand & Schierenbeck (2000) indicate that life-history characteristics (such as perennial habit and herbaceousness), and the purging of genetic load and hybridization may be important before range expansion can occur. It is possible that multiple initial colonizations occur among congeners, as suggested by Silvertown (2004a), and the first species to overcome expansion barriers may be the one to radiate into novel habitats and to displace congeners. Nevertheless, congeners may persist together for millennia before one evolves a competitive advantage that leads to displacement of the others. Once these initial genetic barriers are overcome, expansion into many novel habitats seems likely, and may explain the explosive radiation of only a few taxa. Among congeners, the first to reach this plateau might be serendipitous or it might be related to length of colonization on the island. Thus, dispersal barriers would better explain the wide radiation of monophyletic taxa than either competitive exclusion or niche pre-emption.

Recent work in a microbial model system suggests that the extent of adaptive radiation may be the result of an ecological constraint. The diversity of adaptive radiation in single lineages of *Pseudomonas fluorescens* was shown to peak at intermediate levels of both productivity and disturbance (Kassen *et al*. 2004). An assumption of this model is that adaptive radiation is governed by opportunities arising from unutilized resources (so-called 'vacant niches'). Silvertown (2004a) makes this assumption for the Macaronesian Islands in proposing extensive radiation by niche pre-empting taxa. The pattern proposed by Kassen *et al*. (2004) is remarkably similar to the patterns of diversity and richness predicted by the intermediate disturbance hypothesis (Connell 1978) and the 'humped-back' diversity-productivity model (Grime 1973; Virtanen *et al*. 2001). The mechanism is thought to be related to differential competitiveness among members of a lineage resulting from fitness costs associated with niche specialization. Thus, as a series of extinct volcanic islands subject to frequent disturbance in the past, could Macaronesia represent an intermediate condition in the global landscape of productivity and/or disturbance? If so, then extensive radiation of a few monophyletic taxa might be expected.

Hybrid swarm theory (Seehausen 2004) posits that hybridization is common when populations invade new habitats and that the ecological conditions conducive to hybridization are also conducive to adaptive radiation. Indeed, Seehausen (2004) argues that adaptive radiation is actually facilitated by interspecific hybridization. A good example is the Hawaiian silversword alliance of > 30 species in three genera (*Argyroxyphium*, *Dubautia* and *Wilkesia*) derived from hybridization between two or more North American species of tarweed (*Raillardiopsis muirii*, *Raillardiopsis scabrida*), albeit before dispersal to the Hawaiian islands (Barrier *et al*. 1999). Hybridization between island invasives is not without precedent (e.g. Suehs *et al*. 2004) and can facilitate invasion (Ellstrand & Schierenbeck 2000; Figueroa *et al*. 2003). Thus, hybrid swarm theory predicts that multiple colonizations of closely related taxa will promote both hybridization and adaptive radiation. As noted above, adaptive radiation can be further fuelled under the right ecological conditions (intermediate disturbance or productivity). Branching processes and coalescence, as described above, can then make the resultant pattern as observed today appear monophyletic. Niche pre-emption as suggested by Silvertown (2004a) may be a partial explanation for the loss of taxa during this process but there are many other reasons (e.g. disturbance, disease, stochastic events) why one of the parental hybridizing taxa may become locally extinct over perhaps many years.

In summary, many possibilities exist to explain the wide radiation of apparently monophyletic taxa on oceanic islands, and while competitive exclusion and niche pre-emption remain plausible hypotheses, they are by no means the only ones. The other possibilities that we and HSM have presented are equally as probable. In all likelihood, the stimulus for adaptive radiation is environmental, ecological and genetic, and which stimulus ultimately tips the scales cannot be generalized without a much greater body of evidence.

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