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NEWS AND COMMENTARY

Speciation

Splitting when together

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The longest running controversy in speciation studies is whether species can arise in the absence of geographic barriers. Convincing examples of this phenomenon have proven difficult to find in empirical literature (Coyne and Orr, 2004). Thus, two new examples of sympatric speciation that are recently described in *Nature* (Barluenga *et al*, 2006; Savolainen *et al*, 2006) form an important expansion of the literature.

Darwin (1859) argued that species originate as a byproduct of competition for resources, which by definition requires adjacency or 'sympatry' among diverging populations. In contrast, his most prominent intellectual descendents, and architects of the neo-Darwinian synthesis, reasoned that populations must be geographically isolated or 'allopatric' for speciation to occur; otherwise, populations would be homogenized by gene flow (Dobzhansky, 1937; Mayr, 1942). This conclusion held sway until the latter half of the 20th century, when it was challenged by both theory and empirical data (Maynard Smith, 1966; Bush, 1969).

Theoretical studies indicate that while sympatric speciation is possible, the necessary conditions are considerably more stringent than for speciation in allopatry. Sympatric speciation encounters two main problems that do not necessarily apply to allopatric speciation (Coyne and Orr, 2004); firstly, an association must form between the traits under disruptive selection and those that cause assortative mating. These associations, although favored by selection, are opposed by recombination and thus could be difficult to form in the presence of gene flow. Second, sympatric populations must coexist, which requires ecological divergence to avoid competitive extinction. Again, this problem is avoided in allopatry.

Despite these concerns, sympatric speciation does occur at reasonable frequencies in models that assume strong selection and/or genetic architectures that minimize the antagonism between selection and recombination. What we do not yet know is how common these conditions are in natural populations, although several recent studies imply that they may be less unusual than previously assumed (Hawthorne and Via, 2001; Lexer *et al*, 2003; Ortiz-Barrientos and Noor, 2005).

Empirical studies that attempt to distinguish between sympatric and allopatric speciation offer a way for determining how frequently the former occurs in different groups. However, it is difficult to rule out the possibility of an allopatric phase during the evolutionary history of most sympatric congeners. Indeed, a recent evaluation of the empirical literature performed before these new examples identified only three convincing examples of primary sympatric speciation (Coyne and Orr, 2004). The two new examples, involving palms and cichlid fishes, appear plausible because they occur in situations where an allopatric phase seems very unlikely, and they may help us to understand the kinds of conditions in which sympatry is not a fatal impediment to speciation.

In the palm study, sympatric speciation is thought to have taken place on Lord Howe Island, a very small and isolated island in the South Pacific (Figure 1). The two palms found on the island are each other's closest relatives (ie, sister species), yet they are reproductively isolated by a difference in flowering time. They also have different soil preferences, which may reflect ecological divergence, which has allowed coexistence. Because the two palms are restricted to this very small island, their pollen travels by wind, and their preferred soil substrates intercalate, it is likely that they diverged in sympatry, with ubiquitous mating opportunities between the diverging populations.

Speciation in the cichlid fish appears to have occurred in a small crater lake, Lake Apoyo, in Nicaragua (Figure 1). The two cichlids found in the crater are also sister species; they diverged after the origin of the lake, and one of them is endemic to the lake. Furthermore, the two species forage in different water columns, mate preferentially with individuals of the same species, and hybrids between the two forms have difficulties finding mates. Thus, the cichlid example also appears to satisfy the criteria of phylogenetic sisterhood, significant reproductive isolation, no apparent allopatric phase and sufficient ecological divergence for coexistence.

So what conditions might have facilitated sympatric speciation in these two examples? The two palms are found in soils with very different pH, and growth in the 'wrong' environment presumably has a large cost. Likewise, feeding traits

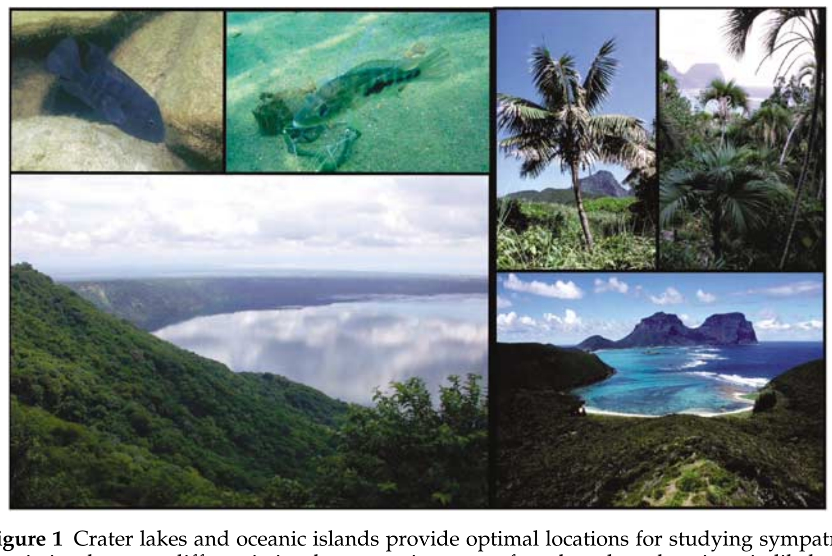

Figure 1 Crater lakes and oceanic islands provide optimal locations for studying sympatric speciation because differentiation between sister taxa found at these locations is likely to have occurred *in situ*. Clockwise from top left, *Amphilophus citrenellus*, *A. zaliosus*, *Howea forsteriana*, *H. belmoreana*, Lord Howe Island, Craterlake Apoyo. Photo credits: Cichlid panel – Marta Barluenga and Ad Conings. Palm panel – William J Baker.

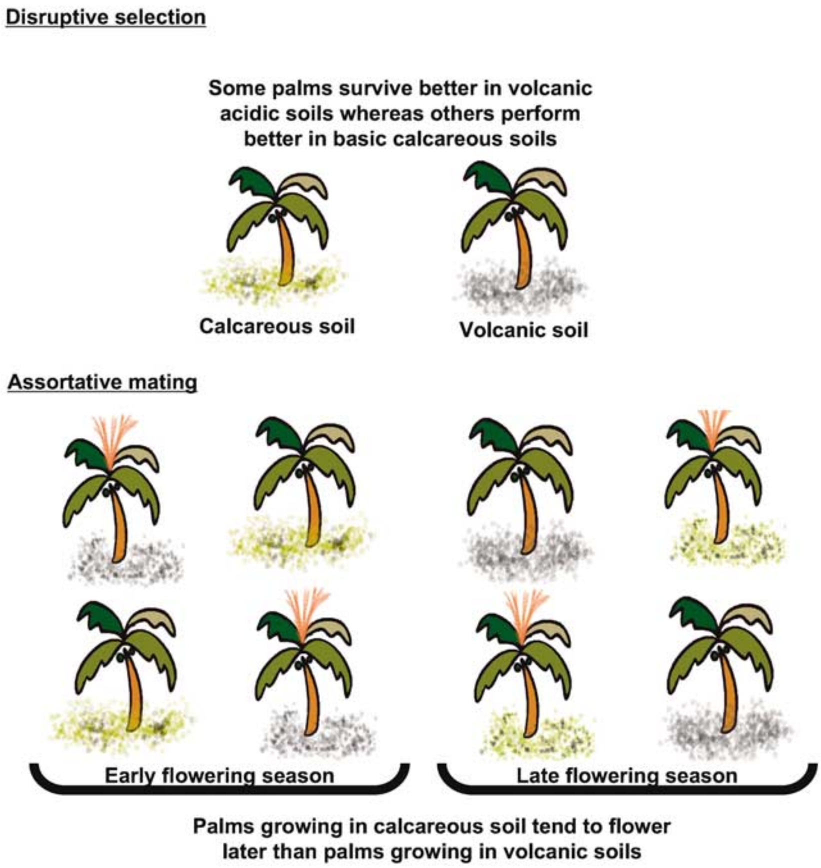

Figure 2 Sympatric speciation occurs most easily when traits under disruptive selection (eg soil preference or foraging behavior) and assortative mating (eg flowering time or body size) are correlated genetically. A possible speciation scenario for the Lord Howe Island palms is shown.

are highly differentiated between the two cichlids, and parallel phenotypic changes have been observed for cichlids from another Nicaraguan Lake. Thus, divergent ecological selection is likely to be strong in both cases, but this needs to be proven through reciprocal transplantation/relocation studies.

Whether there are genetic architectures that minimize the antagonism between divergent selection and recombination is less clear, but again there are tantalizing hints that this might be the case (Figure 2). An interesting feature of the palm example is that one of the species that shows asynchrony in male- and female- flowering time loses this difference in behavior when growing in a different soil type. Thus, this might be an example where developmental plasticity (ie, physiological responses to new substrates) could have initiated evolutionary change (West-Eberhard, 2003), and possibly, by generating a correlation between the trait under disruptive selection (soil preference) and that causing assortative mating (flowering time). However, given that the two species occasionally occur on soil types where flowering time differences are less conspicuous, reproductive barriers different from flowering time, such as conspecific pollen precedence (eg Rieseberg *et al*, 1995) or extrinsic postzygotic isolation in which hybrids perform poorly in both parental habitats, may contribute to the paucity of hybrids on the island.

The case for special genetics is more difficult in the fish example. Cichlids are a hyperdiverse lineage of organisms and provide some of the best-documented examples of sympatric speciation. However, we do not yet know whether ecological divergence and assortative mating traits are correlated genetically in cichlids. If this turns out not to be the case, then it will be difficult to account for the seeming propensity of cichlid fishes for sympatric speciation.

Although speciation in sympatry seems plausible, indeed convincing, in both the studies highlighted here, other explanations cannot be ruled out entirely. For example, hard-line advocates of allopatric speciation might argue for allopatric differentiation and multiple colonizations of Lord Howe Island and Lake Apoyo by palms and cichlids, respectively. Coconuts can travel thousands of kilometers on the ocean, hurricanes can dump fishes into crater lakes and hybridization can erase evidence of independent origins. Although we consider these explanations to be unlikely, they do highlight the need for further study of the strength of selection and genetic correlations in both pairs of taxa. If the conditions required by theory for sympatric speciation do exist in these taxa and other putative examples, then controversy over this mode of speciation might finally be put to rest.

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Editor's suggested reading

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