

EVOLUTIONARY BIOLOGY

Sympatric plant speciation in islands?

Arising from: V. Savolainen *et al.* *Nature* **441**, 210–213 (2006)

Comparative studies of populations, particularly with the help of molecular markers, are necessary to understand the mechanisms of speciation in isolated oceanic archipelagos. Savolainen *et al.*¹ present comparative data on two endemic species of the palm genus *Howea* in Lord Howe Island, from which they infer that speciation was sympatric — that is, divergence had occurred in the absence of geographic isolation. However, the landscape of oceanic islands changes dramatically over time, with many disappearing under the sea after 6 million years or more, and Lord Howe Island is in a very late stage of its ontogeny. An alternative explanation, therefore, is that these two species did not evolve *in situ* but instead that they arose allopatrically after becoming geographically isolated at a time when the island was much larger and more diverse ecologically.

Aside from well-known mechanisms of chromosomal polyploidy, examples of homoploid sympatric speciation in plants are rare. Savolainen *et al.*¹ present interesting comparative morphological, geographical, ecological and molecular (AFLP, or amplified DNA-fragment length polymorphism) data regarding relationships between the two species of *Howea* palms endemic to Lord Howe Island. Considering that the distributions of the two taxa now overlap, the authors regard this as a good example of sympatric plant speciation. The difficulty with this interpretation is that it does not take into account island ontogeny and its possible impact on the two species. Sympat-

ric speciation in islands, therefore, may still not have been convincingly demonstrated.

Lord Howe Island has a geomorphology that suggests strong erosion and surface loss, which correlates with its advanced age of 6.4–6.9 Myr. Dating from molecular sequences reveal the genus *Howea* to have diverged from progenitors 4.5–5.5 Myr ago, which is compatible with the island's age. By the same methods, the two species are judged to be 0.5–1.9 Myr old, at which time the island would still have been much larger than today. Loss of terrestrial area is more rapid during the later stages of island ontogeny, when the sea covers the last parts of the land.

Many other examples exist of sympatric and closely related plant species in oceanic islands. Such a pattern is evident among six species of *Robinsonia* (Asteraceae) from Masatierra Island in the Juan Fernandez archipelago in Chile². My colleagues and I have estimated that this island, which is about 4 Myr old³, has lost up to 95% of its original surface area⁴. The pattern we now see can best be interpreted as refugial, with these species being packed together (sympatrically) in the remaining small surface area. The original mode of speciation would have been ecogeographical (allopatric).

An alternative hypothesis for the origin of the two endemic species of *Howea* on Lord Howe Island, therefore, is by allopatric speciation in different ecological (perhaps calcarenite) zones, when the island was much younger and much larger. The low degree of AFLP divergence between the two species of

Howea does not necessarily argue for sympatric speciation. Island congeners typically show very little genetic divergence in DNA sequences and isozymes⁵. An absence of broad surveys prohibits generalizations at this point, but the limited AFLP data available indicate that very little divergence may have occurred between closely related species in islands that have speciated allopatrically⁶.

Before jumping to conclusions about sympatric speciation in oceanic islands, we need to exercise caution and factor in our best estimate of island geomorphic and habitat change, which together have had a major impact on genetic and species diversity⁷.

Tod F. Stuessy

Department of Systematic and Evolutionary Botany, University of Vienna, 1030 Vienna, Austria

e-mail: tod.stuessy@univie.ac.at

1. Savolainen, V. *et al.* *Nature* **441**, 210–213 (2006).
2. Sanders, R. W., Stuessy, T. F., Marticorena, C. & Silva, O. M. *Opera Bot.* **92**, 195–215 (1987).
3. Stuessy, T. F., Foland, K. A., Sutter, J. F., Sanders, R. W. & Silva, O. M. *Science* **225**, 49–51 (1984).
4. Stuessy, T. F., Crawford, D. J., Marticorena, C. & Rodriguez, R. in *Evolution and Speciation of Island Plants* (eds Stuessy, T. F. & Ono, M.) 121–138 (Cambridge Univ. Press, 1998).
5. Crawford, D. J. & Stuessy, T. F. in *Evolution and Diversification of Land Plants* (eds Iwatsuki, K. & Raven, P. H.) 249–267 (Springer, Tokyo, 1997).
6. Parsons, Y. M. & Shaw, K. L. *Mol. Ecol.* **10**, 1765–1772 (2001).
7. Stuessy, T. F., Greimler, J. & Dirnböck, T. *Biol. Skrift.* **55**, 89–101 (2005).

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Savolainen *et al.* reply

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Stuessy¹ questions our conclusions of sympatric speciation in a case study of palms on Lord Howe Island² and proposes an alternative hypothesis, whereby the two *Howea* species evolved allopatrically when the island was larger and less eroded. Stuessy also argues that low genetic divergence does not necessarily indicate speciation in sympatry¹. We agree that it is important not to jump to conclusions, but we have good estimates of the size and geological history of Lord Howe Island at the time of the speciation event^{3,4}, and both are fully compatible with sympatric speciation. Stuessy also misinterprets the results from our

AFLP (amplified DNA-fragment length polymorphism) genome scan: we did not assert that low AFLP divergence *per se* is evidence for sympatric speciation, but rather that the distribution of these genetic divergence values across the genome is strongly supportive of speciation with gene flow involving disruptive or divergent selection².

Evidence from bathymetry around the island indicates that its past extent has not exceeded 30 km long by 23 km wide³; today the island is roughly 12 km long and, on average, 1.5 km wide. The original height of the island is estimated to be 1,000 m, comparable with 875 m

for Mount Gower today³. The presence of an evenly distributed, wave-cut platform surrounding Lord Howe Island indicates that erosion has been mainly coastal and equal from all sides. Consequently, Quaternary calcarenite deposits, which created divergent ecological selection pressures conducive to *Howea* species divergence², have formed evenly around the island⁴; these are so closely intercalated with volcanic rocks that allopatric speciation due to ecogeographic isolation, as Stuessy proposes¹, is unrealistic.

The geomorphological history of Lord Howe Island must also be seen in the light of the breeding system of *Howea*. Even at its greatest extent, the island would have been small compared with the gene dispersal capacity of these woody, wind-pollinated outcrossers. Indeed, our analysis of molecular variance revealed extremely homogeneous population structure in both palms, which is compatible

with widespread gene flow². It is therefore difficult to imagine how geographic barriers to gene exchange would have formed on the island. The interlinked ecological differences of both species are still clearly visible — that is, in phenology and soil pH (ref. 2), which are both properties that are interdependent in other plants⁵.

Our AFLP genome scan is consistent with speciation in the face of gene flow, involving divergent selection on a limited number of genes. The expected distribution of interspecific divergence (F_{ST}) for species that evolved in allopatry is different from that expected for species that diverged with gene flow^{6–8}. It is the shape of the distribution of F_{ST} in the genome that matters: F_{ST} is expected to follow an L-shaped

distribution for sympatric divergence, as in our case study², whereas genetic differences accumulate throughout the genome in allopatry and lead to a bell-shaped distribution or a distribution that is biased towards large values of F_{ST} . Regardless of Stuessy's concerns, the question now is not whether sympatric speciation exists, but how common it might be^{9,10}.

Vincent Savolainen*, **Christian Lexer***,
Marie-Charlotte Anstett†, **Ian Hutton‡**,
J. J. Clarkson*, **M. V. Norup*S**, **M. P. Powell***,
D. Springate*, **N. Salamin||**, **William J. Baker***

*Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3DS, UK

e-mail: v.savolainen@rbgkew.org.uk

†Centre for Evolutionary and Functional Ecology, UMR 5175, 34293 Montpellier cedex 5, France

‡PO Box 157, Lord Howe Island, New South Wales 2898, Australia

SDepartment of Systematic Botany, University of Aarhus, 8000 Aarhus, Denmark

||Department of Ecology and Evolution, University of Lausanne, 1015 Lausanne, Switzerland

1. Stuessy, T. *Nature* **443**, doi:10.1038/nature05216 (2006).
2. Savolainen, V. *et al. Nature* **441**, 210–213 (2006).
3. McDougall, I. *et al. J. Geol. Soc. Austr.* **28**, 155–176 (1981).
4. Brooke, B. P. *et al. Quat. Sci. Rev.* **22**, 859–880 (2003).
5. Ollerton, J. *Heredity* **95**, 181–182 (2005).
6. Luikart, G. *et al. Nature Rev. Genet.* **4**, 981–994 (2003).
7. Via, S. *Trends Ecol. Evol.* **16**, 381–390 (2001).
8. Wu, C. I. *J. Evol. Biol.* **14**, 851–865 (2001).
9. Pennisi, E. *Science* **311**, 1372–1374 (2006).
10. Ortiz-Barrientos, D. & Rieseberg, L. H. *Heredity* **97**, 2–3 (2006).

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