

*al.* extend their interpretation to ocean basins in which water injected into the oceanic crust plays the same role as meteoric water in continental aquifers. Their article therefore does justice to the careful warning given by Oxburgh and O'Nions (8), who advised that "the systematics of the relation between the fluxes of helium and heat depend on transport processes." This warning was unfortunately lost in the turmoil of the debate between the advocates of whole-mantle versus layered-mantle convection.

One of the cornerstones of layered-mantle convection is therefore weakening. The remaining evidence essentially revolves around our understanding of the properties and inventories of rare gases. We are still awaiting incontrovertible data on rare-gas solubility in mantle minerals and melts, which would consolidate the dominant interpretation of the  $^3\text{He}/^4\text{He}$  evidence in oceanic basalts. Helium-3 is a stable nuclide essentially unaffected by deep-seated radioactive processes. Even if helium turns out to be particularly incompatible, enough undegassed mantle material with high  $^3\text{He}/^4\text{He}$  ratios may be concealed in the lower mantle as streaks inter-layered with recycled material (11). In addition, the argument based on the inventory of  $^{40}\text{Ar}$  in Earth is crucially dependent

on our knowledge of the terrestrial concentration of potassium, an element that is known to be extremely volatile during planetary accretion.

By coincidence, the consensus on the heat/helium imbalance at the surface of Earth is being challenged at almost the same moment as new experiments overturn the well-entrenched idea that high  $^3\text{He}/^4\text{He}$  ratios in basalts are the hallmark of primitive mantle.  $^3\text{He}$  is a stable isotope of helium, whereas  $^4\text{He}$  ( $\alpha$  particles) is continuously produced by the decay of uranium and thorium. High  $^3\text{He}/^4\text{He}$  ratios in hotspot basalts (e.g., Hawaii) with respect to mid-ocean ridge basalts have been held as prime evidence that the deep mantle never lost its primordial gases. Measurement of the helium solubility in mantle minerals (12) suggests instead that a high  $^3\text{He}/^4\text{He}$  mantle ratio may not be primordial (3, 4) but rather corresponds to residues of earlier stages of melting (5, 13, 14).

We should not let the heritage of layered-mantle convection models fall into oblivion, however. Numerical models of mantle convection repeatedly suggest that radial transport is particularly slow across the 660-km discontinuity and display episodic surges of layered-mantle convection regime (14). The article by Castro *et al.* nevertheless provides the first rigorous framework against one of

the strongest arguments used to support the role of the 660-km discontinuity as a convection boundary, and the authors should be commended for their work. Further full 2D and 3D models of large well-characterized aquifer systems around the world will soon let us reevaluate the terrestrial heat and helium fluxes and provide a new perspective on the thermal regime of our planet.

#### References

1. R. van der Hilst, R. Engdahl, W. Spakman, G. Nolet, *Nature* **353**, 37 (1991).
2. S. P. Grand, *J. Geophys. Res.* **99**, 11591 (1994).
3. M. D. Kurz, W. J. Jenkins, S. R. Hart, *Nature* **297**, 43 (1982).
4. C. J. Allègre, T. Staudacher, P. Sarda, M. Kurz, *Nature* **303**, 762 (1983).
5. N. Coltice, Y. Ricard, *Earth Planet. Sci. Lett.* **174**, 125 (1999).
6. C. J. Allègre, A. W. Hofmann, R. K. O'Nions, *Geophys. Res. Lett.* **23**, 3555 (1996).
7. R. K. O'Nions, E. R. Oxburgh, *Nature* **306**, 429 (1983).
8. E. R. Oxburgh, R. K. O'Nions, *Science* **237**, 1583 (1987).
9. P. E. van Keken, C. Ballentine, D. Porcelli, *Earth Planet. Sci. Lett.* **188**, 421 (2001).
10. M. C. Castro, D. Patriarche, P. Goblet, *Earth Planet. Sci. Lett.* **237**, 893 (2005).
11. M. Boyet, M. O. Garcia, R. Pick, F. Albarède, *Geophys. Res. Lett.* **32**, 10.1029/2004GL021873 (2005).
12. S. W. Parman, M. D. Kurz, S. R. Hart, T. L. Grove, *Nature* **437**, 1140 (2005).
13. D. Graham, J. Lupton, F. Albarède, M. Condomines, *Nature* **347**, 545 (1990).
14. S. Xie, P. J. Tackley, *Phys. Earth Planet. Inter.* **146**, 417 (2004).

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## ECOLOGY

# Population Evolution and Island Biogeography

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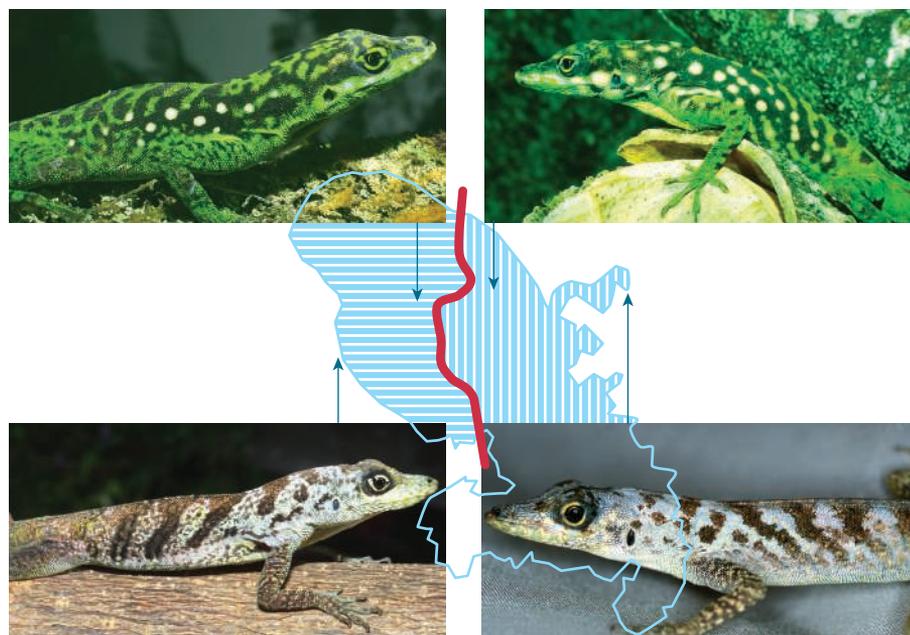
In most areas of empirical science, including biology, we take an experimental approach for granted. However, in evolutionary and related studies, large-scale natural or field experiments are rare because the large spatial and temporal scales of evolutionary and biogeographical processes render experimentation problematic. Classically, biogeography is about large-scale pattern: How many species are there on an island? Is the number related to extent of isolation, island size, or complexity of vegetation? For example, why are there so many tree lizard (anole) species on each of the Greater Antilles but only one or two on each of the Lesser Antilles? Is it simply island size that is accountable, even though the small islands are environmen-

tally heterogeneous and complex (1)? This is not readily subject to direct experimentation. However, these large-scale biogeographic patterns are mediated by small-scale population-level processes. These include ecological processes such as competition between species and habitat usage, and evolutionary processes such as adaptation by natural selection, ancestor-descendant relationships, and speciation (splitting into distinct species, which do not interbreed). Exceptionally, it may be possible to manipulate these fundamental population processes experimentally to gain insight into biogeographic patterns, although even population-level experimentation is difficult. For example, experimental introduction of small Caribbean anoles onto islands, and experimental translocation between large enclosures within islands, have revealed much about the evolutionary and ecological population processes underlying

their biogeography. Large-scale translocation of the small tree lizard *Anolis oculatus* (Dominica, Lesser Antilles) has demonstrated the rapid effect of natural selection on a wide range of genetically controlled traits in response to wet or dry habitats (2, 3), thus explaining the nature and cause of the geographic variation. In addition, experimental introduction of *Anolis sagrei* onto Bahamian islands has shown how predators can alter the behavior, niche usage, and their selection for prey (4). These studies also suggested how introduced predators may render their prey more vulnerable to extinction by catastrophes such as hurricanes (5).

On page 1807 in this issue, Schoener *et al.* (6) show how the survival of resident anoles on islands with introduced predator lizards depends on vegetation height. On islands without the introduced predator, anoles survive better in habitats with shorter vegetation, but on islands with the introduced predator, anoles survive better in habitats with taller vegetation. Island size on its own did not appear to have a significant effect. Hence, the authors take the important step of linking a population process (survival) to a key feature of island biogeography (vegetation type), and this direct demonstration, using a field experi-

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**No evidence for the geographic speciation predicted by biogeographic pattern.** Broad biogeographic pattern suggests geographic speciation in Lesser Antillean anoles, yet on Martinique, where once separate island species now meet in secondary contact (red line), population-based genetic studies show no evidence of their reproductive isolation (9). However, there is strong parallel adaptation to the habitat zonation and some evidence of reduced interbreeding among these habitat types (ecotypes) (9). Xeric coastal ecotypes of anoles are brown and striped (lower photographs; arrows indicate locality of origin). Where lineages meet, in the montane rainforest, they show parallel evolution of green montane ecotypes (upper photographs), irrespective of their independent island history and deep molecular phylogenetic divergence.

ment, is novel. This relationship is important because island biogeographic patterns are determined by such population processes. Although population phenomena underlie central aspects of island biogeographic theory, these related disciplines are often pursued without extensive cross-reference. For instance, the species-area relationship (number of species per island compared to size of island) in island biogeography is usually considered in isolation of the population processes that drive speciation. Comparative island biogeographic analysis of the distribution and number of species of native Caribbean island anoles concludes that “within-island” speciation is rare or nonexistent on small islands (7). However, this proposition has been made in the absence of population-based genetic evidence, and thus biogeographic pattern is suggesting population process, rather than population process informing biogeographic theory. Moreover, what precisely does “within-island” mean? It has become an axiom of evolutionary ecology that the historical component should be taken into account. This, quite rightly, means that the history of an organism (phylogeny) should be considered. But in island biogeography, should we not also be considering the geological history? We may anthropocentrically regard an island that exists now as a “real” single entity, yet it may have been a

single entity for only a brief portion of its history. For example, the island of Martinique in the Lesser Antilles may once have comprised up to five separate islands, some more than 20 million years old, which have spent only a fraction of their existence as part of the single island of Martinique (8). Biogeographic patterning suggests that each Lesser Antillean island has one anole species (per clade), implying that each island may have been dominated by allopatric speciation via island colonization. In other words, each island is naturally inhabited by a single anole species by virtue of having evolved into a new species after colonization of a new island because it was geographically, and hence genetically, isolated from its ancestor. This widely accepted view is perhaps immune to challenge because it is virtually impossible to directly test the reproductive isolation of allopatric species. However, it may be possible to test one aspect of this theory by using population-level analysis. The allopatric speciation hypothesis predicts that the endemic forms on ancient islands should act as “good” species and not freely interbreed on contact with a different species. Such secondary contact exists between the anoles from the precursor islands of Martinique (see the figure). However, population-based genetic studies of nuclear gene flow do not support this pre-

dition of no interbreeding on secondary contact of these populations (9). Therefore it may be more appropriate for population-based studies to inform biogeographic theory, than for biogeographic pattern to suggest the nature of the population process.

Field experiments on aspects of population biology that are relevant to biogeography are replete with challenges. These problems include maintaining conditions that are as natural as possible such as natural densities of organisms, maintaining discrete experimental units such as small islets or enclosures, having a size and number of replicate units that are large enough to give statistical significance but are still logistically manageable, and having effects that are intense enough to yield results in the time frame of the project and variables with sufficient variance to elicit a response. Island anoles in general, and *A. sagrei* in the islands of the Bahamas in particular, provide a model system that overcomes many of these problems. The small size of anoles, their high population density, numerous studies providing background information on their evolutionary ecology, and their presence on small discrete islands with varying vegetation types make island anoles a valuable model system for both experimental (1–6) and comparative (1, 8–10) studies in evolution and biogeography.

Perhaps the larger challenge will be relating population ecology and population evolution to broader scale spatial variation in the environment. Schoener *et al.* have shown that demographics are certainly sensitive to changes in species composition and that this is habitat specific. Anoles adapt closely to the environmental and climatic zones that exist on even small islands (1–3, 8). Can similar experimental studies be used to provide insight into the speed and limits of adaptation to climate change of both individual species and whole communities?

#### References and Notes

1. J. B. Losos, R. S. Thorpe, in *Adaptive Speciation*, U. Dieckmann, M. Doebeli, J. A. J. Metz, D. Tautz, Eds. (Cambridge Univ. Press, Cambridge, UK, 2005), pp. 322–344.
2. A. Malhotra, R. S. Thorpe, *Nature* **353**, 347 (1991).
3. R. S. Thorpe, J. T. Reardon, A. Malhotra, *Am. Nat.* **165**, 495 (2005).
4. J. B. Losos, T. W. Schoener, D. A. Spiller, *Nature* **432**, 505 (2004).
5. T. W. Schoener, D. A. Spiller, J. B. Losos, *Nature* **412**, 183 (2001).
6. T. W. Schoener, J. B. Losos, D. A. Spiller, *Science* **310**, 1807 (2005).
7. J. B. Losos, D. Schluter, *Nature* **408**, 847 (2000).
8. R. S. Thorpe, A. G. Stenson, *Mol. Ecol.* **12**, 117 (2003).
9. R. Ogden, R. S. Thorpe, *Proc. Natl. Acad. Sci. U.S.A.* **99**, 13612 (2002).
10. R. Calsbeek, T. B. Smith, *Nature* **426**, 552 (2003).
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