Journal Club

An evolutionary slant on species–area curves

Uncertainty about the past has made it difficult to evaluate the relative roles of ecological and historical processes in generating species diversity. Although diversity is predicted to be higher on larger islands compared with that on smaller islands because of the effect of area on immigration and extinction rates, ecological theories do not fully account for positive species–area relationships if the source of new species is intra-island speciation, rather than immigration. In such cases, it becomes an evolutionary question of why the diversities differ between islands. Speciation rates are expected to be higher in larger areas, but until now, there had been no quantitative test of this theory. By reconstructing the number of immigration and speciation events on a phylogeny of Caribbean island *Anolis* lizards and comparing these quantities with island area, Losos and Schluter[1] test the evolutionary contribution to species–area relationships.

Their study showed that, above a threshold island size, speciation surpasses immigration as a source of new species. On large islands, species are derived *in situ* from ancestral lineages, but on small islands, the species are always distantly related, and thus must have immigrated. As predicted, speciation rates also scaled positively with island area. Using computer simulations, the authors show that neither the number of ancestral lineages, nor differences in the time islands harbored species accounted for the increased number of speciation events on larger islands. Although a declining extinction rate with increasing island area could produce a positive species–area relationship, Losos and Schluter demonstrate that such an explanation is improbable. Estimates derived from fitting the phylogeny to a birth–death model

indicated that the extinction rate was below that for speciation, and far too low to produce an apparent pattern of increased speciation rate on large islands. Moreover, they showed that, on large islands, higher proportions of the lizard communities were comprised of morphologically and ecologically similar species (i.e. 'superspecies complexes'). If speciation rates were comparable among islands, the proportion of species represented by superspecies complexes should arguably be similar.

Losos and Schluter's study shows that the impact of history on species distributions extends beyond that of chance or accidents of ancestry, but instead, is consistent with evolutionary theory. They also demonstrate that historical effects reflect themselves in patterns of ecomorphology. The proportion of species in superspecies complexes implies that allopatric speciation was common on the largest islands, but became less frequent with decreasing island area, thereby generating a positive species–area relationship. An explanation based on a link between habitat diversity and speciation rate was insufficient because some lineages from old, topographically and climatically diverse islands had not speciated. This suggests that the spatial context of speciation, rather than ecological selection pressures, was more important in producing the positive species–area relationship in Caribbean *Anolis* lizards. Thus, historical approaches not only complement ecological studies of diversity patterns, but an evolutionary perspective is also essential for understanding community structure.

1 Losos, J.B. and Schluter, D. (2000) Analysis of an evolutionary species–area relationship. *Nature* 408, 847–850

L. Lacey Knowles
knowles@u.arizona.edu