Darwin's finches have reached their limits on the Galapagos

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A small Galápagos ground finch (*Geospiza fuliginosa*), Pinta Island, Galápagos. There is no more room for new species on the Galápagos islands, unless one of the existing species becomes extinct. Credit: Ruben Heleno

The evolution of birds on the Galápagos Islands, the cradle of Darwin's theory of evolution, is a two-speed process. Most bird species are still diversifying, while the famous Darwin's finches have already reached an equilibrium, in which new species can only appear when an existing one becomes extinct. This finding expands the classical theory on island evolution put forward in the 1960s. The study is published online on June 23 in *Ecology Letters*.

Islands are seen as natural laboratories for the study of evolution. They form isolated ecosystems with barriers to migration. Classical Island Theory predicts that a dynamic equilibrium will occur between immigration and extinction of species. Recent theory adds that as species diversity increases, ever more ecological niches become occupied, which has a negative effect on immigration (new immigrants from outside of the Galápagos cannot settle) and diversification (radiation into new species is blocked).

Evolutionary dynamics

'However, this has never been tested in detail, for lack of data and the right analytical tools', explains Rampal Etienne, Associate Professor of Theoretical and Evolutionary Community Ecology at the University of Groningen, the Netherlands. Together with Luis Valente (University of Potsdam, Germany) and Albert Phillimore (University of Edinburgh, UK), he developed DAISIE, a mathematical model that uses phylogenetic data on living species to reconstruct evolutionary dynamics. DAISIE stands for Dynamic Assembly of Islands by Speciation, Immigration and Extinction, and was named after famous radiations of daisy-like plants on Hawaii.

A Floreana mockingbird, Champion island, Galápagos. Mockingbirds are still diversifying on the Galápagos islands. Credit: Ruben Heleno

DAISIE was fed with the phylogenetic trees of existing bird species on the Galápagos Islands. These were constructed with genomic data that has become available in recent years. DAISIE then estimates diversity limits and rates of immigration, speciation and extinction per lineage.

'The analysis shows that for the finches, diversity does indeed have a negative effect. There is no more room for new species, unless one of the existing species becomes extinct, so the islands are saturated regarding finch-type species', Etienne explains. This does not mean the radiation is static. 'We found that the rates of both evolution and extinction are very high for Darwin's finches. That is probably why these birds have reached an equilibrium.'

Isolated ecosystems

Galápagos warbler, *Dendroica petechia aureola*, Santiago island, Galápagos. Birds - with the exception of Darwin's finches -- are still diversifying on the Galápagos islands. Credit: Luis Valente

Other species like mockingbirds have not yet reached equilibrium, which contrasts sharply with the current view that oceanic islands are at equilibrium. 'Our data shows that they are evolving more slowly and are still diversifying.' In a million years or so, more mockingbird species may have appeared - granted that conditions on the islands remain the same.

The study shows that the DAISIE model - which the authors have made available as a library in the free and widely used R software environment - is a valuable tool for the study of evolutionary dynamics on islands. It includes speciation and thus extends existing island theory, which is based on immigration and extinction. Etienne: 'And of course, it works for all isolated ecosystems, not just islands but also lakes or mountain tops.'

Apart from explaining evolutionary history, DAISIE also predicts future diversity. 'This could be interesting from a conservation point of view: we are not just conserving existing species, but also future diversity.'

Provided by University of Groningen