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- Hickerson, M. & Meyer, C. (2008) Testing comparative phylogeographic models of marine vicariance and dispersal using a hierarchical Bayesian approach. *BMC Evolutionary Biology*, 8, 322.
- Kallimanis, A.S., Bergmeier, E., Panitsa, M., Georghiou, K., Delipetrou, P. & Dimopoulos, P. (2010) Biogeographical determinants for total and endemic species richness in a continental archipelago. *Biodiversity and Conservation*, 19, 1225-1235.
- Lambeck, K., Esat, T.M. & Potter, E.-K. (2002) Links between climate and sea levels for the past three million years. *Nature*, 419, 199-206.
- Li, J.-W., Yeung, C.K.L., Tsai, P.-W., et al. (2010a) Rejecting strictly allopatric speciation on a continental island: prolonged postdivergence gene flow between Taiwan (*Leucodioptron taewanus*, Passeriformes Timaliidae) and Chinese (*L. canorum canorum*) hwameis. *Molecular Ecology*, 19, 494-507.
- Li, S.-H., Yeung, C.K.L., Han, L., Manh Hung, L., Wang, C.-X., Ding, P. & Yao, C.-T. (2010b) Genetic introgression between an introduced babbler, the Chinese hwamei *Leucodioptron c. canorum*, and the endemic Taiwan hwamei *L. taewanus*: a multiple marker systems analysis. *Journal of Avian Biology*, 41, 64-73.
- Losos, J.B. & Ricklefs, R.E. (2009) Adaptation and diversification on islands. *Nature*, 457, 830-836.
- MacArthur, R.H. & Wilson, E.O. (1967) *The theory of island biogeography*. Princeton University Press, Princeton, New Jersey.
- Mayr, E. (1942) *Systematics and the origin of species, from the viewpoint of a zoologist*. Columbia University Press, New York.
- McDowall, R.M. (2002) Accumulating evidence for a dispersal biogeography of southern cool temperate freshwater fishes. *Journal of Biogeography*, 29, 207-219.
- Raymo, M.E., Mitrovica, J.X., O'Leary, M.J., DeConto, R.M. & Hearty, P.J. (2011) Departures from eustasy in Pliocene sea-level records. *Nature Geoscience*, 4, 328-332.
- Whittaker, R.J. & Fernández-Palacios, J.M. (2007) *Island biogeography. Ecology, evolution and conservation*. Oxford University Press, Oxford.

Edited by Spyros Sfenthourakis

update

Escaping the trap of low sample size in island biogeography

Ecologists and evolutionary biologists have been fascinated by island biodiversity at least since the first travels of 18th century naturalists. Islands' sometimes exuberant diversity – full of rare forms and endemic species or varieties – their character of discrete entities and their isolation from the mainland make islands exceptional natural laboratories for the development of ecological and evolutionary theory. Perhaps unsurprisingly, they have been home to many major theoretical advances in these disciplines during the last 50 years (see Whittaker & Fernández-Palacios 2007), from which the seminal Equilibrium Theory of Island Biogeography (ETIB, MacArthur and Wilson 1967) is just the most outstanding example.

In spite of the importance of islands and archipelagos for the development of biogeographical theory, the stubborn persistence of archipelagos and island groups to come in low island numbers and the tendency of different

characteristics to be collinear makes it difficult to evaluate hypotheses and extract conclusions about the processes originating from the diversity and structure of their assemblages. For example, finding a significant relationship (at the 0.05 level) between any two island descriptors for the seven main islands of the Canarian archipelago using simple least-squares regression models requires percentages of explained variation (adjusted r^2) of about 50%. This problem is further aggravated when working with patterns of within-island diversification, because many islands may be too small to host speciation processes (see e.g. Losos & Schluter 2000), therefore reducing the number of islands that can be used for these particular analyses in each archipelago. Needless to say, discriminating between three or four non-mutually exclusive hypotheses represented by predictors with different degrees of collinearity is typically a difficult task in island biogeography.

In addition, differences in a number of characteristics – species pool, geographic location, geological origin or history, among others – provide each archipelago – and each taxon within an archipelago – with its own idiosyncrasy (see Whittaker & Fernández-Palacios 2007, Santos et al. 2010). This impedes analysis of several island groups together, using standard statistical techniques, except perhaps in the case of relatively coherent regions such as the Aegean or Macaronesian islands, and then only to some extent (e.g. Sfenthourakis 1996, Triantis et al. 2010). These limitations have forced island biogeographers to push their results to the limit, and many times to rely on anecdote to explain the large differences between different archipelagos in many biogeographical relationships, some of them as fundamental as the species–area relationship (Triantis et al. 2012).

The limitations listed above make it difficult to reach unequivocal conclusions about the relative importance of different factors for the generation and maintenance of island diversity. Thus, several debates with no easy solution have accumulated over the years, such as the recent discussion on whether island diversity may be enhancing diversification rates, which started with the proposal of Emerson and Kolm (2005) and was followed in subsequent issues of *Nature* (vol. 468 iss. 7064, 2005), *Ecography* (vol. 30 iss. 3, 2007) and *Ecology* (vol. 88 iss. 8, 2007), among other places. To date, the solution to this has mostly been the development of theoretical models that incorporate new aspects or processes into the basic body of theory provided by MacArthur and Wilson's (1967) ETIB. We can recognize two main groups of these models, namely simple predictions about the relationships between diversity and certain parameters, or complex process-based models providing mathematically explicit descriptions of the processes regulating island diversity. A good example of the former is the proposal of the General Dynamic Model of Oceanic Island Biogeography (GDM, Whittaker et al. 2008), which merges the geological evolution of oceanic islands with the basic ETIB predictions. This emerged from the debate on the relationship between island diver-

sity and diversification rates, quoted above. The advances provided by this kind of approach have been limited because they tend to focus on very basic principles that are often not mutually exclusive, which makes it necessary to add several of them into more complex models. This results in models with large numbers of parameters that are therefore difficult to evaluate with the limited number of archipelagos available, given the abovementioned risk of relying on explanations that are too particular. Process-based models can provide deeper insights by combining basic ecological and evolutionary theory with the already large body of knowledge about island diversity patterns (for a great example see Rosindell and Phillimore 2011). However, evaluating the validity of their predictions is still limited by the low sample sizes and limited data available about island biotas (see Hortal et al. 2009).

There may, however, be other ways of escaping from the trap of low sample size in island biogeography, thanks to the use of statistical tools that are already being used in other fields of ecology. In a *forum* paper in *Ecography*, Bunnefeld and Phillimore (2012) argue that Linear Mixed Models (LMM) are particularly suited to working with the data structure commonly found in island biogeography studies. In LMM predictors are divided into fixed and random effects. Fixed effects are those that are being studied – and for which we aim to estimate regression parameters and/or evaluate significance. Random effects identify different groups within the data – such as archipelagos, taxa or regions. This allows estimation of the general effects of one or several predictors across several datasets in a single analysis, providing an elegant way of estimating the explanatory power of a given hypothesis across many particular cases, while at the same time accounting for non-independence in the data and reducing the number of degrees of freedom used in the analysis. Bunnefeld and Phillimore (2012) use LMM to re-evaluate the datasets originally used by Whittaker et al. (2008), finding further support for the generality of GDM predictions once the particular geological history of each archipelago and the particularities of each taxon are accounted for.

The applications of LMM in island biogeography are not restricted to the joint inclusion of many archipelagos into single analyses. In another paper already available online in *Ecography*, Steinbauer et al. (2012) use LMM to study whether isolation from their mainland sources and geological history determine the overall diversification of seed plants in different altitudinal bands throughout the Canary Islands. In this case, they found support for both GDM predictions and their initial hypothesis that overall diversification rates are higher for higher-altitude ecosystems, which are significantly more isolated from their sources of colonizers than low-altitude ones. This example shows how LMM can be easily used to detect and evaluate general patterns using data from heterogeneous sources, as claimed by Bunnefeld and Phillimore (2012), as well as the utility of this approach for evaluating the joint effect of several hypotheses when their predictions are clearly stated. From my knowledge about the characteristics of island diversity data, I believe that LMM provides a robust and promising way of accounting for the low sample sizes that are the norm in this research field. Thus, I join Bunnefeld and Phillimore (2012) in recommending that LMM or similar approaches become the standard in island biogeography studies.

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References

- Bunnefeld, N. & Phillimore, A.B. (2012) Island, archipelago and taxon effects: mixed models as a means of dealing with the imperfect design of nature's experiments. *Ecography*, 35, 15–23.
- Emerson, B.C. & Kolm, N. (2005) Species diversity can drive speciation. *Nature*, 434, 1015–1017.
- Hortal, J., Triantis, K.A., Meiri, S., Thébault, E. & Sfenthourakis, S. (2009) Island species richness increases with habitat diversity. *American Naturalist*, 173, E205–E217.
- Losos, J.B. & Schluter, D. (2000) Analysis of an evolutionary species–area relationship. *Nature*, 408, 847–850.
- MacArthur, R.H. & Wilson, E.O. (1967) *The theory of island biogeography*. Princeton University Press, Princeton.
- Rosindell, J. & Phillimore, A.B. (2011) A unified model of island biogeography sheds light on the zone of radiation. *Ecology Letters*, 14, 552–560.
- Santos, A.M.C., Whittaker, R.J., Triantis, K.A., Borges, P.A.V., Jones, O.R., Quicke, D.L.J. & Hortal, J. (2010) Are species–area relationships from entire archipelagos congruent with those of their constituent islands? *Global Ecology and Biogeography*, 19, 527–540.
- Sfenthourakis, S. (1996) The species–area relationship of terrestrial isopods (Isopoda; Oniscidea) from the Aegean archipelago (Greece): a comparative study. *Global Ecology and Biogeography Letters*, 5, 149–157.
- Steinbauer, M.J., Otto, R., Naranjo-Cigala, A., Beierkuhnlein, C. & Fernández-Palacios, J.-M. (2012) Increase of island endemism with altitude – speciation processes on oceanic islands. *Ecography*, 35, 23–32.
- Triantis, K.A., Borges, P.A.V., Hortal, J. & Whittaker, R.J. (2010). The Macaronesian Archipelago: patterns of species richness and endemism of arthropods. In *Terrestrial arthropods of Macaronesia – Biodiversity, ecology and evolution* (ed. by A.R.M. Serrano, P.A.V. Borges, M. Boieiro and P. Oromí), pp. 49–71. Sociedade Portuguesa de Entomologia, Lisboa.
- Triantis, K.A., Guilhaumon, F. & Whittaker, R.J. (2012) The island species–area relationship: biology and statistics. *Journal of Biogeography*, 39, 215–231.
- Whittaker, R.J. & Fernández-Palacios, J.M. (2007) *Island biogeography. Ecology, evolution, and conservation*. Second edition. Oxford University Press, Oxford.
- Whittaker, R.J., Triantis, K.A. & Ladle, R.J. (2008) A general dynamic theory of oceanic island biogeography. *Journal of Biogeography*, 35, 977–994.

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