



COMMENTARY



## Island biology and the consequences of interspecific interactions

Dan Simberloff and his work have had an immeasurable impact on biogeography and on biogeographers. In recognition of his contributions, the International Biogeography Society awarded him the prestigious Alfred Russel Wallace Award at its biennial meeting in Bayreuth, Germany, in January, 2015. The Wallace Award is given to an eminent scholar to recognize his/her lifetime of outstanding contributions. Dan Simberloff certainly fits this description. Previous recipients include John Avise, Jack Briggs, James H. Brown, Jared Diamond and Robert E. Ricklefs.

Dan's lifetime of outstanding contributions began in the late 1960s, when he partnered with E.O. Wilson to test experimentally the ideas of the nascent Theory of Island Biogeography (Simberloff & Wilson, 1969, 1970). We all know about this experiment, or at least we should, as the study features in almost every ecology textbook in existence. The work was, and still is, ahead of its time. When Simberloff started working with Wilson, experiments were rare in ecology, and especially in biogeography, as they still are (several recent authors have called for a more experimental biogeography). Simberloff and Wilson's herculean experiments on mangrove islands off the coast of Florida appeared to confirm the emerging Theory of Island Biogeography and contributed to its becoming a dominant paradigm in biogeography. Wilson (2010) provides an excellent overview of the work, with some rare photos from the field as well.

Simberloff could have sat on his laurels and let the accolades and acolytes come to him. But instead, soon after the publication of his classic papers with Wilson, Dan dug deeper into the details of the experiment and showed, in a paper published in *Science* in 1976 (Simberloff, 1976), that most of the turnover of insect species on the islands was of transient, ephemeral species, which was in conflict with the basic tenets of the Theory of Island Biogeography. Dan is recognized as a paradigm-smashing ecologist, or at least as

someone who challenges the bandwagons du jour. However, we often forget that one of the first examples of such critical re-examination of a biogeographical bandwagon was the one based on his own award-winning work. The ability to challenge the established view of the day and to avoid blindly accepting published work (especially one's own work) should be at the heart of the scientific endeavour.

Despite Dan's pointing out these fundamental issues with the interpretation of the mangrove experiment, his work with Wilson spurred a decade of attempts to apply island biogeography theory to reserve design and conservation biology, much to Dan's chagrin and despite his clear-headed papers on the subject (e.g. Simberloff & Abele, 1976). The debates about the use and mis-use of the Theory of Island Biogeography in reserve design continued throughout the mid-1970s and into the 1980s, with Dan and his colleagues on one side, pushing for an empirical data-based approach to addressing the issue. At about the same time, a new 'discussion' was emerging in community ecology, and again, Simberloff and his colleagues were on one side, taking on the established views of the day (Connor & Simberloff, 1979). The 'discussions' among Simberloff, Diamond, Connor, Strong, Roughgarden and others were about the processes that might (or might not) structure communities and whether one could infer process (usually interspecific competition) by examining a pattern, usually the distribution of species among oceanic islands. Simberloff and his colleagues championed the null models approach in community ecology and biogeography and again took on the dominant paradigms of the day (Simberloff, 1983). These heated discussions about how to interpret patterns in nature (or, as Simberloff might put it, how to avoid over-interpreting patterns in nature) have cooled a little of late, but not by much. As a consequence of these discussions, our science is much more rigorous, and the use of null models in biogeogra-

phy is accepted practice, and even required by most astute reviewers and journal editors.

Dan's work on the Theory of Island Biogeography (and his own re-evaluation of his work) and his promotion of null models in ecology and biogeography were clarion calls for rigour, for refusing to accept blindly the prevailing dogma of the day, for a reliance on data rather than ideology. And these are hallmarks of Dan's approach in the numerous other fields he has pioneered (or challenged), including the threats posed by invasive species (Simberloff & Von Holle, 1999), the unintended consequences of biological control (Simberloff & Stiling, 1996), the utility (or lack thereof) of corridors (Simberloff *et al.*, 1992) and assisted migration as conservation tools (Ricciardi & Simberloff, 2009), and the ecological and evolutionary consequences of character displacement (Dayan & Simberloff, 2005). And throughout his career, Dan has worked with and mentored some of the very best ecologists and biogeographers. He never fails to acknowledge them or to admit how much inspiration they have given him. Finally, that brings me to the paper that Dan presented when he received the Wallace Award in Bayreuth; the printed version of which stems from Arijana Barun's dissertation.

The paper by Barun *et al.* (2015) is based on many measurements of mongoose and marten skulls from museum collections and on field-collected data as part of Barun's dissertation with Simberloff. It seeks to examine two inter-related topics at the core of much of community ecology and biogeography – character release and character displacement. In short, the data demonstrate a slightly more complicated story than simple character displacement being observed when the competitors co-occur and character release when they do not. The mongoose tends to have smaller canines and skulls when it co-occurs with the marten, as predicted under character displacement, but it is not larger where it occurs by itself, which would be predicted if character

release were occurring. Marten skulls, in contrast, tend to be shorter on islands where the mongoose is absent than where it is present, indicating character release. But marten canine diameters are similar across all islands.

Barun *et al.* (2015) is rather more than a tidy story of character displacement and character release in a couple of small mammal species on some islands in the Adriatic. Instead, Barun *et al.* (2015) exemplifies and summarizes much of Dan's diverse interests and strengths:

1. The paper is about patterns on islands, a recurrent theme in much of Dan's work since his own PhD.

2. Although the paper ostensibly tests several biogeographical hypotheses (e.g. character displacement, character release, the 'island rule', and Bergmann's rule), there is no presumption about what should be found. Instead, Barun and colleagues simply let the data tell them what they tell them.

3. The mongoose, one of the classic examples of biocontrol gone bad, is a notoriously noxious invasive species that disrupts native communities almost everywhere it has been introduced.

4. The paper is really about inferring process (interspecific competition) from patterns (body sizes among islands).

5. And finally, Barun *et al.* (2015) stress the necessity of knowing one's natural history (and historical) information about the focal taxa. It would be one thing to download all of the data from some online repository, but a much richer story arises when time is spent in the field and in the museum with the organisms.

Hence, this paper typifies Dan, at least to me. Much of what makes Dan such an

incredible biogeographer, natural historian and mentor are evident throughout the manuscript. But Dan is not receiving such a prestigious award for this one paper. Instead, Dan is receiving the Wallace Award from the IBS for a lifetime of achievements. His work has helped make biogeography into a better science. And his mentorship, friendship, and advocacy have shaped new generations of ecologists and biogeographers. Biogeography is better because of Dan, and there are few, if any biogeographers who are better than Dan Simberloff.

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Editor: Robert Whittaker

doi:10.1111/jbi.12603