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symposium summary

Island biogeography

A contributed session at the 5th International Biogeography Society Conference – Heraklion, Greece, 7–11 January 2011

It is now almost 50 years since the publication of Robert H. MacArthur and Edward O. Wilson's 1963 paper, *An Equilibrium Theory of Insular Zoogeography* which led to their famous book, *The Theory of Island Biogeography* (MacArthur and Wilson 1967). These publications were instrumental in a switch from a static, historically oriented biogeography, based in the direct interpretation of the data collected in the field, to a 'dynamic' equilibrium paradigm, based on a synthetic approach to biogeographical processes.

By their nature, the processes underlying biogeographic distributions and evolution on (remote) islands occur on large scales of time and space and remain among the most difficult to study and understand. Although some of the topics emphasized by MacArthur and Wilson still remain relatively unexplored, recent advances in island theory demonstrate that we are moving towards a new synthesis, identifying and incorporating aspects of the island systems that were not considered in the past. All the talks in the island biogeography session pointed in this direction.

One of the first lessons taught to us by Wallace, decades before MacArthur and Wilson, is that comparisons among different archipelagos and biogeographic regions of the globe can offer significant insights and increase our understanding of the processes regulating biodiversity across time and space (see Wallace 1887). Daniel Carstensen and colleagues compared the biogeographical patterns of birds in Wallacea and the West Indies, adopting a network approach to detect biogeographical modules (i.e. sub-regions of islands compartmentalized on the basis of a common avifauna) and the roles of each island according to its spatial location and the topology of the geographical network. They discussed the relative importance of island features and species richness on the local and regional fauna of the two biogeographical regions. Similarly, Silvia Aranda and co-workers compared, within the framework

of the *Theory of Island Biogeography*, the effects of area, isolation, geological age and climate on bryophyte species richness on Macaronesian Islands. They provided evidence that, in addition to area, it is necessary to quantify other variables that are also critical for the establishment of biodiversity and at the same time have high explanatory power (such as island age and climate), if we are to build up a more predictive science of species richness variation across island systems.

However, island area remains the most powerful single variable in explaining variation in the number of species occupying an island and the species–area relationship (SAR) is one of ecology's few laws. Even and Kathleen Tjørve showed that we should consider with caution the common assumption that the power law of Arrhenius is appropriate for both sample-area (mainland) SARs and isolate (island) SARs. Especially regarding isolate SARs, they argue that the form of the relationship is actually sigmoid when the finest scales are included. Based on this assumption, they proposed a new species–area model and presented results from different archipelagos and taxa.

Fifty years ago E.O. Wilson, studying Melanesian ants, coined the term 'taxon cycle' to describe 'the inferred cyclical evolution of species [of Melanesian ants], from the ability to live in marginal habitats and disperse widely, to preference for more central, species-rich habitats with an associated loss of dispersal ability, and back again' (Wilson 1961). However, the taxon cycle has, until recently, been difficult to test (see Ricklefs and Bermingham 2002). Evan Economo and Eli Sarnat evaluated taxon cycle predictions with a new dataset on habitat distributions of the entire Fijian ant fauna and a community phylogeny for one of the genera present in that archipelago. They provided evidence that as lineages progress to higher levels of endemism, they undergo shifts from marginal to interior primary habitats, from ecological generalism to specialization, and from

high to low population density, consistent with one of the major predictions of the taxon cycle.

One of major driving forces considered in the taxon cycle and most importantly in the *Theory of Island Biogeography* is (natural) extinction. The extinctions caused directly and indirectly by humans colonizing isolated islands of the globe have been dramatic (Steadman 2006). Alison Boyer and Walter Jetz quantified the distribution of functional diversity, a major component of biological diversity, in 45 pre-historic island bird communities of the Pacific and documented its reduction via species extinctions over the past 3,500 years. They concluded that the loss of functional diversity in the system under study is highly predictable from the pre-extinction composition of communities, with island age and isolation being less important determinants.

One of the major challenges for the *Theory of Island Biogeography* has been understanding the origin of the diversity patterns on oceanic islands. The conceptual model of MacArthur and Wilson (1967) has been less successful and is arguably less complete when applied to oceanic island systems. Although they already recognized that on the more remote islands increasing proportions of the biota are the result of *in situ* evolutionary change, they chose to focus on the immigration–extinction dynamics for simplicity. The recognition of this shortfall has led to the introduction of new theories (e.g. Whittaker et al. 2008) but other challenges remain, such as species–abundance distributions on islands. James Rosindell and Albert Phillimore presented a new unified model of island biogeography (Rosindell and Phillimore 2011), based on the neutral theory of biodiversity and biogeography (Hubbell 2001), aiming to tackle these major issues. Most of their model's predictions are consistent with a broad range of patterns in empirical data and existing theory. This integration of classic island biogeography with neutral theory provides a critical addition to the existing theoretical framework for describing and understanding the evolutionary biogeography of oceanic islands.

It is an exciting era for island biographers; it is now more obvious than ever that no theory is

an island. We are moving towards refining existing theories, introducing new ones and eventually new syntheses. I hope that, in the next IBS meeting in Miami (2013), held 100 years after the passing of Alfred Russel Wallace, and 50 years after the publication of MacArthur and Wilson's (1963) seminal article, island biogeographers will be able to celebrate new theories; *we still have some of the Cretan spirit, raki, left...*

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