

## Dream islands and island dreams

Alessandro Minelli

Department of Biology, University of Padova, Via Ugo Bassi 58 B, I 35131 Padova, Italy; email: alessandro.minelli@unipd.it

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**ABSTRACT** The contribution to the development of biogeography and evolutionary biology offered by investigations on insular floras and faunas is briefly reviewed. Implications of the dynamic nature of insular biota for faunistic and floristic research are stressed.

**KEY WORDS** allopatric speciation; chronogeonomy; dispersal; island biota; vicariance.

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### EXPLORING ISLANDS

Ever since Darwin visited the Galapagos Islands in 1835, the study of insular biotas has offered factual evidence of critical importance for the development of evolutionary biology (e.g., Grant, 1998), but also unparalleled contributions to biogeography (e.g., Carlquist, 1966). This is especially true of the oceanic islands, with the Hawaiian archipelago eventually becoming a cherished treasure trove for naturalists and population geneticists alike, ready to spend their lives studying the archipelago's hundreds of *Drosophila* Fallén, 1823 species, or to document distribution and interrelationships of the amazingly diverse tree-dwelling snails of the genus *Achatinella* Swainson, 1828 (Cook & Kondo, 1960), or to reconstruct the evolutionary history of the endemic, nectar-feeding drepanid birds. A jump across the Pacific brings us to Moorea, and to the local *Partula* Férussac, 1821 snails, another group of land gastropods that features among the most popular taxa in evolutionary biology since Crampton's (1916, 1925, 1932) classical investigations.

Several monographic studies of insular biota are by now classics of evolutionary biology and/or biogeography. A very short, selective list includes Alfred Russell Wallace's *Island Life* (1880), Henry

Brougham Guppy's (1906) monograph on plant dispersal across the Pacific, the books on the Galapagos' Darwin finches by David Lambert Lack (1945, 1947) and Peter R. Grant (1986), and Sherwin Carlquist's comprehensive books (1965, 1974, 1980) on the origin and adaptations of insular plants and animals.

Naturalists' fascination with insular biota helps understanding the prominent role long acknowledged in biogeography to long-distance dispersal in explaining distributions.

Dispersalist interpretations have been extensively challenged in the last few decades, since the advent of the vicariance models of a new biogeography rooted in cladistics, beginning with Brundin's (1966) long essay on transantarctic relationships; for classic reference texts on vicariance biogeography, see Nelson & Platnick (1981), Nelson & Rosen (1981) and Humphries & Parenti (1986); for a comparative perspective on biogeographic models based on vicariance vs. dispersal, see Morrone & Crisci (1995).

Vicariance models have their obvious merits when applied to continental biotas. However, when investigating the origin of insular faunas and floras, the traditional interpretations based on dispersal still deserve consideration. Still of interest are a few

classical works on land molluscs of the Pacific area, such as Vagvolgyi (1975), as well as others devoted to land plants (e.g., Fosberg, 1948, 1956, 1963) or insects (e.g., Zimmermann, 1948; Gressitt, 1956, 1961; Gressitt & Yoshimoto, 1963).

### CONCEPTUAL MODELS

Since Darwin (1859), the study of insular biota has offered precious examples of the evolutionary scenario currently known as allopatric speciation (Mayr, 1942; White, 1978; Coyne & Orr, 2004; Grant & Grant, 2008), but has also stimulated the formulation of other important concepts in evolutionary biology, as the founder effect (Mayr, 1942; see also Barton & Charlesworth, 1984) or, more recently, the perhaps less popular notion of taxon cycle (Wilson, 1959, 1961; see also Ricklefs, 1970; Whittaker, 1998; Ricklefs & Bermingham, 1999). As defined by Ricklefs & Bermingham (2002), “taxon cycles are sequential phases of expansion and contraction of the ranges of species, associated generally with shifts in ecological distribution. The important contribution of the taxon cycle to biogeographical analysis is its emphasis on evolutionary and ecological interactions among colonizing and resident species, which influence their extinction dynamics and establish patterns of geographical distribution. Taxon cycles were inferred originally from the distribution of species across island archipelagos, where a correlation was noted between gaps in island occupancy and the degree of phenotypic differentiation. This pattern implied that phases of colonization were followed by range contraction.”

This concept offers a bridge between evolutionary biology and biogeography. Within the latter, however, the single most important contribution offered by the study of insular biota has been the development of the theoretical models of insular biogeography (McArthur & Wilson, 1963, 1967; Wilson, 1969), by which the species composition of insular biota is explained in terms of combined dynamics of colonization and extinction.

### EXPERIMENTAL MODELS

The quantitative nature of MacArthur and Wilson’s models invited soon to test them experimentally.

A first test was performed on a set of very small and low islands off the coast of Florida. Here, the existing fauna was carefully inventoried, then it was completely eliminated by fumigation, thus setting time to zero before starting to record (re)colonization and survival/extinction dynamics (Simberloff, 1969; Simberloff & Wilson, 1969, 1970; Wilson & Simberloff, 1969). It is fair to remember, however, that Nature had already offered a broadly similar opportunity on a grand scale, when the island of Krakatau was the theatre of the famous dramatic explosion (1883) that annihilated most if not all of its original biota. Unfortunately, the local fauna and flora had not been inventoried before the explosion. However, subsequent recolonization was studied over about one century and has been eventually documented and discussed in important monographs (Docters van Leeuwen, 1936; Dammerman, 1948; Whittaker et al., 1989; Thornton, 1996).

### ISLAND AS METAPHORE

In geography, an island is a piece of land surrounded by water. In ecology, however, there are many units that deserve to be called islands because of the sharp boundaries that delimit them in respect to a radically different surrounding landscape, where the inhabitants of the ‘ecological island’ could not survive permanently. Thus, islands are bare mountaintops separated from the nearest mountaintops by green and perhaps forested valleys. Ecological islands are crater lakes fully lacking connection to other water bodies. To some extent, caves are also a kind of islands, although their actual limits do not coincide, as a rule, with the spaces potentially accessible to exploration by humans, because of more or less extensive interstitial spaces that may represent inhabitable corridors for the subterranean fauna.

Discussing the mammalian faunas of mountaintops, Brown (1971) characterized these as true relicts, rather than biota materializing equilibria between rates of colonization and extinction, as predicted by MacArthur and Wilson’s model of insular biogeography. In the same years, however, the potential usefulness of this model in describing the biota of ecological islands was demonstrated by Culver (1970) for subterranean aquatic arthropods and by Vuilleumier (1970) for the birds communities inhabiting the isolated paramos of the Northern Andes.

The 'splendid isolation' (to use the words adopted by Simpson (1980) in reconstructing the history of long separation and recent temporary interchange between the North American and South American faunas) of several faunistically rich lakes has been long studied, revealing strict parallels with the evolution of the faunas (and, to a more limited extent, the floras) of larger islands such as New Caledonia (Chazeau 1993; Morat, 1993) or Madagascar (Goodman & Benstead, 2003). Let's just mention Lake Baikal (Kozhov, 1963), with its unique diversity ranging over fishes, snails, amphipods, planarians and other groups, and the great African lakes (Victoria, Malawi, Tanganyika), whose huge cohorts of cichlid fishes have offered some of the most extensively investigated histories in speciation (see Goldschmidt, 1996 for a popular account on Lake Victoria cichlids, under the significant title of Darwin's dreampond). Similarly, extensive karstic areas such as those accompanying the Southern margin of the Alps (in turn, part of a more extensive system ranging from the Pyrenees to the mountains of Anatolia) hosts a huge number of strictly localized species of subterranean arthropods (especially carabids and cholevid beetles among the terrestrial forms, and amphipods among the aquatic ones) comparable to the multiplicity of single-island endemics found e.g. in the Hawaiian archipelago. One more example of 'insular' fragmentation of a lineage in a continental setting is offered from single-mountaintop endemics such as the numerous camaenid snails distributed on mountain ranges of South-Eastern Australia (Smith, 1984).

A very peculiar way to use the metaphor of the ecological island is its application to host-parasite relationships (Brooks, 1979), where parasites (or parasitoids) are described as potential colonizers of 'islands' represented by the available host species, on each of which the colonizer may eventually survive, more or less permanently, or go rapidly extinct.

### WHY ARE ISLAND A NATURALIST'S DREAM MODELS?

The most remote oceanic islands are at the same time a cherished subject of everyman's dreams, and exemplary locations where to study speciation and dispersal.

However, if on the emotional level the attractiveness of islands is fundamentally dependent on the adventurous journey we must undertake before putting our foot on them, an island's attractiveness for the biogeographer or the evolutionary biologist lies foremost in its clearcut physical boundaries.

Narrow straits between selected islands have allowed biogeographers to fix the borderline between the Oriental and the Australian Regions, although without unanimity of consent - the choice being offered including Wallace's line, based on mammals and birds, and placed between Bali and Lombok (Wallace, 1876), and the more eastward traced lines of Weber and Lydekker (cf. Mayr, 1944; van Steenis, 1950; Whitmore, 1981).

Having precise boundaries means also that we can precisely determine an island's distance from other islands, or from the nearest continent - basic parameters in MacArthur and Wilson's model. Good for biology - in so far as using number means scientific, modern, safe.

### FROM DREAM TO REAL LIFE

Remote islands, however, are difficult targets for potential colonizers. With increasing distance from a potential source (a continent, or another island), the process of colonization goes on progressively slower, thus offering limited chance to compensate for extinction. On the other hand, extinction is always happening, especially on small islands, where it may be difficult for many animals and plants to maintain a population of viable size. The problem may become especially acute for species that have developed the prima facie paradoxical syndrome of insular gigantism. Among animals, this is exemplified by the huge tortoises of Aldabra and the Galapagos. More numerous examples are offered by plants, where several genera represented on continents by small herbaceous species have evolved giant, woody representatives on several archipelagos. There are many examples among the Asteraceae (Hemsley, 1885; Carlquist, 1974, 1980), e.g. *Bidens* Linnaeus, 1753 with giant species in Southern Polynesia, a phenomenon also found in some *Senecio* Linnaeus, 1753 of New Zealand, and some *Centaurea* Linnaeus, 1753 of the Canary Islands, not to mention the extraordinary Hawaiian composites traditionally classified

in the genus *Wilkesia* A. Gray, 1852 and *Argyroxiphium* DC, 1836 (Keck, 1936; Carlquist, 1980). Further examples are provided e.g. by *Echium* Linnaeus, 1753 (Boraginaceae) and *Euphorbia* Linnaeus, 1753 (Euphorbiaceae) in Madeira, the Canary Islands and the Cape Verde Islands.

Additionally, an island's very existence is also to some extent precarious. The Hawaiian archipelago provides a dramatic example of the regular cycle through which individual volcanic islands first emerge from the sea, then grow through repeated eruptions but eventually lose connection to the deep magmatic channels and start being demolished, reducing to small emerged rocks to be eventually cancelled from the world's list of islands.

There is no need to offer detail about the devastating consequences on insular biotas, of oceanic islands especially, of human temporary or permanent settlement, with the accompanying introduction of exotic animals and plants. With the arrival of man, the faunistic and floristic history of islands turns soon into a history of extinctions. Islands feature very prominently indeed in all surveys on plant and especially animal extinctions in historical times (for a summary, see Balouet, 1990; worth reading is still Greenway's (1956) old, but exemplary monograph on the extinct birds of the world), as well as in the major works on introduced species (for example, Long's (1981, 2003) monographs, on introduced birds and mammals, respectively). Alcover et al. (1998) calculated that the arrival of humans is directly or indirectly responsible for the extinction of at least 27% of autochthonous mammal species that evolved on the world's oceanic and oceanic-like islands, a percentage rising to 35% when flying mammals are excluded.

As a consequence of their intrinsic fragility, insular biota deserve special priorities in conservation planning (Diamond, 1975).

There are interesting lessons to be learned from these dramatic stories at global level - lessons, indeed, that should inform the biogeographer in his/her daily work at documenting and interpreting species distributions. The core lesson is, that local species composition may change at a pace we cannot ignore. The list of all plant or bird species recorded for a given area over one century may not correspond to that area's actual flora or avifauna at any time. You can not (or should not) imagine an ecological network involving all those spe-

cies - they have never been all together in the area you are investigating, and quite probably will never be in the future. Geographic precision in recording findings is certainly precious, but it may be inadequate, if the spatial information is not accompanied by the record's date. Distribution maps ignoring time of recorded presences must be replaced by chronogeonomies (Brandmayr et al., 2006). The amazing turnover in the beetle fauna recorded over just fifteen years by Owen (1991) in her garden in Cambridge may well serve as a warning against the ecological implausibility of total species lists for an island, be it geographical or ecological, accumulated through decades of observations.

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