
INVITED REVIEW

Darwin on island plants

SHERWIN CARLQUIST FLS*

Santa Barbara Botanic Garden, 1212 Mission Canyon Road, Santa Barbara, CA 93105, USA

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Islands played a key role in Charles Darwin's observations and experiments on plant dispersal. By means of these experiments, he expunged the old idea that a given species could originate at multiple times and in multiple places. More importantly, by seeing the capabilities for dispersal of plant seeds, fruits and branches, he was able to develop ideas of how plants reach islands and thus he is one of the founders of plant biogeography. For facts regarding floristic distribution of plants, Darwin relied on other workers, most notably Sir Joseph Dalton Hooker. Among his insights were the differences between oceanic and continental islands on a floristic basis, ideas on how age of island and distance from mainland areas influenced composition of island floras, the nature of endemism on islands and the role islands and archipelagos served as stepping stones in dispersal. Ingenious at proposing hypotheses, but always respectful of facts, Darwin sought explanations for plant adaptations on islands at a time when knowledge of island botany was little more than floristic in nature. These explanations are compared with selected recent works in island botany. © 2009 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2009, 161, 20–25.

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One could make a case that Darwin's contributions to botany concerned mostly phenomena other than those found on islands. His books on insectivorous plants, orchid pollination and movements in plants derive from the later portion of his life, not from his years aboard HMS Beagle, during which he visited islands. In fact, Darwin had little preparation for field botany at that time. He commented (1845), regarding plant endemism in the Galápagos:

'... thus, *Scalesia*, a remarkable arborescent genus of the Compositae, is confined to the archipelago: it has six species: one from Chatham, one from Albermarle, one from Charles Island, two from James Island... Again, *Euphorbia*, a mundane [= cosmopolitan] and widely distributed genus, has here eight species, of which seven are confined to the archipelago, and not one found on any two islands: *Acalypha* and *Borreria*, both mundane genera, have respectively six and seven species, none of which have the same species on two islands, with the exception of one *Borreria*, which does occur

on two islands. The species of the Compositae are particularly local.'

The observations are based on identifications by Sir Joseph Dalton Hooker, noted Kew botanist on whose expertise in insular (and continental) floras Darwin relied heavily. In fact, one can congratulate Darwin on the wisdom of using Hooker as a resource rather than trying to train himself into a self-sufficient plant taxonomist. Darwin's specimens from the Beagle voyage were examined by specialists and Darwin, writing in the preface to the (1845) *Journal of Researches*, some years after the Beagle returned to England (2 October 1836) cited the usefulness of Hooker's (1847a, b) work on the flora of the Galápagos Islands. The relative paucity and openness of the Galápagos flora permitted Darwin to collect a significant portion of the Galápagos flora, from which some conclusions could readily be drawn.

By contrast, complex floras baffled Darwin. Such was the case with the flora of south-western Australia, which today is regarded as a wonderfully rich floristic island-like area within Australia, showing

*Corresponding author. E-mail: s.carlquist@verizon.net

insular evolutionary tendencies magnificently (Carlquist, 1974). Darwin's visit to King George's Sound (today, the coast near Albany and vicinity) during a season favourable for seeing at least moderate flowering in the area is noteworthy:

'February 7th. – The Beagle sailed from Tasmania, and on the 6th of the ensuing month, reached King George's Sound, situated close to the S. W. corner of Australia. We stayed there eight days, and we did not during our voyage pass a more dull and uninteresting time. The country, viewed from an eminence, appears a woody plain, with here and there rounded and partly bare hills of granite protruding. One day I went out with a party, in the hopes of seeing a kangaroo hunt, and walked over a good many miles of country. Everywhere we found the soil sandy, and very poor; it supported either a coarse vegetation of thin, low brushwood and wiry grass, or a forest of stunted trees. The scenery resembled that of the high sandstone platform of the Blue Mountains [near Sydney, eastern Australia]; the Casuarina (a tree somewhat resembling a Scotch fir) is, however, here in greater number, and the Eucalyptus in rather less. In the open parts there were many grass-trees [*Xanthorrhoea* Sm.], – a plant which, in appearance, has some affinity with the palm; but instead of being surmounted by a crown of noble fronds, it can boast merely a tuft of very coarse grass-like leaves. The general bright colour of the brushwood and other plants, viewed from a distance, seemed to promise fertility. A single walk, however, was enough to dispel any such illusion; and he who thinks with me will never wish to walk again in so uninviting a country.'

Ironically, a south-western Australian genus of Myrtaceae named for Darwin's grandfather Erasmus Darwin, *Darwinia* Rudge, is rich in evolutionary phenomena like those of islands: endemism to mountain tops, shift in pollination modes, loss of dispersibility in seeds (Carlquist, 1974).

We see, then, the value of floristic simplicity where only a brief visit is possible. We also are witnessing the limitations faced by a single naturalist to any given area during the early stages of biological exploration. The timing of the Beagle voyage coincided with post-colonization interest in scientific exploration. Not surprisingly, the animals of regions new to European biologists were more striking to them than the plants. However, ease of collection made plants easy objects for attention by field naturalists of the era and, if the appeal of animals motivated visits by naturalists more strongly, plants were not neglected and knowledge of plants grew accordingly.

DECODING DISPERSAL

Study of how plants might have arrived on islands was one of Darwin's great contributions to island biology. The pages devoted to 'Means of Dispersal' in *Origin of Species* were a crucial advance in our understanding of island biogeography. Surprisingly, a major

reason for these studies was Darwin's desire to disprove the idea, commonly believed by Gmelin and others in the 18th century, that 'the same species must have been independently created at many distinct points.' Dispersal, Darwin rightly reasoned, must be effective if a particular species arose only once in time and space and was able to reach remote localities such as islands. Islands provided the critical case: dispersal to oceanic islands had to be explained.

Darwin even had a perception of islands changing over time with respect to dispersal:

'I freely admit the former existence of many islands, now buried beneath the sea, which may have served as halting places for plants and for many animals during their migration.'

The demonstration that islands have been not merely target areas for dispersal, but also stepping stones ['halting places'] in its progress has, in fact, been demonstrated clearly for plants only recently (e.g. Harbaugh *et al.*, 2009).

In Darwin's time, original results were commonly reported in book form. This practice has now all but vanished, unfortunately. With shift to papers as a way of scientific reportage, we have lost the feeling that the writer of a book is an investigative scientist and an original observer. A book writer who reports original work shows how science works and retains continuity between context, discovery and conclusion. Darwin (1859) undertook seed, fruit and branch flotation experiments. He found that some seeds could germinate after exposure to saltwater, although many could not. He reported that certain small seeds (Hydrophyllaceae and Polemoniaceae) did not float, so that they 'could not have been floated across wide spaces of the sea.' He noticed that dried seeds and fruits floated better than green ones. Perceptively, he showed that 'dried plants bearing fruits could float even if the seeds themselves would not.' He notes that:

'Altogether, out of the 94 dried plants, 18 floated for above 28 days; and some of the 18 floated for a very much longer period. So that as 64/87 kinds of seeds germinated after an immersion of 28 days; and as 18/94 distinct species with ripe fruit (but not all of the same species as in the foregoing experiment) floated, after being dried, for above 28 days, we may conclude, as far as anything may be inferred from these scanty facts, that the seeds of 14/100 kinds of plants of any country might be floated by sea currents during 28 days, and would retain their power of germination.'

Dispersal of fruits and seeds by seawater flotation is often imagined by those less well acquainted with dispersal on a world basis to account for transport from continents to islands. In fact, seawater flotation accounts for dispersal of little more than coastal plants of islands (Carlquist, 1967). Although perhaps only dimly aware of this because of his limited

floristic points of reference, Darwin nevertheless saw that transportation of seeds by birds accounted for a large proportion of long-distance plant dispersal:

'Living birds can hardly fail to be highly effective agents in the transportation of seeds. I could give many facts showing how frequently birds of many kinds are blown by gales to vast distances across the ocean. We may I think safely assume that under such circumstances their rate of flight would often be 35 miles an hour, and some authors have given a far higher estimate. I have never seen an instance of nutritious seeds [e.g. grasses] passing through the intestines of a bird; but hard seeds of fruit will pass uninjured through even the digestive organs of a turkey. In the course of two months, I picked up in my garden 12 kinds of seeds, out of the excrement of small birds, and these seemed perfect, and some of them, which I tried, germinated. But the following fact is more important: the crops of birds do not secrete gastric juice, and do not injure in the least, as I know by trial, the germination of seeds; now, after a bird has found and devoured a large supply of food, it is positively asserted that all the grains do not pass into the gizzard for 12 or even 18 hours. A bird in this interval might easily be blown to the distance of 500 miles . . .'

Such experiments have been bettered only recently by such workers as Proctor (1968), who worked with a shore bird (killdeer) known to migrate over long distances. Actually, marine and shore birds can serve for intercontinental dispersal (Carlquist, 1983) if their migratory routes follow a route between continents. The Pacific Flyway thus accounts for disjunctions in plant distributions between Chile and California (see Constance, 1963; Raven, 1963). Darwin was unaware of such patterns, which during his times had not been highlighted, and thus was sceptical that they existed:

'These means, however, would suffice for occasional transport across tracts of sea some hundred miles in breadth, or from island to island, or from a continent to a neighbouring island, but not from one continent to another.'

Scepticism or disbelief about intercontinental over-water dispersal persisted until recent times and was a fiercely held tenet of the early proponents of vicariance biogeography (Rosen, 1978). Vicariance biogeographers wished to incorporate knowledge about tectonic plate movement into biogeography. By seeking methodological precision, they were forced to exclude events of chance dispersal which would confuse distributional patterns or 'tracks' (Rosen, 1978). In order to establish vicariance biogeography, the early workers in that field were forced to deny that chance dispersal plays any appreciable role in biogeography. In Rosen's time, molecular-based phylogenetic trees were not available. However, molecular-based phylogenies (when overlain by geographical distributions) now clearly show examples of the existence of intercontinental dispersal and long-

distance dispersal (e.g. Morrell, Porter & Friar, 2000; Coleman *et al.*, 2003; Simpson *et al.*, 2004; Martin-Bravo, Vargas & Luceno, 2009).

Dispersal externally on bird surfaces (a form of exozoochory) is a plausible example of long-distance dispersal and such examples were eagerly sought by Darwin:

'Prof. Newton sent me the leg of a red-legged partridge (*Cacabis rufa*) which had been wounded and could not fly, with a ball of hard earth adhering to it, and weighing six and a half ounces. The earth had been kept for three years, but when broken, watered, and placed under a bell glass, no less than 82 plants sprung from it: these consisted of 12 monocotyledons, including the common oat, and at least one kind of grass, and of 70 dicotyledons, which consisted, judging from the young leaves, of at least three distinct species. With such facts before us, can there be doubt that the many birds which are annually blown by gales across great spaces of ocean and which annually migrate – for instance, the millions of quails across the Mediterranean – must occasionally transport a few seeds embedded in dirt adhering to their feet or beaks?'

Darwin's thinking about dispersal extended to differentiating between transport and establishment. He keenly saw that establishment of a species in a new habitat requires equivalency in ecology between the source area and the target area and that timing of an arrival is critical because of the potential presence of competitors or predators:

'Out of a hundred kinds of seeds or animals transported to an island . . . perhaps not more than one would be so well fitted to its home as to become naturalised. But this is no valid argument against what would be effected by occasional means of transport, during the long lapse of geological time, whilst the island was being upheaved, and before it had become fully stocked with inhabitants. On almost bare land, with few or no destructive insects or birds living there, nearly every seed which chanced to arrive, if fitted for the climate, would germinate or survive.'

BIOGEOGRAPHIC BEGINNINGS

Darwin has some claims to beginning the field of plant biogeography, just as does Alfred Russel Wallace, whose faunistic comparisons ('Wallace's Line') are seminal in the field. Many others could be cited, as could many points of origin for particular ideas. Wallace had, of course, personally seen faunistic differences first-hand. Darwin, at the mercy of the Beagle's itinerary for his information, was more limited in his comparisons. However, Darwin did derive comparisons of island regions from the floristic work of leading botanists, especially Hooker. The basis for biogeography is not sudden insight, but slow accumulation of floristic, faunistic and geological informa-

tion. Not surprisingly, Darwin's observations where plants are concerned include the Galápagos Islands:

'Dr. Hooker has shown that in the Galápagos Islands the proportional number of the different orders are very different from what they are elsewhere. All such differences in number, and the absence of certain whole groups of animals and plants, are generally accounted for by supposed differences in the physical conditions of the islands; but this explanation is not a little doubtful. Facility of immigration seems to have been fully as important as the nature of the conditions.'

Darwin is correct in saying that absence of groups by virtue of lack of suitable habitats is 'doubtful.' Absence can be because of low dispersal capability, as with conifers, notably absent on oceanic islands. Animals are cited by Darwin ('New Zealand gigantic wingless birds') more often than plants, perhaps a nod to readers whose familiarity with kinds of plants, then as now, is not as great as their knowledge of animals.

The difference between continental and oceanic islands is already becoming evident: 'Although New Zealand is here spoken of as an oceanic island, it is in some degree whether it should be so ranked; it is of large size and not separated from Australia by a profoundly deep sea.' Darwin favoured thinking of New Zealand and New Caledonia as 'appurtenances of Australia.' Both of these are now considered continental islands with links to Australia in pre-marsupial time, as evidenced by the conifers they share (*Agathis* Salisb., *Araucaria* Juss.).

Darwin's well-known work on volcanic islands and their conversion into atolls (1845) shows that he was making a distinction between oceanic and continental islands. He lacked only the lists of plant and animal families on particular oceanic and continental islands in order to certify the difference. The age of exploration, limited by the capacities of sailing ships, did not yet permit Darwin to compare the floras of oceanic and continental islands adequately. Amazingly, Darwin did recognize that mountain tops could be biogeographically insular (1859): 'Mountains are islands on the land. . . .'

Collections by Darwin and others were sufficient, however, for instances of endemism to be identified in the Galápagos flora. He even cited (1845) in tabular form, an analysis of Fabaceae in which he listed the number of species that were confined to one island, confined to the archipelago etc. In the *Journal of Researches* (1845), Darwin attributed differences in restriction of species to the action of ocean currents and separations by ocean depths. Later, in *Origin of Species* (1859), Darwin was able to see the mutability of species as a cause for endemism:

'... species occasionally having to arrive after long intervals in the new and isolated district, and having to compete with

new associates, would be eminently liable to modification, and would often produce groups of modified descendents.'

This remains adequate as a blanket statement, amazing for its time although necessarily vague. The tabulation of endemic plant species in the Galápagos is essentially the first expression of quantitative biogeography, making later contributions, such as that of MacArthur & Wilson (1968), seem almost inevitable sequiturs.

AVENUES OF ADAPTATION

Once the process of evolutionary change had been proposed by Darwin, he tirelessly sought examples of its workings. One of the fascinating concepts we owe to Darwin was the idea of secondary woodiness in island plants (1859):

'Again, islands often possess trees or bushes belonging to orders which elsewhere include only herbaceous species; now trees, as Alph. de Candolle has shown, generally have, whatever the cause may be, confined ranges. Hence trees would be little likely to reach distance oceanic islands, and an herbaceous plant, which had no chance of successfully competing with the many fully developed trees growing on a continent might, when established on an island, gain an advantage over other herbaceous plants by growing taller and taller and overtopping them. In this case, natural selection would tend to add to the stature of the plant, to whatever order it belonged, and thus first convert it into a bush and then into a tree.'

Darwin was certainly right about the phenomenon of secondary woodiness. That in itself is rather amazing, considering that secondary woodiness, although demonstrated for particular groups on the Canary Islands and Madeira (Carlquist, 1970a, b, 1974), was discounted or denied even in recent times (Bramwell, 1972; Sunding, 1979; Cronk, 1992). The existence of secondary woodiness on insular areas was, in fact, obvious in Macaronesia, although most clearly visible in the Hawaiian flora (Carlquist, 1974; Carlquist, Baldwin & Carr, 2003), as demonstrated by multiple types of evidence. The Hawaiian flora was neglected by European workers, but is, in fact, the ultimate proving ground for evolutionary processes on oceanic islands. Secondary woodiness in the Canarian and Madeiran floras has now been established on the basis of DNA-based phylogenetic analyses for such genera as *Echium* L. (Kim *et al.*, 1996) and *Sonchus* L. (Böhle, Hilger & Martin, 1996).

Loss of dispersibility was noted by Darwin for island beetles (1859):

'Many remarkable little facts could be given with respect to the inhabitants of oceanic islands. For instance, in certain islands not tenanted by a single mammal, some of the endemic plants have beautifully hooked seeds; yet few relations are

more manifest than that hooks serve for the transportal of seeds in the wool or fur of quadruped. But a hooked seed might be carried to an island by other means; and the plant then becoming modified would form an endemic species, still retaining its hooks, which would form useless appendages like the shrivelled wings under the soldered wing covers of many insular beetles.'

Beetles do lose flight on islands, but perhaps often not for the reason Darwin suggested (beetles that do not use their wings 'will have had the best chance of surviving from not being blown out to sea'). Zimmerman (1948) found that many beetles inhabit under-story habitats in leaf litter and other places where wind was unlikely to be a factor. Zimmerman cited, instead, a tendency for a beetle to remain confined to an ecologically suitable habitat and for wings to vanish as flight (an energy-intensive activity) is no longer necessary for feeding or for evasion of predators. Darwin did apparently see some possible loss of wind dispersal in island plant species (letter to J. D. Hooker, 7 March 1855). Loss of dispersibility is wonderfully manifest in the Pacific species of *Bidens* L. (Carlquist, 1966a), where loss of awns and of stiff hairs likely to catch on feathers is evident as species change ecological preferences and adapt to inland sites. The Hawaiian flora as a whole contains numerous good examples of loss of dispersibility (Carlquist, 1966b). Recently, loss of dispersibility (reduction of the pappus on achenes of Asteraceae) has been shown by Cody & Overton (1996) in *Hypochaeris* L. and *Lactuca* L. (Asteraceae) in a matter of a few generations on off-shore islets. Darwin was unaware of the many examples, which would, in fact, have reinforced his ideas. Plant seeds and fruits carried by means of hooks, barbs and bristles on quadruped fur on mainland areas reach oceanic islands and tend to disperse within islands on bird feathers, a fact hinted by Darwin ('... carried to an island by other means . . .'), who was familiar with dispersal on continental areas but did not have a chance to see the most pertinent island floras.

Interestingly, the adaptive aspects of the Darwin's finches were appreciated only when his collections were assembled in England. At that point, the fact that these diverse birds all belonged to one family became evident, and notes on their habits made in the field could be correlated with bill shapes and sizes as well as other features. The relative simplicity of the Galápagos flora and fauna placed these adaptations in relief. Darwin was on shore on the Galápagos Islands long enough to make observations that would not have been possible on quick day trips to one or two of the islands.

The underlying point here that the Beagle voyage shows us is the importance of field work and observations made over a sufficient period of time. Natural habitats are the testing grounds for adaptive radiation and, while that phenomenon became evident with

respect to the Darwin's finches, it could not be demonstrated on the basis of the island plants collected on the Beagle voyage. There is too narrow a range in ecological diversity (e.g. temperature and rainfall gradients) to have fostered much adaptive radiation in Galápagos plants. Such phenomena would have been better illustrated on the Canary Islands (which the Beagle did visit, but landing of the ship's party was forbidden because of a quarantine at the time). Adaptive evolutionary diversification within the Hawaiian flora is bewilderingly rich. It could be appreciated only in the days following Hillebrand's (1888) flora. The appreciation of plant adaptive radiation had to wait for the production of such floras and these, in turn, were dependent on maturation of the age of biological exploration. During the years when visits by sailing vessels were the predominant mode of transportation, true acquaintanceship with adaptive radiation in island plants was not possible. Easier access to islands by airplanes, and travel within them by automobiles, led to the kinds of observation that floristic books and papers do not (and cannot, by their nature) offer. When species of a plant group which has diversified on an island or archipelagic area can be compared in the field with each other and with their habitats, and when experimental and observational work can be carried out on them in laboratories, the full range of patterns becomes evident. For example, the fact that the silver-sword complex (*Argyroxiphium* DC. and allies) in the Hawaiian Islands represents an example of adaptive radiation *par excellence*, exceeding even the Darwin's finches, remained unappreciated until relatively recently (Carlquist *et al.*, 2003).

CONTEXTS OF ISLAND PLANT DISCOVERIES

Each period of science brings its own discoveries but also suffers from its own limitations of technique and information. The efforts of scientists at any one time are often directed toward transcending concepts by adept study and acute insight into what can be uncovered in a given period of time. In terms of technique, Darwin's accomplishments were relatively simple, but direct observation without complex optical equipment can still yield much today. For example, loss of dispersibility in fruits of island Asteraceae was not described until a century after *Origin of Species* (Carlquist, 1966a) and another 30 years transpired before experimental work demonstrated such changes over time (Cody & Overton, 1996). Conceptually, Darwin went well beyond the thinking of his time, by fitting plants, animals and geological history into the overarching concepts of mutability of species. His concepts reached the limits of what could be hypothesized

without knowledge of genetics, cytogenetics and gene action and without instrumentation unavailable in Darwin's time. One should not regard Darwin's ideas as limited by the technical advances of the time: in fact, all periods of science must operate within technical limitations. What is consistently amazing when one reads *Voyage of Researches* (1945) and *Origin of Species* (1869) is Darwin's daring and willingness to go beyond his fellow scientists in formulating hypotheses about how dispersal took plants to islands and how they changed after their arrival. In retrospect, we revere these insights as hypotheses, although similar thoughts today are all too often branded as speculations by scientists who value safety more than progress. Not all of the hypotheses in *Origin of Species* are unflawed, but that surely is one of the strengths of that book: it exemplifies broad vision and venture, qualities always uncommon and always welcome in the science of any time.

REFERENCES

- Bramwell D. 1972.** Endemism in the flora of the Canary Islands. In: Valentine DH, ed. *Taxonomy, phytogeography, and evolution*. London: Academic Press, 141–159.
- Böhle U-R, Hilger HH, Martin WF. 1996.** Island colonization and evolution of the insular woody habit in *Echium* l. (Boraginaceae). *Proceedings of the National Academy of Sciences of the USA* **93**: 11740–11745.
- Carlquist S. 1966a.** The biota of long-distance dispersal. II. Loss of dispersibility in Pacific Compositae. *Evolution* **20**: 30–48.
- Carlquist S. 1966b.** The biota of long-distance dispersal III. Loss of dispersibility in the Hawaiian flora. *Brittonia* **18**: 310–335.
- Carlquist S. 1967.** The biota of long-distance dispersal. IV. Plant dispersal to Pacific islands. *Bulletin of the Torrey Botanical Club* **94**: 129–162.
- Carlquist S. 1970a.** Wood anatomy of *Echium* (Boraginaceae). *Aliso* **7**: 183–199.
- Carlquist S. 1970b.** Wood anatomy of insular species of *Plantago* and the problem of insular woodiness. *Bulletin of the Torrey Botanical Club* **97**: 353–361.
- Carlquist S. 1974.** *Island biology*. New York: Columbia University Press.
- Carlquist S. 1983.** Intercontinental dispersal. *Sonderband der Naturwissenschaftliche Verhandlungen Hamburg* **7**: 37–47.
- Carlquist S, Baldwin BG, Carr GD, eds. 2003.** *Tarweeds and silverswords. Evolution of the madinae (Asteraceae)*. St. Louis, MO: Missouri Botanical Garden Press.
- Cody ML, Overton JM. 1996.** Short-term evolution of reduced dispersal in island plant populations. *Journal of Ecology* **84**: 53–61.
- Coleman M, Liston A, Kadereit JW, Abbott RJ. 2003.** Repeat intercontinental dispersal and Pleistocene speciation in disjunct Mediterranean and desert *Senecio* (Asteraceae). *American Journal of Botany* **90**: 1446–1454.
- Constance L. 1963.** Amphitropical relationships in the herbaceous flora of the Pacific Coast of North and South America: a symposium. Introduction. *Quarterly Review of Biology* **38**: 109–116.
- Cronk QCB. 1992.** Relict floras of Atlantic islands. *Biological Journal of the Linnean Society* **46**: 91–103.
- Darwin C. 1845.** *Journal of researches into the natural history and geology of the countries visited during the voyage of H.M.S. Beagle round the world*. Ed. 2. Reprint edition. New York: The Modern Library.
- Darwin C. 1859.** *The origin of species*. Reprint edition. New York: Random House.
- Harbaugh D, Wagner WL, Allan GJ, Zimmer EA. 2009.** The Hawaiian archipelago is a stepping stone for dispersal in the Pacifica: an example from the genus *Melicope* (Rutaceae). *Journal of Biogeography* **36**: 230–241.
- Hillebrand W. 1888.** *Flora of the Hawaiian Islands*. London: Williams and Norgate.
- Hooker JD. 1847a.** An enumeration of the plants of the Galapagos Islands with descriptions of those which are new. *Transactions of the Linnean Society* **20**: 163–233.
- Hooker JD. 1847b.** On the vegetation of the Galapagos Islands as compared with that of some other tropical islands of the continent of America. *Transactions of the Linnean Society* **20**: 235–262.
- Kim S-C, Crawford DJ, Francisco-Ortega J, Santos-Guerra A. 1996.** A common origin for woody *Sonchus* and five related genera in the Macaronesian islands: Molecular evidence for extensive radiation. *Proceedings of the National Academy of Sciences of the USA* **93**: 7743–7748.
- MacArthur RH, Wilson EO. 1968.** *The theory of island biogeography*. Princeton, NJ: Princeton University Press.
- Martin-Bravo S, Vargas P, Luceno M. 2009.** Is *Oligomeris* (Resedaceae) indigenous to North America? Molecular evidence for a natural colonization from the Old World. *American Journal of Botany* **96**: 507–518.
- Morrell P, Porter JH, Friar EA. 2000.** Intercontinental dispersal: the origin of the widespread South American plant species *Gilia laciniata* (Polemoniaceae) from a rare California and Oregon coastal endemic. *Plant Systematics and Evolution* **224**: 13–32.
- Proctor VW. 1968.** Long-distance dispersal of seeds by retention in digestive tract of birds. *Science* **160**: 321–322.
- Raven P. 1963.** Amphitropical relationships in the floras of North and South America. *Quarterly Review of Biology* **38**: 151–177.
- Rosen D. 1978.** Vicariance patterns and historical explanations in biogeography. *Systematic Zoology* **27**: 159–188.
- Simpson BB, Weeks A, Helfgott DM, Larkin LL. 2004.** Species relationships in *Krameria* (Krameriaceae) based on ITS sequences and morphology: implications for character utility and biogeography. *Systematic Botany* **29**: 97–108.
- Sunding P. 1979.** Origins of the Macaronesian flora. In: Bramwell DH, ed. *Plants and islands*. London: Academic Press, 13–40.
- Zimmerman EC. 1948.** *Insects of Hawaii. vol. 1. Introduction*. Honolulu: University of Hawaii Press.