Aliso: A Journal of Systematic and Floristic Botany

Volume 16 | Issue 2 Article 3

1998

Shifting Paradigms in Island Biology

Sherwin Carlquist
Santa Barbara Botanic Garden

Aliso, 16(2), pp. 85–88

SHIFTING PARADIGMS IN ISLAND BIOLOGY

SHERWIN CARLQUIST

Santa Barbara Botanic Garden
1212 Mission Canyon Road
Santa Barbara, CA 93105[1]

ABSTRACT

The ease of travel by jet aircraft has opened up island areas not only for study but also for introduction of weeds, pests, and pathogens. We are at a critical juncture in the study of island organisms, which have become more accessible at the same time that they are vanishing. With the urgency for study of island organisms, we have many new tools, especially molecular ones, which have validated the existence of long-distance dispersal in unexpected ways. These tools, together with the ease of staying for longer periods on islands, have permitted us to understand many aspects of evolutionary adaptation on islands: thus, knowledge of biology of island organisms has been accelerated. From the beginning of the age of exploration to the mid twentieth century, there was a preponderant interest in floristics and faunistics of island organisms, but most workers are now concerned with evolutionary and biogeographical studies. Interest in mathematical models of island organisms, originally a pure science concern, is now applied to conservation problems on islands and islandlike mainland areas. Each organism, however, presents unique conservation problems, some perhaps insoluble, and we must place a higher priority on studying native island species while they are still with us in reasonable abundance.

Key Words: Conservation, island biology, long-distance dispersal.

INTRODUCTION

Over the 50 years since I first became interested in island biology, our knowledge of island biotas has gained more than in the preceding 100 or more years. More importantly, however, there have been numerous shifts in the way we look at plants and animals on islands—changes not just in techniques of study, but in concepts as well. Island plants and animals are in the forefront of our understanding of evolution, providing us with striking materials and examples of how evolution occurs. At the same time, island plants and animals are threatened in a way that could not have been imagined when Darwin visited the Galapagos Islands, and a concerted conservation effort that did not exist 50 years ago has sprung into existence.

If island floras and faunas seemed relatively intact 50 years ago, plants and animals introduced during the age of exploration were already making inroads: some of the races (or species) of Galapagos tortoises and Hawaiian honeycreeper finches were already extinct 50 years ago, and extinctions in dryland Hawaiian plants had already begun well before that because of the spread of introduced vertebrates and insects as well as agricultural use of the land. We could easily have lost many more native species without having acquired much more than museum specimens and not having developed knowledge on these organisms, but our understanding of island organisms has changed because means of travel to islands improved radically within the decades after World War II. Biologists today are the beneficiaries of jet travel, which takes us to many major islands and island groups that were relatively difficult to reach 50 years ago. At the same time, extinction and endangerment of island species, although accelerating, has not moved so far that we have only a few vestiges of interesting island organisms left for study. Peter and Rosemary Grant (e.g., Grant 1986) study natural selection of Darwin's finches on a day-to-day basis on virtually pristine Daphne Major in the Galapagos, a long-term study celebrated in the recent popular book by Weiner (1995), *The Beak of the Finch.* The multiple aspects of adaptive radiation of the Hawaiian silversword complex can be documented by Baldwin and Robichaux (1995) because virtually all of the species of this complex are still alive, although some are currently disappearing or possibly extinct. Accounts such as Baldwin and Robichaux's comprise a book I consider to represent a major advance and landmark in our understanding and synthesizing of island biology, *Hawaiian Biogeography—Evolution on a Hot Spot Archipelago,* edited by Wagner and Funk (1995). Thus, island biologists today live in a unique window in time: they can reach islands readily for study in a time period when island plants and animals are still available. At the risk of being pessimistic, I suspect that the accelerating endangerment of indigenous island species will lead to the extinction of

---

[1] Address for correspondence with author: 4539 Via Huerto, Santa Barbara, CA 93110.

numerous species over the next several decades, and those species that survive in small populations and are carefully protected are likely to become unavailable to the public without special permission. Ironically, the ease of travel to islands that benefits biologists furthers the endangerment of native island organisms.

MATERIALS AND METHODS

One of the interesting shifts in our understanding of island biology has been in demonstrating the role played by long-distance dispersal to oceanic and even to continental islands. We tend to forget that the earliest students of islands believed in the effectiveness of long-distance dispersal. Hooker divided islands into continental and oceanic with remarkable accuracy, thereby setting the stage for acceptance of long-distance dispersal as a means of populating the latter islands. Darwin saw that when the same species occurs on an island and on a mainland area, one has two possibilities: the species has evolved twice independently, or long-distance dispersal has operated. Darwin logically chose the latter as the explanation, and began a tradition that continued until challenged by the methods of vicariance biogeography several decades ago. Adherents of vicariance biogeography doubted or even denied the existence of long-distance dispersal, because such dispersal could only provide a "noise level" that would disturb patterns they developed on the basis of the orderly migrations they envisioned as the result of tectonic events. Some adherents of vicariance biogeography hypothesized now-vanished lands such as a continent, "Pacifica," as a way of explaining distribution patterns in the Pacific, and even at present, some biologists regard the floras and faunas of Atlantic islands as relictual from the early Tertiary rather than the products of dispersal in relatively recent time. The infrequency of successful chance dispersals that lead to endemic species and the difficulty of seeing actual dispersal events of made long-distance dispersal a vulnerable hypothesis, rejected by the more extreme adherents of vicariance biogeography.

Advances in science provide unexpected changes in our thinking. As one such example, the modes of origins of oceanic islands did not become clear until Wegener's theories of continental drift became thoroughly accepted around 1970. The recentness of volcanic islands has become evident only as we developed the potassium-argon ratio method for dating them, and the accuracy of this technique has improved considerably in recent decades. Likewise, the theory of long-distance dispersal to oceanic islands received massive support from study of DNA, which can not only pinpoint source areas from which groups that arrived on islands dispersed, but can yield details of the changes in those groups as they evolved throughout an archipelago. The precision and overwhelming statistical likelihood of interpretations based on analyses of various DNA sites have provided a tool unimaginable in its power only a few years ago, and have inconspicuously supplanted the methodologies of vicariance biogeography as ways of deriving phylogenetic and biogeographic data. These advances, so fascinatingly documented in the book of Wagner and Funk (1995), could not have been imagined even as recently as 20 years ago.

ADAPTATIONS AND EVOLUTIONARY CHANGES

The use of DNA analysis when combined with cladistics based on macromorphology of island organisms offers much more than the identification of geographic origins and phylogenetic trees of island species, and instances of these remarkable byproducts are worth noting. For example, the work on *Schiedea* (Wagner et al., 1995) shows the history of fluctuation of that genus between wet and dry areas and its shifts in sexual conditions. Changes in altitudinal preferences in *Cyanea* of the Lobeliaceae are demonstrated by the cladograms of Givnish et al. (1995). A phylogenetic increase in woodiness in the Hawaiian silversword complex is an inevitable conclusion of the work of Baldwin and Robichaux (1995). Patterson (1995) confirms the hypothesis (Carlquist 1974) that Hawaiian species of *Scaevola* (Goodeniaceae) are derived from more than one event of dispersal to the Hawaiian Islands. In many of the cladograms of the Wagner and Funk (1995) book, we are given insights into the likely site of arrival of dispersing organisms and, because of the sequential nature of island-building in the Hawaiian chain, we are given evidence for the timing of these events. We may soon expect to demonstrate other biological phenomena on islands using the agency of cladograms based on DNA and macromorphology: changes in habit, changes in pollinators, changes in ecological preferences, changes in physiology, and changes in diet in the case of animals. Thus, the value of cladistics as used by the authors in the book of Wagner and Funk (1995) is much more than a construction of trees. To the degree we ask questions about the biology of island organisms depicted in those trees, we will be able to demonstrate with a high degree of statistical likelihood the changing natural history of island organisms. The evolution of organisms on islands, as in organisms on mainland areas, features progressive shifts in adaptations, so we will be able to see, with the new tools at hand, the direction and nature of those shifts. We can liken this to being with Darwin when he looked at the divergent adaptations of the geospizid finches on the Galapagos, and being able to tell him which adaptations preceded which others, and on which islands and when particular shifts in

diets, habitats, colors, sizes, and songs occurred. Interest in adaptations on islands is certainly not new—it is clear in Darwin's *Journal of a Naturalist* and in Wallace's *Island Life* and *The Malay Archipelago*. However, in the decades after the work of Darwin and Wallace, there was primarily an interest in cataloging species on islands. The dominant interest in floristics and faunistics during that period of time derived from the ease of bringing specimens back from islands compared with the difficulty of living on islands long enough to see the nature of adaptations and the likely explanations for them. When I became interested in adaptations in the Hawaiian and other island floras, I found few studies of adaptations of species on islands, and most of such studies, like those of Perkins (1913) and Zimmermann (1948) dealt with animals. The ease of travel to islands and the visits by students interested in phylogenetics of island groups are probably the sources for the development of interest in evolutionary adaptations on islands in recent years.

CONSERVATION

Thus, the paradigm shift offered by the cladistics based on DNA and macromorphology is not just a byproduct of the construction of phylogenetic trees, but the opening of grand vistas of how organisms disperse and evolve. The mathematical models of species numbers on islands and similar phenomena offered by MacArthur and Wilson (1967) have fascinated workers; however, instead of offering insights primarily into biogeography, as suggested in the title of their book, their work now proves to be helpful in developing concepts and strategies for conservation of island organisms. Another unexpected outcome of the concerns of MacArthur and Wilson is the use of their ideas in conservation on mainland areas, not just island areas. Increasingly in today's world, all natural areas **are** islands separated from each other not by water but by disturbed and developed areas. In accordance with their own interests in birds and in insects, MacArthur and Wilson (1967), derived their models from island birds and insects. When applied to mainland areas, these ideas must be altered in order to serve for conservation of groups absent on oceanic islands, such as mammals and conifers. Indeed, we do not yet know with any certainty how much or in what direction to alter their models for the purposes of conservation efforts, although we do know we are dealing with islandlike populations. The idea of a partially intact fringe or boundary zone as a way of protecting an undisturbed natural area is in use today, but is an idea that does not apply to islands separated by water and was thus not conceived by MacArthur and Wilson. Natural areas on islands are now islands within islands, and the concept of a protecting boundary zone applies to island populations as well.

However, conservation of island organisms has aspects that have been realized only recently. When I visited the Hawaiian Islands in the 1950s and 1960s, I talked to the manager of a large parcel of natural forest on the island of Hawaii. The trustees who represented the ownership of this forest wanted the area to yield cash, so they ordered the manager to plant exotic timber trees, although no lumber mills existed and the numbers of trees were likely too small to sustain a lumber mill economically. What if none of these tree species were economically feasible, I asked, wouldn't some of them become weeds and persist, displacing native vegetation? No, there was no chance of that, he stated firmly, they had invited an ecologist from an eastern United States university who told them that native trees always displace introduced species. As anyone who has visited Hawaii knows, that simply is not true. In fact, the new flora of the Hawaiian Islands (Wagner et al. 1990) shows that there are 956 native species of flowering plants and 861 species of naturalized introduced flowering plants. The number of exotics is increasing each year, but, more significantly, the proportion of the landscape occupied by introduced plants is growing, and the weedier of the introduced species are still increasing in areas they occupy. Hawaiian native plants are peculiarly vulnerable because they have not evolved in relation to herbivores or other pests or pathogens present on mainland areas. When exotic species which are capable of naturalizing in Hawaii and which are relatively resistant to mainland herbivores and pathogens are introduced, they outdo many of the Hawaiian native species. How long can native species survive, which can be saved, and which must by default disappear? We now have a new picture of conservation of plants on islands that shows that on some islands, such as the Hawaiian Islands, many plant species may be extremely vulnerable, whereas on other islands, the natives can hold their own much better. And on any given island, there is a range among the native species in resiliency—some natives are quite weedy, other natives are seemingly impossible to save, and many lie somewhere in between. Both the realization that island plants and animals form special cases with respect to conservation and the development of programs that take into account differential survivability of species are relatively new changes in the way we view conservation of island biotas.

OPPORTUNITIES FOR STUDY AND PUBLICITY

Another change in the way we look at islands caused by the endangerment of island floras and faunas is an obvious one: we should study them now, while

many of the native species are still there. Although obviously this is desirable, I did not foresee that there would be intensification of efforts by biologists to study island organisms relatively recently. Today, the fascinating results of DNA analysis have led the way in attracting many younger biologists to islands. Islands remain just as remarkable as museums of evolution as they have always been, and now we have a large assemblage of tools, including the powerful molecular ones, that permit us to develop far more information than we could have twenty or thirty years ago. Consequently, I am much more hopeful than I could have been a few years ago that we will, in fact, understand the unique stories of at least the more striking groups of island plants and animals before their numbers are lessened to the point where such studies would no longer be possible. However, such studies require enterprising individuals, so I encourage each of you to be one of those people. The opportunities for study of some island groups and some island areas will not last indefinitely, so I invite especially the younger among you to enjoy the special privilege of studying island life. In addition, I beg all of you willing to write about island organisms to contribute both scientific studies and popular articles. The lesson of conservation is that the public tends not to be interested in conserving organisms they don't know about. Developing the evolutionary stories of island plants and animals and telling the public about the inherent interest of those particular species may prove to be the most effective tactics some of us can use to save island plants and animals.

LITERATURE CITED

BALDWIN, B., AND R. H. ROBICHAUX. 1995. Historical biogeography and ecology of the Hawaiian silversword alliance (Asteraceae), pp. 259–287. *In* W. L. Wagner and V. A. Funk [eds.], Hawaiian biogeography. Evolution on a hot spot archipelago. Smithsonian Institution Press, Washington, D. C.

CARLQUIST, S. 1974. Island biology. Columbia University Press, New York. 660 p.

GIVNISH, T. J., K. J. SYTSMA, J. F. SMITH, AND W. J. HAHN. 1995. Molecular evolution, adaptive radiation, and geographic speciation in *Cyanea* (Campanulaceae, Lobelioideae), pp. 288–337. *In* W. L. Wagner and V. A. Funk [eds.], Hawaiian Biogeography. Evolution on a hot spot archipelago. Smithsonian Institution Press, Washington, DC.

GRANT, P. R. 1986. Ecology and evolution of Darwin's Finches. Princeton University Press, Princeton NJ.

MACARTHUR, R. H., AND E. O. WILSON. 1967. The theory of island biogeography. Princeton University Press, Princeton, NJ. 203 p.

PATTERSON, R. 1995. Phylogenetic analysis of Hawaiian and other Pacific species of *Scaevola* (Goodeniaceae), pp. 363–378. *In* W. L. Wagner and V. Funk [eds.], Hawaiian biogeography. Evolution on a hot spot archipelago. Smithsonian Institution Press, Washington, D. C.

PERKINS, R. C. L. 1913. Introduction. *In* R. C. L. Perkins [ed.], Fauna Hawaiiensis, **1**(6): xv-ccxxviii. Cambridge University Press, Cambridge.

WAGNER, W. L., D. R. HERBST, AND S. H. SOHMER. 1990. Manual of the flowering plants of Hawai'i. University of Hawaii Press and Bishop Museum Press, Honolulu. 1853 p.

———, AND V. A. FUNK [EDS.] 1995. Hawaiian biogeography—Evolution on a hot spot archipelago. Smithsonian Institution Press, Washington, D. C. 467 p.

———, S. G. WELLER, AND A. K. SAKAI. 1995. Phylogeny in *Schiedea* and *Alsinodendron* (Caryophyllaceae), pp. 221–258. *In* W. L. Wagner and V. A. Funk [eds.], Hawaiian biogeography. Evolution on a hot spot archipelago. Smithsonian Institution Press, Washington, D. C.

WEINER, J. 1995. The beak of the finch. Vintage Books, New York. 332 p.

ZIMMERMANN, E. C. 1948. Introduction. *In* E. C. Zimmermann [ed.], Insects of Hawaii, **1**:1–206. University of Hawaii Press, Honolulu.