DISPERSAL OF PLANTS AND ANIMALS TO OCEANIC ISLANDS

J. M. B. Smith
University of New England, Armidale, Australia

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Summary

Oceanic islands, lacking connections to other land, have acquired their terrestrial plants and animals by dispersal across ocean barriers. Not all types of organism are similarly capable of crossing such barriers, and this is reflected in the disharmonic compositions of oceanic island biotas. Some birds and insects actively fly to islands. Buoyant seeds and a few animals may be drifted there, and a larger variety of organisms may be carried across the ocean on natural rafts. Spores, small seeds, and small invertebrates may be passively carried by winds. Many seeds, and some invertebrates, are transported in or on birds. Dispersal across narrow ocean gaps occurs much more frequently, but very wide gaps are also crossed. Recently formed islands (e.g., Surtsey, Krakatau) indicate how immigrants are dispersed. They, and comparisons with relatively older islands (e.g., Macquarie, Galapagos, Hawaii), also demonstrate that as island communities become more complex and stable, fewer newly arriving organisms are able to establish populations. Barriers to dispersal appear generally easier to overcome than barriers to establishment. Humans have broken down both these sorts of barrier, so that

islands have now become invaded by many alien organisms that previously were unable to colonize them.

1. Introduction: Dispersal across Marine Barriers

By definition, oceanic islands have never (or in some cases, not since being sterilized by volcanic or glacial activity) had any terrestrial link with other landmasses, so the very presence of terrestrial plants and animals on them shows that dispersal has occurred across marine barriers. The processes of such dispersal have long fascinated naturalists and also have relevance to the movement of organisms between other, less isolated regions.

Many examples of dispersal of live animals, seeds, or spores to oceanic islands have actually been observed, rarely in some cases and routinely in others. Nevertheless, oceanic island biotas typically appear unbalanced in that they lack altogether some types of organisms that might be expected on purely ecological grounds, and overall they include relatively small numbers of species. This has led to their often having been described as disharmonic or depauperate, and raised the question as to whether it is a failure of dispersal that restricts the size and composition of oceanic island biotas. The present section briefly reviews and exemplifies dispersal to provide a background to consideration elsewhere in this volume of other questions concerning post-dispersal persistence and evolution, and the conservation of island biotas. The recent increase in rates of dispersal of organisms across marine barriers as a result of human activities is also briefly discussed.

1.1 The Scale of Dispersal across Marine Barriers

It might be thought that the organisms most frequently encountered on oceanic islands would be those with the greatest ability to disperse and the most obvious dispersal mechanisms. To a large degree this is true. For example, land birds with the power of flight frequently have been noted as arriving on oceanic islands, and are present as residents on almost all islands that are large and varied enough to permit their survival. Similarly, the beachside vegetation of such islands is typically dominated by species whose seeds or fruits can readily be shown to remain buoyant and viable in seawater for weeks and sometimes for years. On the other hand, terrestrial mammals that cannot fly, and plants with relatively large, winged seeds that are typically dispersed only a short distance, are generally absent from oceanic islands unless carried there by people.

But other organisms lacking any obvious dispersal capacity may also be found on oceanic islands. In some cases this apparent paradox can be explained by evolutionary loss of their dispersal capacity after their arrival. Good dispersal ability may be selected against on small islands, where well-dispersed individuals might be carried out to sea and lost while their less mobile fellows remain safe ashore. This is thought to have led, for example, to the flightlessness of beetles at Madeira and the progressive loss of hooks on the fruits of *Fitchia*, a relative of daisies that occurs on tropical Pacific islands. It may also be the case that dispersal ability is lost by some island organisms over evolutionary time because its function in facilitating escape from predators has no benefit on species-poor islands where predators are absent.

In a few cases, relatively poor dispersal ability seems actually to result in more frequent arrival on oceanic islands. Rails are a group of birds with notoriously weak flying power, yet they appear routinely on islands. This is in contrast to some stronger fliers such as birds of prey, which despite their aerial powers occur less commonly on remote islands. One case is that of the peregrine falcon (*Falco peregrinus*), renowned for its strong and rapid flight, which although having a nearly worldwide distribution in continental areas, is absent from most islands including some very large ones like New Zealand. The explanation may lie in the reaction of the birds to being caught in gales that threaten to drive them offshore towards remote islands. Weak fliers may not attempt to fight against the wind, reserving their energies for staying aloft and alive, whereas strong fliers may struggle to regain the shore or die in the attempt. Likewise, flowering plants that successfully reach oceanic islands do not all have obvious mechanisms facilitating such dispersal. While many examples can be found of island plants with seeds or fruits that are clearly adapted to dispersal over barriers, in most island floras other plants have no such apparent mechanisms but nevertheless have also succeeded in crossing an oceanic barrier.

New Zealand may provide a particularly striking example. Geologically, New Zealand is a micro-continent rather than a truly oceanic island. It broke away from the larger continental area of Antarctica/Australia in late Cretaceous time. It has conventionally been assumed that its biota was largely “inherited” from this former landmass. However, some researchers have concluded recently on the basis of geological, including fossil, evidence that the entire island became submerged in Neogene time, and has been recolonized by oversea dispersal since its more recent re-emergence above sea level. If this is true it means that many plants conventionally thought to be very poorly dispersed, such as the southern beech *Nothofagus*, nevertheless somehow crossed the (by then) wide sea barrier between Australia and New Zealand.

Organisms may reach oceanic islands entirely passively without any intervention by the organisms themselves, by ocean drift, on the wind, or by transport on or in a flying animal. Alternatively, they may move actively to the island by swimming or flying. Different dispersal mechanisms have different effective ranges. A few vertebrates (e.g., monitor lizards, elephants, some snakes) may easily swim across a strait a few kilometers wide, but have no chance of similarly crossing hundreds of kilometers of ocean. At the other extreme, some buoyant, long-lived seeds may be drifted halfway around the world as easily as across a narrow channel. With increasing ocean distance, the overall rates of successful dispersal drop sharply, with some mechanisms (e.g., bird dispersal of seeds compared with wind dispersal) becoming relatively more important over longer distances.

Islands that in historic times have newly emerged from the ocean (e.g., Surtsey) or been sterilized by volcanic activity (e.g., Krakatau) provide portraits of the processes whereby organisms reach and in some cases establish permanent populations on oceanic islands. Older oceanic islands show how colonists may then form stable (but vulnerable) communities of plants and animals, both through the accumulation of further colonizing species, and through ecological and evolutionary changes within the island communities themselves. Such case studies demonstrate that while many organisms may arrive on an island, most do not survive, especially as the island's resident biota becomes richer and more complex. Establishment of permanent populations following successful dispersal may be a far larger hurdle to potential colonists than being dispersed to an island in the first place.

Section 2 (below) briefly reviews and exemplifies ways in which organisms cross marine barriers to reach oceanic islands. In Section 3 some examples of islands and their biotas are briefly reviewed, and in Section 4 aspects of dispersal to oceanic islands are discussed more widely.

2. Dispersal Mechanisms

Organisms may reach an oceanic island either actively, by their own movement (albeit commonly assisted by winds or currents), or entirely passively.

2.1 Active Dispersal

Some terrestrial vertebrates can swim and may reach islands in this way, especially if distances are short (truly marine vertebrates such as seals and penguins with an exceptional capacity to swim are excluded from consideration here). However, the main means of active dispersal to oceanic islands is flying.

Birds are recorded arriving at oceanic islands with surprising frequency. For example, at Macquarie Island in the southern Pacific Ocean (see Section 3.3), over a period of fifty years many nonresident species have been observed on one or several occasions. They include waders, swifts, bronze-cuckoos, snipes, ducks, herons, egrets, raptors, grebes, coots, crake, swifts, finches, thrushes, pipits, and silvereyes. In one typical year, December 1995–November 1996, two cattle egrets (*Ardeola ibis*), one song thrush (*Turdus philomelos*), one tree martin (*Petrochelidon nigricans*), two masked lapwings (*Vanellus miles*), two blackbirds (*Turdus merula*), and four mallards (*Anas platyrhynchos*, possibly hybrids with *A. superciliosa*) were noted, with at least two more, probably vagrant, passerine birds seen but not identified. Several of these were seen after strong winds from the northeast, and it is thought that all came from New Zealand, nearly 1000 km distant in that direction. Given the size of the island and the paucity of observers, this must have been only a small fraction of those actually arriving. Early in the twentieth century, two exotic bird species introduced to New Zealand from Europe, the starling (*Sturnus vulgaris*) and the redpoll (*Acanthis flammea*), spontaneously established permanent populations on Macquarie Island, perhaps aided by the prior extinction of the only two native land birds, probably by predation by introduced cats and rats.

The same island provides examples of insects flying across marine barriers. One moth species (*Agrostis ipsilon*) has been recorded in autumn in several years, having flown with northeast gales from New Zealand. In spring 1996, two other moth species (*Dasypodia selenophora* and *Persectania ewingii*) and a butterfly (*Vanessa kershawi*) were found, in two cases still alive, after flying from Australia more than 1200 km to the northwest. In this case radiosonde data showed a temperature inversion existed for less than 24 hours at 600–1000 m above sea level, in which the air was warmer than 5

°C and moving at a velocity sufficient for the insects to reach the island overnight. All the species involved are known to migrate within Australia, although not before as far as Macquarie Island. None survived for long in the cold climate of Macquarie Island, but they nevertheless dramatically demonstrated how some insects might colonize distant oceanic islands.

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summarizing the biology of islands, placing dispersal within the context of modern ecological and biogeographical theory.]

Biographical Sketch

Jeremy Michael Bayliss Smith was born and educated in Britain, then lived in Malaysia and Singapore before entering academic life in Australia. His degrees are from Cambridge, Singapore, and Australian National universities, his doctoral thesis for the last being on the biogeography of the high altitude flora of New Guinea. From 1974 until 2000 he worked at the University of New England, Armidale, New South Wales, Australia, initially as a lecturer and later as an associate professor in biogeography. His research interests have been diverse but mainly in the broad areas of tropical high mountain ecology, seed dispersal by oceanic currents, and biological invasions, particularly by woody plants. He has undertaken field research in various places including Borneo, New Guinea, Venezuela, and many parts of eastern Australia, as well as on islands in the Pacific and subantarctic regions. In 1996 he was station leader of the research station at Macquarie Island, and in 2001 he performed the same role at Davis Station, Antarctica. He is the author of about 100 papers, monographs and book chapters covering a broad range of biogeographical and ecological topics.