

Long-distance dispersal: a framework for hypothesis testing

Rosemary G. Gillespie¹, Bruce G. Baldwin², Jonathan M. Waters³, Ceridwen I. Fraser³, Raisa Nikula³ and George K. Roderick¹

¹ Essig Museum of Entomology and Environmental Science Policy and Management, University of California, Berkeley, CA 94720-3114, USA

² Jepson Herbarium and Department of Integrative Biology, University of California, Berkeley, CA 94720-2465, USA

³ Department of Zoology, University of Otago, Dunedin 9054, New Zealand

Tests of hypotheses about the biogeographical consequences of long-distance dispersal have long eluded biologists, largely because of the rarity and presumed unpredictability of such events. Here, we examine data for terrestrial (including littoral) organisms in the Pacific to show that knowledge of dispersal by wind, birds and oceanic drift or rafting, coupled with information about the natural environment and biology of the organisms, can be used to generate broad biogeographic predictions. We then examine the predictions in the context of the origin, frequency of arrival and location of establishment of dispersed organisms, as well as subsequent patterns of endemism and diversification on remote islands. The predicted patterns are being increasingly supported by phylogenetic data for both terrestrial and littoral organisms.

Modes of dispersal as a framework for predictions

Although the importance of long-distance dispersal (LDD) in establishing the biotas of remote islands is well known, the rarity and presumed unpredictability of such events has precluded development of testable hypotheses [1–5]. However, although a single rare LDD event may indeed be impossible to predict, an understanding of the mechanisms involved in LDD over extended (evolutionary) time periods can lend predictability to the process [5]. Here, we argue that understanding the different modes of LDD and associated dispersal adaptations (and exaptations) in the context of geological, paleontological, evolutionary and ecological data can lead to predictions concerning the origin, frequency of arrival and location of establishment of dispersed organisms, as well as subsequent patterns of endemism and diversification. Our discussion focuses primarily on terrestrial environments (extending to the low water mark), but similar features of predictability can apply in purely marine systems [6], despite obvious differences in physical medium and associated biological dispersibility [7]. Microbes are also excluded from our discussion, as biogeographic information for these taxa remains limited. However, the only difference expected for microorganisms will be related to their size, which imposes no constraint *per se* on their dispersal, except that of self-propulsion [8]. We focus on the Pacific, where the

importance of LDD is perhaps best illustrated, and where recent progress in understanding the affinities of multiple insular lineages, coupled with growing knowledge of ecologies, makes it an appropriate and timely test-bed for the predictability of LDD and its ecological and evolutionary consequences.

The contrasting modes of dispersal for particular organisms [9] form the bases for a framework leading to predictions. Long-distance dispersal in the Pacific occurs through three primary vectors: wind, birds and ocean currents (Figure 1). Key elements contributing to the effectiveness of these vectors as dispersal agents are their sustained velocity and directionality, together with their capacity to pick up and transport propagules. The likelihood of a propagule to be vectored will depend on its mechanism

Glossary

Climate matching: occupation of habitats of similar climate; often used to compare the area of origin with regions that the taxon colonizes.

Dispersal: unidirectional movement of an individual away from its place of birth [5]. Contrast with 'dispersion'.

Dispersal biogeography: an explanation for the geographical distribution of organisms based on processes of dispersal.

Dispersal kernel: a probability density function characterizing the spatial distribution of dispersal units originating from a common source [9].

Dispersion: the distribution of organisms in space and time.

Exaptation: the use of a structure or feature for a function other than that for which it was developed through natural selection. Here, traits that evolved for short distance dispersal can serve as exaptations for LDD.

Niche conservatism: the tendency of species to retain ancestral ecological characteristics.

Precinctiveness: reproduction such that most propagules are shed within a limited zone of stable conditions to which a species is ecologically specialized [20].

Propagule pressure: the frequency and number of individual arrival events.

Radiation zone: a geographical limit between island and source populations, beyond which evolutionary divergence has occurred. Although divergence requires reduced connectivity, other factors also typically have a role (Box 2).

Subfossil: biological remains in which the fossilization process is not complete, typically retaining organic material.

Taxon cycle: sequential phases of expansion and contraction of the ranges of species, associated generally with shifts in ecological distribution. Initially developed by Wilson [66] as an explanation for cycles of distribution of taxa on archipelagos, with Stage 1 colonists being recent and widespread, and colonists in Stages 2–4 becoming progressively more restricted and specialized to interior habitats.

Taxonomic disharmony: the unrepresentative assembly of taxa characteristic of remote ecological communities relative to continental source regions.

Vicariance biogeography: an explanation for the geographical distribution of organisms based on geological events.

Corresponding author: Gillespie, R.G. (gillespie@berkeley.edu)

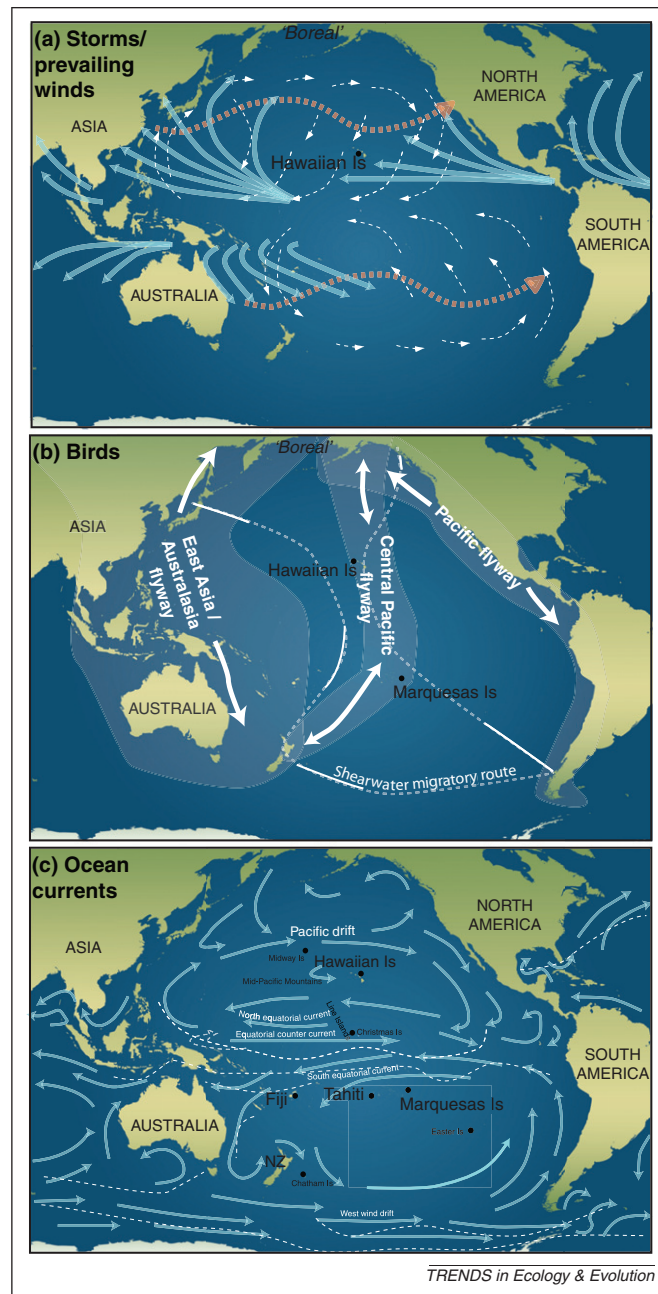


Figure 1. Contrasting modes of long-distance dispersal. (a) Storms and prevailing winds: generalized storm tracks (unbroken blue lines, based on NASA data from 1985 to 2005); eastward subtropical jet streams (broken orange lines); prevailing trade winds (light, low-altitude winds, broken white lines). (b) Bird migratory routes: major migratory pathways (unbroken lines); possible routes used by shearwaters and petrels (broken lines) [71]. (c) Oceanic currents: major currents (unbroken lines); episodic rafting routes [40] (broken lines). Although broadly consistent across oceans, circulation patterns can shift with season, weather patterns and other factors [72]. The North and South Equatorial Currents both flow east-to-west and average 0.7–1 km/h. The Equatorial Counter Current runs west-to-east and averages 1.4–2.2 km/h, although its position and velocity varies seasonally, especially during El Niño events [73]. This current is a potential means by which organisms reach the eastern Pacific from the west [74]. The Antarctic Circumpolar Current (or West Wind Drift) flows west-to-east around Antarctica at approximately 2.75 km/h and is a means by which rafting organisms may travel between New Zealand and South America in less than 1 year [54].

of association with the vector, coupled with its ability to withstand the environment to which it is exposed during transit, attributes that impose strong filters to the kind of organisms involved (Box 1). Features of the new environment that affect the ability to establish will impose additional filters.

Dispersal by wind

Transport during storms, including hurricanes and cyclones, when air currents can lift organisms and carry them great distances quickly (>100 km/h) [10], is a widely

recognized mechanism facilitating the successful colonization of remote islands, especially for arthropods [11]. Given that hurricanes and cyclones usually follow the same general tracks (at least in recorded history), we argue that they will tend to disperse wind-borne propagules in predictable directions. In the northeast Pacific, for example, hurricanes tend to travel from east to west (America to the mid-ocean; http://www.nasa.gov/mission_pages/hurricanes/main/index.html; Figure 1). The low-altitude trade winds move more slowly (ca. 20–30 km/h), and do not blow directly over any continental area [12], so are less likely to have had a role

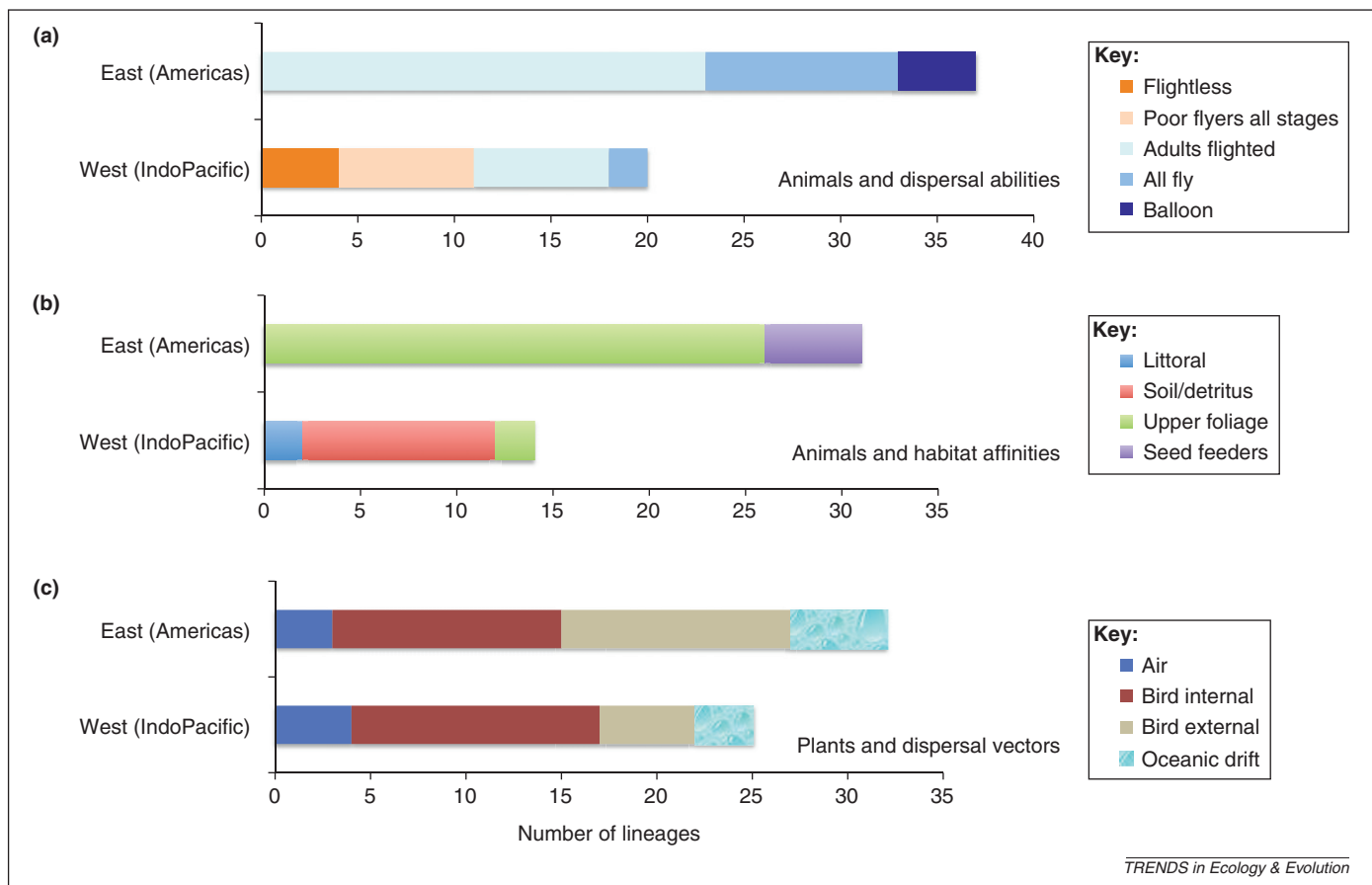


Figure 2. Associations of dispersal abilities and habitat affinities with directionality of colonization for terrestrial animals and plants of Hawaii. Summaries are compiled from data in Table S1 in the supplementary material online, which includes only taxa for which relationships outside the archipelago have been assessed and, thus, the source of colonists can be inferred. (a) Hypothesized flight ability of colonizing terrestrial animals (mammals, birds, mollusks and arthropods). Categories of 'flightless' and 'poor flyers' are those that do not have specific adaptations for aerial dispersal at any life stage. Category of 'all fly' is limited to birds, and 'balloon' to spiders. (b) Hypothesized habitat associations of colonizing animal lineages. Taxa for which habitat affinities of colonists are unknown (e.g. snails) are not included. (c) Hypothesized dispersal vectors of colonizing plants (angiosperms [75] and ferns) for lineages resolved by molecular phylogenetic data (thus biased against those with only 1 or 2 taxa).

in long-distance transportation of medium-large propagules [13]. However, they may be effective over short distances [14] and for small propagules. Finally, the subtropical jet streams are high-altitude (10–16 km), strong (100–150 km/h) winds that blow from west to east in both hemispheres [15]. However, at these high altitudes, the conditions of low temperature, decreased atmospheric pressure and direct solar radiation probably preclude survival of most animal propagules [16]. Thus, among the different winds, extreme storms (because of their speed, strength and variable altitude) are more probable dispersal vectors, at least for animals. We can now examine whether these predictions are met.

Directionality

For the Hawaiian Islands, taxa known for aerial dispersal abilities (birds and spiders in particular) have generally colonized from the east (Figure 2; Table S1 in the supplementary material online), in agreement with the direction of extreme storms (Figure 1). Trade winds (and storms) are frequently implicated in the wind dispersal of Hawaiian ferns, consistent with the ability of fern spores to survive an aerial existence for long periods [15]. In addition, Hawaiian fern lineages show evidence of repeated dispersal from Indomalaya, reflecting the direction of the subtropical

jet stream [17], which is also consistent with the ability of fern and fungal spores to survive extreme conditions [15].

Dispersal itinerary

For many highly dispersive taxa, the probability of dispersal declines only marginally with distance, falling more rapidly for less dispersive taxa (Box 2). Accordingly, highly dispersive taxa are likely to arrive at remote locations through one dispersal event rather than several events in a stepping-stone route, because the probability of a single longer dispersal event is greater than the combined probability of two consecutive shorter dispersal events [4]. This effect may be compounded by loss of dispersal ability upon initial island colonization (Box 3). The consequence is a higher probability of highly wind-dispersed dispersive taxa colonizing islands directly and independently from a mainland source, a prediction borne out by data from several lineages, including spiders and birds [18] (Box 1).

Arrival point and subsequent diversification

Following arrival, additional impediments to establishment can also be important [19,20]. Successful colonization and establishment are more likely in environments that approximately match the source environment [21]. Thus, for taxa from higher latitudes colonizing lower latitudes by

Box 1. Colonizing filters and taxonomic disharmony

Colonization of remote islands depends on factors that impose filters to successful establishment, resulting in taxonomic disharmony.

Wind, birds, or ocean currents as dispersal vectors

Dispersal to remote islands is largely limited to aerial transport, bird vectors, or oceanic rafting (Figure 1, main text). Although the dispersal strategies associated with these vectors have generally evolved for local movement, the same traits can allow LDD in some taxa [9]. As a result, there is an overrepresentation on remote islands of taxa that come from lineages that disperse in these ways [19]; for example, taxa that are small for a given lineage, as seen in some snails [76]. Moreover, the same kinds of taxa with certain dispersal abilities frequently colonize remote archipelagoes multiple times from a mainland source [18]. For example, fulgoroid planthoppers have colonized different remote islands of Oceania independently [77], as have sandalwoods to some extent [78].

Climate matching and niche conservatism

The physical environment can limit colonization, although the importance of this filter can be modified by phenotypic plasticity, allowing the organism to establish in a less than optimal habitat and then adapt under selection [79]. Given the availability of habitat,

colonizing taxa will tend to occupy environments similar to those of their source areas. For example, organisms from higher latitudes are most likely to become established at lower latitudes in higher elevation habitats with climatic conditions matching their original environment [22]. Similarly, lower elevations at low latitudes should be more easily colonized by taxa from tropical sites. Indeed, recent observations imply that some cold-adapted sub-Antarctic taxa rafting to warmer coasts of mainland New Zealand have been unable to establish upon arrival [54].

Symbioses and facilitation

For taxa that live inside other organisms or are associated with particular substrates, establishment can occur more readily if they arrive with (or after the establishment of) their substrate, symbiont or host [80,81]. Surprisingly, even some highly specialized mutualisms are maintained (or recovered) following independent colonization of remote islands by the different partners [82].

Escape from predators, parasites and competitors

Although the presence of some organisms facilitates establishment, the absence of others can be important [83], a phenomenon well documented through studies of successful invasions where predators are lacking [84].

wind dispersal, successful colonization is more likely to occur in higher elevation habitats (Box 1). Subsequently, for taxa that move readily across large (transoceanic) distances, gene exchange between migrants will limit the effects of local selection, and one would predict little or no diversification within an archipelago (Box 2). Illustrating this, a large proportion of lineages that occur in the Hawaiian Islands, both plants and animals, have not diversified, and are represented in the islands by a single species (or two, often reflecting separate colonization events) [20,22,23].

However, for many taxa, colonization of remote islands is extremely rare (Box 2). For these taxa, connectivity with source populations will be very low, and genetic divergence from source populations will be probable, either through drift or adaptation, including ecological shifts associated with the new environment and a reduction in dispersal ability (precinctiveness) [24,25]. These processes appear to form the basis for diversification of ancestrally wind-dispersed taxa at small spatial scales, such as within an archipelago (Box 3).

Dispersal by birds

Birds, in particular strong flyers and migratory species, can be vectors for LDD. There are several avenues of bird dispersal in the Pacific. First, some birds (e.g. Pacific golden-plover, *Pluvialis fulva*; wandering tattler, *Tringa incana*; bristle-thighed curlew, *Numenius tahitiensis*; and ruddy turnstone, *Arenaria interpres*) regularly use the central Pacific migratory flyway that runs north–south across the equator (Figure 1). Second, dispersal may occur through accidental displacement. For example, of the 336 birds recorded in Hawaii, a surprising 52% have been recorded as arriving naturally in modern times, either as regular or occasional visitors (49%), or breeders (pelagic albatrosses, petrels, etc.; 3%) [26]; of the visitors, most were accidentally displaced migrants that normally travel between boreal North America and South America or between northern Eurasia and Australasia, or both. Third, some birds have wide ranges

across islands. For example, in southern Polynesia, species currently or historically widespread through the islands, such as pigeons (*Ducula* and *Columba* spp.), lorikeets (e.g. *Vini kuhlii*) and thrushes (e.g. *Turdus poliocephalus*) [27], were or are probable important dispersal vectors.

Although ‘landbirds’ and cuckoos (9% of visitors to Hawaii) might be expected to be most important for dispersing propagules to and from inland sites, migratory plovers and other shorebirds (27% of visitors to Hawaii) probably also have a role, as some of these frequent inland habitats. Taxa that are dispersed by birds frequently illustrate adaptations involving mechanisms for attachment to animals or passage through their guts (e.g. many angiosperm disseminules [20], but also snails [28] are known to survive passage through bird guts). Other taxa can be associated with bird vectors accidentally, such as insects that feed within seeds that themselves have mechanisms for transportation by birds [29].

The particular importance of birds as vectors lies in the regularity, speed and distance they travel [13]. Moreover, in contrast to winds, which frequently move east–west and not across the equator, the common migratory flyways run approximately north–south, with less migration in other directions. However, in the South Pacific, the movement of widespread birds between islands is more likely to create a pattern of dispersal from west to east [30]. We can now assess whether there is any predictable pattern to LDD by birds.

Directionality

Among plants, Baldwin and Wagner [22] used seed and fruit morphology to show that a large proportion of Hawaiian lineages of temperate or boreal North American origin probably arrived by bird transport (Figure 2), as predicted by migratory routes and the potential for birds to be blown off course (Figure 1). Some Hawaiian arthropod lineages show similar affinities with the north, a pattern suggested for many Lepidoptera (see Table S1 in the supplementary material online). Although requiring confirmation with

Box 2. Modes of LDD predict the spatial scale of genetic divergence.

Patterns of connectivity (Nm = number of migrants/generation) for taxa with different modes of dispersal as a function of distance help predict the scale at which genetic divergence leading to speciation is possible.

In Figure 1, highly dispersive taxa and those with directed flight (blue line) typically have wide ranges with little divergence (a migratory bird and a coconut are shown). When connectivity is less (green or yellow lines), rare long-distance colonizers can diverge from ancestral source pools, particularly with subsequent divergent selection as described below (a ballooning spider and sticky fruits of tar vine, *Boerhavia* spp., Caryophyllales; and barbed seeds of beggartick *Bidens* spp., Asteraceae, are shown). Taxa with very limited dispersal ability (red line) can diverge at the smallest spatial scales, even within archipelagoes or within islands (a flightless *Rhyncogonus* weevil, *Succinea* snail and mygalomorph spider are shown). Although organisms often have a characteristic mode of dispersal, tendency to disperse can not only be variable within a lifespan [9] but also over evolutionary time, with consequences for diversification and speciation. For example, species with normally limited dispersal ability, when attached to a bird vector or a drifting mat of vegetation, can become highly dispersive [(a) arrows] while

associated with the vector. By contrast, over evolutionary time, descendants of a ballooning spider may lose the ability to balloon (see Box 3) or seeds may lose their stickiness or barbs [(b) arrows], and thus have the potential for diversification at much smaller spatial scales.

Several methods have been proposed for estimating the probability of LDD and its consequences, including the use of effective dispersal kernels [5] and modeling of population parameters [49]. Ideally, information about LDD not only predicts the spatial scale at which genetic divergence is likely, but also serves as a null model to understand the importance of selection and other factors in processes of speciation in remote habitats. However, quantifying the relationships between gene flow and divergence has been problematic, largely because direct observations of LDD are difficult, if not impossible, for many taxa. At shorter distances, such as within islands, genetic divergence has been linked to the scale of speciation [85]. However, at longer distances, predicting the scale of speciation for taxa with different dispersal modes is more difficult for several reasons, including the variable nature of colonization and survival, unknown effects of selection, and the non-random importance of some loci on genetic divergence leading to speciation [86].

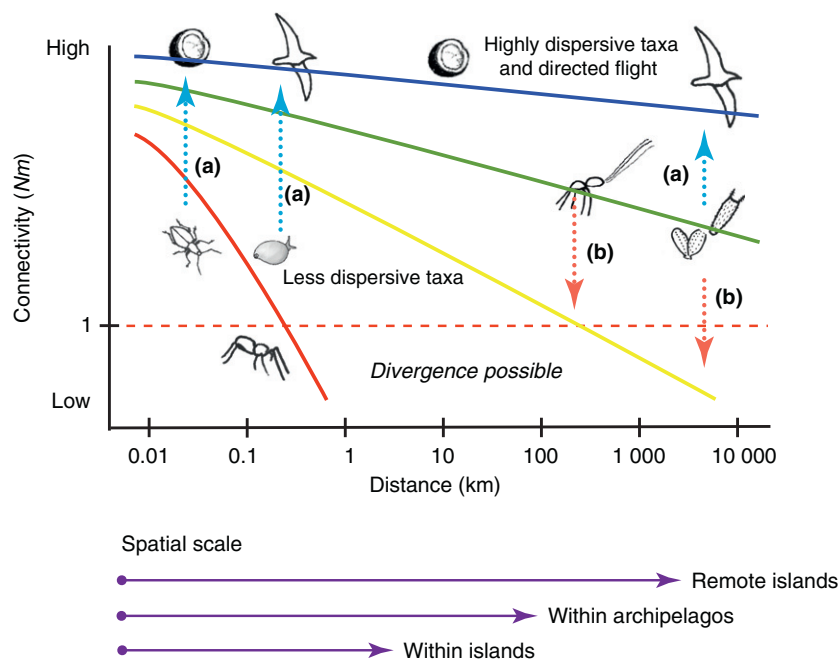


Figure 1. Effect of dispersal on colonization and genetic isolation.

phylogenetic data, the pattern supports the idea that insects feeding within seeds would show a pattern of colonization matching that of their plant hosts.

Dispersal itinerary

If a taxon hypothesized to be vectored by birds is present on multiple archipelagos in the north and south Pacific, one would expect relationships to match migratory routes, a pattern found in several angiosperms [22,31] and spiders [32]. Dispersal by birds into remote Oceania may include a multi-step process of transport into the South Pacific, followed by north-south transport by other birds. Although dispersal pathways are less predictable when multiple vectors are involved, affinities of many Hawaiian angiosperms

with Indomalayan or Neotropical taxa are most readily explained by accidental arrivals (or now-extinct birds), some intersecting with migratory bird routes.

Genetic divergence and adaptation, including potential loss of traits for dispersal by birds, would be expected for taxa that arrive very rarely (Box 2). Such modification has been inferred for a diversity of Hawaiian angiosperms [25], associated with considerable genetic isolation of populations within and across islands [23]. For those organisms that maintain associations with bird vectors (for whatever reason, Box 3), the chance of colonization of additional islands remains, but will be diminished if habitat shifts lead to dispersal by birds with smaller ranges (e.g. forest birds).

Box 3. Loss of dispersal ability on islands?

Changes in dispersal ability subsequent to colonization are partly predictable. Some situations (the first two detailed below) predict no modification in dispersal strategy, whereas others (the next four below), which assume that a lack of gene flow allows local selection and that organisms have a dispersal mode upon which selection can act, predict a reduced dispersal ability. In each case, selection will oppose the tendency for reduced dispersal if movement is required for other activities.

Resulting dispersal not associated with a dispersal strategy

When dispersal occurs because of an attribute of the organism that has some primary function unrelated to dispersal, selection against dispersal is not likely. For example, an egg mass that is sticky for purposes of protection can inadvertently get stuck to the feathers of a bird.

Maintenance of genetic connectivity

The genetic consequences of LDD depend on whether dispersal carries the individual away from its genetic deme (Box 2). Populations continually connected to a source by gene flow are unlikely to diverge, so their dispersal mode remains unchanged.

Selection against individuals that disperse

Individuals that reach an isolated island and then continue to disperse widely will almost certainly be unsuccessful and thus be removed from the local deme [87], whereas those that do not will

remain within the island habitat, resulting in selection for reduced dispersal distance. This tendency will be most relevant for organisms with non-directional dispersal strategies that prevent them from returning to the island gene pool, such as ballooning spiders and Lepidoptera larvae. For species that are capable of returning after displacement, selection for reduction in dispersal will be less.

Disassociation from the vector

The tendency to adapt, diversify, or switch habitats on remote islands can result in disassociation from the vector that carried the organism to the island [25]. As a result, selection maintaining the trait (e.g. barbs or sticky seeds) that facilitated association with the initial vector of colonization (e.g. migratory bird) can cease.

Dispersal reduction as a byproduct of ecological or evolutionary changes

Shifts from pioneering to more stable habitats can result in less dispersive propagules as a byproduct of the transition. For example, some small-seeded herbs have evolved woodiness or arborescence [88], accompanied by selection for fewer, larger seeds of reduced longevity [24,25].

Costly dispersal no longer required

Dispersal ability may be lost if not required and its maintenance demands energy. For example, flight allows birds and insects to escape predators, but without predators, selection can lead to wing reduction.

Arrival point and subsequent diversification

Because bird-dispersed taxa often colonize islands along migration routes from temperate locales, they will tend to establish initially at high elevations (similar to their original habitat) on tropical islands and generally only on islands that have such habitat [22]. Bird-mediated transport to tropical islands from tropical latitudes is expected to be less common than dispersal from boreal or temperate regions, because the central Pacific migratory route does not cross major tropical landmasses. However, any propagule that does arrive from tropical habitats should have a greater chance of establishment because of the greater availability of similar habitats, especially on lower islands. This argument is consistent with the sizable number of vascular plants with Australasian and Indomalayan origins [33].

Dispersal by ocean currents

The ability of organisms to disperse by oceanic drift or rafting on ocean flotsam is dictated by a complex interaction between ocean dynamics, geomorphology, proximity to the ocean and survival *en route*. Ocean currents are generally slow (approximately 0.7–2.7 km/h) and flow in predictable directions (Figure 1), although both parameters can be modified somewhat by storms. Moreover, because the presence of islands affects water circulation patterns [34], the appearance of islands during episodic lowering of eustatic sea levels (associated with glacial cycles) would have modified paleocurrents. In addition, distances between islands have changed considerably over space and time for two reasons. First, volcanic hotspot islands in the Pacific have a finite lifespan from formation to almost complete loss of the above-water volcanic core after 4–6 million years [35].

Box 4. Testing dispersal predictions: next steps

Hypothesized syndromes of dispersal and their consequences can be tested directly or indirectly, with additional insights gained from knowledge of functional groups, fossil data and semi-natural experiments.

Observations of LDD

Actual observations of LDD remain limited, although recent technological advances are making long-distance tagging more feasible (e.g. tracking bird migratory routes [71]). Functional studies can provide information on the survival and use of vectors (e.g. snails in bird guts [28]). Finally, surrogates for actual dispersal can also be used to estimate features of LDD, including directionality and survivability (e.g. analysis of storm debris objects [9] and ocean trash [89]).

Taxonomic assessment and phylogenetic analyses

Understanding colonization routes and changes in dispersibility requires thorough taxonomic sampling across islands and interpretation in the context of relatives outside those islands. Phylogenetic information is now available for multiple lineages on remote Pacific islands, with a good understanding of relationships across archipelagoes. However, the data are incomplete and additional information is needed not only for many extant lineages (e.g. arthropods), but also for fossils, to reveal taxa that have become extinct or have shifted range, in particular since human arrival [27].

Genomic analyses

Genomic tools allow insights into functional changes in dispersal and can potentially be used to test predictions of change in dispersal. For example, it may be possible to use these approaches to detect predicted signatures of selection at the molecular level for traits associated with loss of dispersal or change in vector [90].

Niche modeling

Sophisticated niche modeling is now available to allow assessment of arrival location in a phylogenetic context. Climatic and landscape variables can be mapped for all species within a clade [91], making it possible to construct a set of different 'cost surfaces' for each species based on known suitable habitats and under different predicted dispersal scenarios. For example, low-cost pathways under bird dispersal models would be along migratory or foraging pathways (e.g. [92]).

Computational techniques for modeling evolutionary data

Different dispersal strategies predict different patterns of diversification subsequent to establishment. Phylogenetic comparative methods provide new insights into such events [93]. Models such as hierarchical approximate Bayesian computation (HABC) [94] can be used to quantify and compare multi-species patterns in range expansion and colonization, and patterns of speciation or divergence. Together, these tools promise insights into the historical demography of even recent colonization events [95].

Second, exposure of land by marine regressions provides additional stepping-stones in the ocean. For example, numerous islands existed historically in the area of the current Line Islands and mid-Pacific mountains [30,36] (Figure 1), probably providing stepping stones to more recent islands [37]. Although the frequent appearance and disappearance of islands (often limited to coastal habitats that are the inevitable point of contact for rafting taxa) is also relevant to wind- and bird-dispersed taxa, the special relevance for rafting taxa is that it serves to reduce interarchipelago and interisland distances for organisms that cannot tolerate the extended transit times of oceanic drift.

Surviving prolonged periods at sea is necessary for rafting. Although some terrestrial organisms have been shown empirically to survive exposure to seawater for ≥ 2 –3 weeks [38], relatively few are expected to survive the many months required to reach some remote Pacific islands, unless they are protected in some way. Organisms in which dispersal occurs in the dormant phase (most angiosperms) are more likely to tolerate such harsh conditions [39]. Alternatively, organisms living in wood or with some other mechanism of protection from seawater can survive relatively well during transport [40]. However, traversing the vast expanses of the Pacific Ocean would be challenging for most terrestrial organisms. For example, the 3000-km stretch between the Marquesas and Hawaii would take approximately 65 days to traverse if there was a direct current of 1.9 km/h (the average velocity of the Equatorial Countercurrent).

Marine intertidal or fully terrestrial taxa with adaptations for dispersal by oceanic drift [40–43], such as plants with floating fruits and seeds that can readily withstand seawater, are expected to raft more frequently than most terrestrial taxa. Such organisms may show biogeographic patterns corresponding to the ocean surface current systems [44]. By contrast, those in which tolerance to seawater is limited (most terrestrial taxa) will only survive to raft short distances, and might therefore be expected to show a biogeographic pattern of stepping-stone colonization [45]. We now examine the extent to which these predictions hold.

Directionality

Ocean currents provide some directionality to patterns of colonization by drift or rafting. Marine intertidal taxa (e.g. circumpolar *Macrocystis* and *Durvillaea* kelp, *Parawaldeckia* amphipods and *Limnoria* isopods) and those with adaptations for dispersal by oceanic drift [40–43] have been found to be genetically homogeneous within the neighborhood of the Antarctic Circumpolar Current, relative to the more restricted distributions of terrestrial taxa (e.g. [43]). Long-distance rafting is clearly the most plausible explanation for this circumpolar dispersal of floating kelp and its associated epifauna. Some terrestrial taxa that show specific adaptations for oceanic dispersal, including tolerance to seawater and flotation mechanisms, are presumably also dispersed via ocean currents, yielding similarly widespread distributions [46].

Dispersal itinerary

Intertidal taxa that seemingly raft with high frequency show evidence of numerous independent colonization

events on different oceanic islands, as in the rafting sea-star *Parvulastra exigua* [47]. Importantly, rare meteorological [48] and extreme oceanographic events (rather than mean current trajectories) can have a major role [49] in reducing the time required for such events. For instance, although the median transit time estimates for passive dispersal from Australia to New Zealand are approximately 2–3 years, models incorporating oceanographic variability and winds indicate that, under certain conditions, such voyages can be completed in less than 1 year [50]. Under these ‘rare’ conditions, a substantial proportion of rock-lobster (*Jasus*) larvae, for example, should successfully complete the 2000-km transit within their planktonic lifespan, reinforcing independent biological evidence from molecular markers [51–53]. Likewise, rare south-easterly weather systems are apparently responsible for the relatively rapid transport of sub-Antarctic kelp rafts to mainland New Zealand, with biologically estimated dispersal times [54] that are sometimes substantially shorter than the mean dispersal times inferred from oceanographic models [55]. Moreover, modeling of paleocurrents can provide explanations for historical oceanic dispersal events that might have seemed implausible given modern-day oceanographic regimes [56,57].

For terrestrial plants in the Pacific, dispersal by oceanic drift has occurred repeatedly from both the Neotropics and Paleotropics, especially for littoral taxa [22,23,39,58], consistent with the ability of some plants to tolerate long periods at sea owing to their tendency to disperse in a dormant phase. For terrestrial taxa that may not survive long journeys at sea, rafting can still be the predominant mode of dispersal for flightless and poorly flighted arthropods, in particular if they are insulated within rafts of debris or wood [59]. Indeed, rafting in terrestrial animals appears to be most common for those associated with dead wood [11,60], leaf miners, wood borers and other insects that inhabit plant debris [61], or those that attach their eggs to vegetation [49,62]. However, the proximity of islands is likely to have an important role in terrestrial arthropods, dramatically increasing the probability of colonization for terrestrial groups with limited survival tolerance in the open ocean [45]. In Hawaii, the most remote archipelago for terrestrial taxa, colonization by rafting appears to have been largely from the southwest for many insects (Figure 2), as predicted under a stepping-stone colonization model (there are many more islands to the south west than to the east). Indeed, *Rhyncogonus* weevils occur on oceanic islands throughout the Pacific, and appear to have colonized archipelagoes in a sequential stepping-stone fashion [19]. The littoral habitat is (or has been) present on almost every island, large or small, atoll or high. Thus, for organisms such as *Rhyncogonus*, usable habitat will have been relatively abundant even in vast expanses of open ocean, although the amount and extent of habitat will undoubtedly have varied over millennia, with changing climates and volcanic activity.

Arrival point and subsequent diversification

For seawater-resistant taxa (and marine intertidal organisms in particular), habitat affinities dictate the initial tendency to raft. For example, species that graze on

beach-cast macroalgae have more rafting opportunities than do those that graze only on rocky or soft substrates [63]. For these taxa, the predicted tendency will be to remain in coastal areas, as repeated arrival of new propagules will limit divergence, adaptation and any loss of dispersal ability [25] (Box 3). Support for this prediction comes from the prevalence of wide oceanic distributions among angiosperms from littoral environments with rafting dispersal capabilities [20,22,23], as well as from genetic data [58].

Colonization will inevitably occur in the littoral zone for species that use oceanic drift or rafting to reach an island. However, provided selection or limited genetic connectivity with the source, ecological shifts can occur and dispersal ability may be reduced subsequent to arrival (Box 3). Tests of such historical colonization and subsequent differentiation for littoral taxa on remote islands have been impeded by large-scale anthropogenic disturbance and associated extinction at low elevations. Recent work has uncovered a fabulous resource of subfossil remains on multiple Pacific islands that promises insights into the characteristics of the pre-human insular birds and plants [27,64]. This work has shown that, at least among plants, some lineages currently confined to higher elevations (e.g. the mallow *Kokia*, dogbanes *Ochrosia* and *Pteralyxia*, and palm *Pritchardia*) previously occurred at low elevations. However, other lineages that are currently diverse at higher elevations (e.g. silverswords, lobeliads and *Cyrtandra*) probably never occurred at low elevations. Such data are now also becoming available for invertebrates [65]. As predicted, a large proportion of this coastal material consists of organisms that are inferred (e.g. a lineage characterized by flightlessness across the Pacific) to have colonized by rafting [Porch, N. (2009) The insect fossil record and the reconstitution of Indo-Pacific island diversity. A *Pacific Science Intercongress* 2009 presentation].

For organisms colonizing the littoral zone, there may be a progression towards specialization for more terrestrial habitats. Wilson [66] suggested for ants in Melanesia that most colonists disperse through lowland marginal habitats and then extend their distributions into forested and montane habitats on increasingly remote islands; a progression from generalist to specialist that he termed the 'taxon cycle'. Such a cycle has also been identified through detailed molecular studies of West Indian birds [67]. Although phylogenetic analysis of island lineages overall shows little evidence that this cycle of distributional change from littoral habitats to higher elevations leads to analogous speciation trends [68], a better test of possible speciation trends could be provided by restricting analysis to rafting taxa that inevitably arrive in littoral habitats and subsequently undergo differentiation. Indeed, diversification between habitats separated by elevation is a common pattern in oceanic islands [69,70].

Concluding remarks

We have shown here how features characterizing dispersal modes and ecology lead to predictions and testable hypotheses concerning the avenue of arrival and opportunity for diversification of colonizing taxa and even resulting ecological communities in the Pacific (see Box 4 for future

research directions). For example, taxa in Hawaii that are associated with dispersal by birds often show the origins predicted from the combined likelihood of transportation vector and establishment site (i.e. ancestral ecological setting). Terrestrial animal taxa in Hawaii that disperse by winds come primarily from the east as predicted by storm patterns, and those that raft appear to come mostly from the west (Figure 2), as predicted by ocean currents and available interspersed islands serving as stepping stones. Related predictions stem from the amount of connectivity among populations of organisms dispersing through different mechanisms (Box 2) and the extent to which dispersal mechanisms become modified subsequent to colonization (Box 3). Predictability may be complicated by the possibility that a combination of vectors are involved in long-distance dispersal [9]; for example, a propagule carried in the wind might land in the ocean before being carried to land, or a bird may pick up a piece of flotsam, carrying a propagule to land. However, although LDD is an inherently stochastic and rare phenomenon, understanding the dispersal vector, whether wind, birds, or ocean currents, as well as geological, biological and environmental factors that affect these vectors and the ability of the propagule to use them, can reveal predictable patterns of biogeography and subsequent evolutionary modifications associated with a given degree of isolation.

Acknowledgments

We thank members of Evolab at the University of California, Berkeley for discussion and Ran Nathan for comments. Four anonymous reviewers were hugely helpful in shaping the ideas presented. Support provided by NSF, and the Gordon and Betty Moore Foundation.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.tree.2011.08.009](https://doi.org/10.1016/j.tree.2011.08.009).

References

- Nelson, G. and Platnick, N.I. (1981) *Systematics and Biogeography: Cladistics and Vicariance*, Columbia University Press
- Carlquist, S. (1972) Island biology: we've only just begun. *Bioscience* 22, 221–225
- Cowie, R.H. and Holland, B.S. (2006) Dispersal is fundamental to biogeography and the evolution of biodiversity on oceanic islands. *J. Biogeogr.* 33, 193–198
- Crisp, M.D. *et al.* (2011) Hypothesis testing in biogeography. *Trends Ecol. Evol.* 26, 66–72
- Nathan, R. (2006) Long-distance dispersal of plants. *Science* 313, 786–788
- Dawson, M.N. and Hamner, W.M. (2008) A biophysical perspective on dispersal and geography of evolution in the sea. *J. R. Soc.: Interface* 5, 135–150
- Vermeij, G.J. and Grosberg, R.K. (2010) The Great Divergence: when did diversity on land exceed that in the sea? *Integr. Comp. Biol.* 50, 675–682
- Hughes Martiny, J.B. *et al.* (2006) Microbial biogeography: putting microorganisms on the map. *Nat. Rev. Microbiol.* 4, 102–112
- Nathan, R. *et al.* (2008) Mechanisms of long-distance seed dispersal. *Trends Ecol. Evol.* 23, 638–647
- Gressitt, J.L. (1960) The development of insect faunas in Oceania. In *Darwin-Wallace Centenary. Proceedings of the Centenary and Bicentenary Congress of Biology, 1958* (R.D. Purchon, eds), pp. 58–62, University of Malaya
- Zimmerman, E.C. (1948) *Introduction, Insects of Hawaii* (Vol. 1), University of Hawaii Press

- 12 Ziegler, A.C. (2002) *Hawaiian Natural History, Ecology, and Evolution*, University of Hawaii Press
- 13 Holzapfel, E.P. and Harrell, J.C. (1968) Transoceanic dispersal studies of insects. *Pac. Insects* 10, 115–153
- 14 Kirchner, C.H. *et al.* (1997) Flying snails – how far can *Trancatellina* (Pulmonata: Vertiginidae) be blown over the sea? *J. Mollusc. Stud.* 63, 479–487
- 15 Geiger, J.M.O. *et al.* (2007) Molecular biogeography and origins of the Hawaiian fern flora. *Brittonia* 59, 142–158
- 16 Bell, J.R. *et al.* (2005) Ballooning dispersal using silk: world fauna, phylogenies, genetics and models. *Bull. Entomol. Res.* 95, 69–114
- 17 Geiger, J.M.O. and Ranker, T.A. (2005) Molecular phylogenetics and historical biogeography of Hawaiian *Dryopteris* (Dryopteridaceae). *Mol. Syst. Evol.* 34, 392–407
- 18 Gillespie, R.G. *et al.* (2008) Biogeography of French Polynesia: diversification within and between a series of hotspot archipelagoes. *Philos. Trans. R. Soc. Lond.* 363, 3335–3346
- 19 Carlquist, S. (1966) The biota of long-distance dispersal. I. Principles of dispersal and evolution. *Q. Rev. Biol.* 41, 247–270
- 20 Carlquist, S. (1967) The biota of long-distance dispersal. V. Plant dispersal to Pacific Islands. *Bull. Torrey Bot. Club* 94, 129–162
- 21 Cavendar-Bares, J. *et al.* (2009) The merging of community ecology and phylogenetic biology. *Ecol. Lett.* 12, 693–715
- 22 Baldwin, B.G. and Wagner, W.L. (2010) Hawaiian angiosperm radiations of North American origin. *Ann. Bot.* 105, 849–879
- 23 Price, J.P. and Wagner, W.L. (2004) Speciation in Hawaiian angiosperm lineages: cause, consequence, and mode. *Evolution* 58, 2185–2200
- 24 Carlquist, S. (1966) The biota of long-distance dispersal. II. Loss of dispersibility in Pacific Compositae. *Evolution* 20, 30–48
- 25 Carlquist, S. (1966) The biota of long-distance dispersal. III. Loss of dispersibility in the Hawaiian flora. *Brittonia* 18, 310–335
- 26 Pyle, R.L. (2002) Checklist of the birds of Hawaii. *Elepaio* 62, 137–148
- 27 Steadman, D.W. (2006) *Extinction and Biogeography of Tropical Pacific Birds*, University of Chicago Press
- 28 Wada, S. *et al.* (2011) Snails can survive passage through a bird's digestive system. *J. Biogeogr.* DOI: 10.1111/j.1365-2699.2011.02559.x
- 29 Sallabanks, R. and Courtney, S.P. (1992) Frugivory, seed predation, and insect–vertebrate interactions. *Ann. Rev. Entomol.* 37, 377–400
- 30 Kingston, N. *et al.* (2003) The phylogeographical affinities of the Pitcairn Islands – a model for south-eastern Polynesia? *J. Biogeogr.* 30, 1311–1328
- 31 Price, J.P. and Wagner, W.L. (2011) A phylogenetic basis for species–area relationships among three Pacific Island floras. *Am. J. Bot.* 98, 449–459
- 32 Garb, J.E. and Gillespie, R.G. (2009) Diversity despite dispersal: colonization history and phylogeography of Hawaiian crab spiders inferred from multilocus genetic data. *Mol. Ecol.* 18, 1746–1764
- 33 Ballard, H.E.J. and Sytsma, K.J. (2000) Evolution and biogeography of the woody Hawaiian violets (*Viola*, Violaceae): Arctic origins, herbaceous ancestry and bird dispersal. *Evolution* 54, 1521–1532
- 34 Xie, S.P. *et al.* (2001) Far-reaching effects of the Hawaiian Islands on the Pacific Ocean atmosphere system. *Science* 292, 2057–2060
- 35 Craig, D.A. *et al.* (2001) Geographical history of the central-western Pacific black fly subgenus *Inseliellum* (Diptera: Simuliidae: Simulium) based on a reconstructed phylogeny of the species, hot-spot archipelagoes and hydrological considerations. *J. Biogeogr.* 28, 1101–1127
- 36 Clouard, V. and Bonneville, A. (2005) Ages of seamounts, islands, and plateaus on the Pacific plate. In *Plates, Plumes, and Paradigms* (Foulger, G.R. *et al.*, eds), pp. 71–90, Geological Society of America
- 37 Nunn, P.D. (2009) *Vanished Islands and Hidden Continents of the Pacific*, University of Hawaii Press
- 38 Coulson, S.J. *et al.* (2002) Survival of terrestrial soil-dwelling arthropods on and in seawater: implications for trans-oceanic dispersal. *Funct. Ecol.* 16, 353–356
- 39 Thiel, M. and Gutow, L. (2005) The ecology of rafting in the marine environment II. The rafting organisms and community. *Oceanogr. Mar. Biol. Annu. Rev.* 43, 279–418
- 40 Thiel, M. and Haye, P.A. (2006) The ecology of rafting in the marine environment. III. Biogeographical and evolutionary consequences. *Oceanogr. Mar. Biol. Annu. Rev.* 44, 323–429
- 41 McGaughan, A. *et al.* (2010) Biogeography of circum-Antarctic springtails. *Mol. Phylogenet. Evol.* 57, 48–58
- 42 Mortimer, E. *et al.* (2011) Mite dispersal among the Southern Ocean islands and Antarctica before the Last Glacial Maximum. *Proc. R. Soc. B* 278, 1247–1255
- 43 Pugh, P.G.A. and Scott, B. (2002) Biodiversity and biogeography of non-marine Mollusca on the islands of the Southern Ocean. *J. Nat. History* 36, 927–952
- 44 Pugh, P.J.A. (2004) Biogeography of spiders (Araneae: Arachnida) on the islands of the southern ocean. *J. Nat. History* 38, 1461–1487
- 45 MacArthur, R.H. and Wilson, E.O. (1967) *The Theory of Island Biogeography*, Princeton University Press
- 46 Keppel, G. *et al.* (2009) Changing perspectives on the biogeography of the tropical South Pacific: influences of dispersal, vicariance and extinction. *J. Biogeogr.* 36, 1035–1054
- 47 Waters, J.M. and Roy, M.S. (2004) Out of Africa: the slow train to Australasia. *Syst. Biol.* 53, 18–24
- 48 Censky, E.J. *et al.* (1998) Over-water dispersal of lizards due to hurricanes. *Nature* 395, 556
- 49 Paulay, G. and Meyer, C. (2002) Diversification in the Tropical Pacific: comparisons between marine and terrestrial systems and the importance of founder speciation. *Integr. Comp. Biol.* 42, 922–934
- 50 Chiswell, S.M. *et al.* (2003) Trans-Tasman sea-larval transport: is Australia a source for New Zealand rock lobsters? *Mar. Ecol. Prog. Ser.* 247, 173–182
- 51 Ovenden, J.R. *et al.* (1992) Mitochondrial DNA analyses of the red rock lobster *Jasus edwardsii* supports an apparent absence of population subdivision throughout Australasia. *Mar. Biol.* 112, 319–326
- 52 Burrige, C.P. and Smolenski, A.J. (2003) Lack of genetic divergence found with microsatellite DNA markers in the tarakihi *Nemadactylus macropterus*. *N. Z. J. Mar. Freshwa. Res.* 37, 223–230
- 53 Waters, J.M. *et al.* (2005) Phylogeographic disjunction in abundant high-dispersal littoral gastropods. *Mol. Ecol.* 14, 2789–2802
- 54 Fraser, C. *et al.* (2011) Oceanic rafting by a coastal community. *Proc. R. Soc. B* 278, 649–655
- 55 Chiswell, S.M. (2009) Colonisation and connectivity by intertidal limpets among New Zealand, Chatham and Sub-Antarctic Islands. II. Oceanographic connections. *Mar. Ecol. Prog. Ser.* 388, 121–135
- 56 Townsend, T.M. *et al.* (2010) Eastward from Africa: palaeocurrent-mediated chameleon dispersal to the Seychelles islands. *Biol. Lett.* 7, 225–228
- 57 Ali, J.R. and Huber, M. (2010) Mammalian biodiversity on Madagascar controlled by ocean currents. *Nature* 463, 653–657
- 58 Takayama, K. *et al.* (2008) Gene flow and population subdivision in a pantropical plant with sea-drifted seeds *Hibiscus tiliaceus* and allied species: evidence from microsatellite analyses. *Mol. Ecol.* 17, 2730–2742
- 59 Peck, S.B. (2008) Galapagos Islands Insects: colonization, structure, and evolution. In *Encyclopedia of Entomology* (2nd edn) (Capinera, J.L., ed.), pp. 1561–1572, Springer
- 60 Zimmerman, E.C. (1942) Distribution and origin of some eastern oceanic insects. *Am. Nat.* 76, 280–307
- 61 Gressitt, J.L. (1961) Problems in the zoogeography of Pacific and Antarctic insects. *Pac. Insects Monogr.* 2, 1–94
- 62 Perkins, R.C.L. (1907) On a species of *Proterhinus* from Samoa. *Proc. Hawaii. Entomol. Soc.* 1, 87–88
- 63 Donald, K.M. *et al.* (2005) Cladogenesis as the result of long-distance rafting events in Pacific topshells (Gastropoda: Trochidae). *Evolution* 59, 1701–1711
- 64 Burney, D.A. *et al.* (2001) Fossil evidence for a diverse biota from Kaua'i and its transformation since human arrival. *Ecol. Monogr.* 74, 615–641
- 65 Porch, N. (2008) Insect fossils from Pacific Island pre-human and archaeological contexts: reconstructing lost 'Edens' and human impacts. *Quatern. Int.* 328 (Suppl. 1), 167–168
- 66 Wilson, E.O. (1961) The nature of the taxon cycle in the Melanesian ant fauna. *Am. Nat.* 95, 169–193
- 67 Ricklefs, R.E. and Bermingham, E. (2002) The concept of the taxon cycle in biogeography. *Global Ecol. Biogeogr.* 11, 353–361
- 68 Schluter, D. (2000) *The Ecology of Adaptive Radiation*, Oxford University Press
- 69 Liebherr, J.K. (1997) Dispersal and vicariance in Hawaiian platynine carabid beetles (Insecta: Coleoptera). *Pac. Sci.* 51, 424–439

- 70 Taiti, S. *et al.* (2003) Evolution of terrestriality in Hawaiian species of the genus *Ligia* (Isopoda, Oniscidea). *Crustaceana Monogr.* 2, 85–102
- 71 Shaffer, S.A. *et al.* (2006) Migratory shearwaters integrate oceanic resources across the Pacific Ocean in an endless summer. *Proc. Natl. Acad. Sci. U.S.A.* 103, 12799–12802
- 72 Flament, P. *et al.* (1998) The Ocean. In *Atlas of Hawaii* (Juvik, S.P. and Juvik, J.O., eds), pp. 82–86, University of Hawaii Press
- 73 Jokiel, P.L. (1990) Long-distance dispersal by rafting: reemergence of an old hypothesis. *Endeavour* 14, 66–73
- 74 Richmond, R.H.I. *et al.* (1989) The effects of the El Nino-Southern Oscillation on the dispersal of corals and other marine organisms. In *Global Ecological Consequences of the 1982–83 El Nino-Southern Oscillation* (Glynn, P.W., ed.), pp. 127–140, Elsevier North Holland Press
- 75 Sakai, A.K. *et al.* (1995) Origins of dioecy in the Hawaiian flora. *Ecology* 76, 2517–2529
- 76 Vagvolgyi, J. (1975) Body size, aerial dispersal, and origin of the Pacific land snail fauna. *Syst. Zool.* 24, 465–488
- 77 Asche, M. (1997) A review of the systematics of Hawaiian planthoppers (Hemiptera: Fulgoroidea). *Pac. Sci.* 51, 366–376
- 78 Harbaugh, D.T. and Baldwin, B.G. (2007) Phylogeny and biogeography of the sandalwoods (*Santalum*, Santalaceae): repeated dispersals throughout the Pacific. *Am. J. Bot.* 94, 1028–1040
- 79 Price, T.D. *et al.* (2003) The role of phenotypic plasticity in driving genetic evolution. *Proc. R. Soc. B* 270, 1433–1440
- 80 Armbruster, W.S. and Baldwin, B.G. (1998) Switch from specialized to generalized pollination. *Nature* 394, 632
- 81 Nikula, R. *et al.* (2010) Circumpolar dispersal by rafting in two subantarctic kelp-dwelling crustaceans. *Mar. Ecol. Prog. Ser.* 405, 221–230
- 82 Hembry, D.H. *et al.* (2011) Repeated colonization of remote islands by specialized mutualists. *Biol. Lett.* DOI: 10.1098/rsbl.2011.0771
- 83 Ricklefs, R. and Bermingham, E. (2008) The West Indies as a laboratory of biogeography and evolution. *Philos. Trans. R. Soc. Lond.* 363, 2393–2413
- 84 Blossey, B. (2011) The enemy release hypothesis. In *Encyclopedia of Biological Invasions* (Simberloff, D. and Rejmanek, M., eds), pp. 193–196, University of California Press
- 85 Kisel, Y. and Barraclough, T.G. (2010) Speciation has a spatial scale that depends on levels of gene flow. *Am. Nat.* 175
- 86 Beaumont, M. (2005) Adaptation and speciation: what can Fst tell us? *Trends Ecol. Evol.* 20, 435–440
- 87 Riba, M. *et al.* (2009) Darwin's wind hypothesis: does it work for plant dispersal in fragmented habitats? *New Phytol.* 183, 667–677
- 88 Baldwin, B.G. *et al.* (1998) Molecular phylogenetic insights on the origin and evolution of oceanic island plants. In *Molecular Systematics of Plants II: DNA Sequencing* (Soltis, D.E. *et al.*, eds), pp. 410–441, Kluwer Academic Publishers
- 89 Barnes, D.K.A. (2002) Invasions by marine life on plastic debris. *Nature* 416, 808–809
- 90 Ehrenreich, I.M. and Purugganan, M.D. (2006) The molecular genetic basis of plant adaptation. *Am. J. Bot.* 93, 953–962
- 91 Araújo, M.B. and New, M. (2007) Ensemble forecasting of species distributions. *Trends Ecol. Evol.* 22, 42–47
- 92 Epps, C.W. *et al.* (2007) Optimizing dispersal and corridor models using landscape genetics. *J. Appl. Ecol.* 44, 714–724
- 93 Harmon, L.J. *et al.* (2008) The role of geography and ecological opportunity in the diversification of day geckos (*Phelsuma*). *Syst. Biol.* 57, 562–573
- 94 Hickerson, M.J. *et al.* (2007) msBayes: pipeline for testing comparative phylogeographic histories using hierarchical approximate Bayesian computation. *BMC Bioinform.* 8, 268
- 95 Pool, J.E. *et al.* (2010) Population genetic inference from genomic sequence variation. *Genome Res.* 20, 291–300