Review

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Are islands the end of the colonization road?

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Ecologists have, up to now, widely regarded colonization of islands from continents as a one-way journey, mainly because of widely accepted assertions that less diverse island communities are easier to invade. However, continents present large targets and island species should be capable of making the reverse journey, considering they are the direct descendants of successful colonists and provided that they have not lost their dispersal abilities. Recent mapping of geography onto molecular phylogenies has revealed several cases of 'reverse colonization' (from islands to continents). We suggest this phenomenon warrants closer attention in ecology and biogeography. Assessing its significance will contribute to understanding the role of dispersal and establishment in biogeographic distributions and the assembly of natural biotas.

An emerging paradigm shift for island biogeography

The discipline of island biogeography attempts to discover factors that affect species richness across insular communities [1–4]. MacArthur and Wilson [3] revolutionized the discipline when they suggested that diversity on islands represents a balance between the arrival of new species through colonization (or speciation) and the disappearance of old species by extinction. Because open water presents a strong barrier to dispersal by terrestrial taxa, species richness is lower on oceanic islands than on continents, in contrast to continental islands where geographic isolation is not a significant determinant of species richness [5]. The diversity–invasibility theory [6] further postulates that less diverse communities (e.g. islands compared to continents) should be more susceptible to invasion by exotic species because ecological space is less densely packed and interspecific competition is less intense. Conversely, the more densely packed ecological space of continental biotas should be difficult to invade, particularly by island populations for which evolution in low-competition environments might have produced more generalized phenotypes at a competitive disadvantage in diverse communities. The diversity–invasibility theory has received much support from theoretical studies. However, empirical studies indicate a negative relationship between invasibility and diversity only at local scales, competitive interactions being overridden by habitat suitability at larger scales [7,8]. Thus, the relationship between diversity and invasibility remains unresolved.

Based on a long tradition of thinking about invasion ecology and the evolution of dispersal and competitive ability in island taxa (Box 1), ecologists widely consider colonization of islands from continents as a one-way journey. Nevertheless, 'reverse colonization' should be possible, if not likely, for several reasons. Island species are, for the most part, the direct descendants of successful colonists and, provided that adaptation to island life has not resulted in reduced dispersal ability, island inhabitants should be capable of making the reverse journey. Moreover, although islands tend to have fewer species, continents present large targets for colonization. Explicit molecular phylogenies produced from DNA sequence data since the mid-1990s are beginning to reveal geographic relationships most readily interpreted as cases of reverse colonization (e.g. [9–11]). In a recent review of hypotheses related to oceanic island biogeography, Heaney [12] emphasized that the increasing appreciation for this phenomenon might signal an emerging paradigm shift for island biogeography.

In this review, we first summarize factors that influence the direction of colonization between continents and islands. Second, we characterize the prevalence of reverse colonization and evaluate the degree to which islands might be sources of biodiversity for continents. We then emphasize the importance of considering reverse colonization for interpreting biogeographic patterns and highlight the significance that reverse colonization might have for ecological theory in general. Finally, we suggest some

Glossary

Colonization: dispersal by a species to an area not previously inhabited by that species, with subsequent establishment of a viable population.
Dispersal: the spread of organisms to a new area (a complex process comprising emigration, movement and establishment).
Establishment: the settling of an individual at a new locality where it successfully reproduces; at the population level, long-term persistence.
Extinction: the disappearance of a population or species either locally or globally, depending on the context.
Migration: seasonal migration between different habitats or regions which does not result in dispersal.
Movement: for individuals, the displacement phase between leaving a source locality and arriving at a new locality.
Phylogenetic analysis: use of reconstructed evolutionary relationships to determine the history of trait evolution and geographic distribution.
Reverse colonization: expansion of a species range from an area of low species richness to one of high species richness, specifically from island to continent.
Sink: for a species, an area in which extinction exceeds colonization.
Source area: for a species, an area from which populations colonize new places.
Vicariance: the splitting of a species range into two or more fragments by continental movements or climate change.

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Box 1. Why have ecologists accepted 'unidirectional colonization'?

There is a well-established asymmetry in the minds of ecologists, who generally regard continents primarily as source areas and islands as sinks. From Wilson [52] to the development of metapopulation theory, the concept of 'unidirectional colonization' has been well accepted.

In 1961, one of the world's leading naturalists and ecologists, Edward Wilson, championed the concept of unidirectional colonization. In his study of ants from the Moluccas and Melanesian islands, he stated 'The headquarters (of a taxon) can be shifted from a larger to a smaller land mass ... but not in the reverse direction' [52].

A few years later, Wilson and the mathematical ecologist Robert MacArthur collaborated to develop a theory of island biogeography [3]. Their equilibrium theory described a dynamic balance between colonization and extinction and predicted increasing equilibrium diversity with increasing island size and decreasing diversity with greater distance from a colonization source. Although expanded to include a stepping-stone model with the possibility of migration between islands, their theory designates continents as potential sources of colonization for islands. Three core observations and conjectures have reinforced the notion of unidirectional colonization. First, more species are available as potential colonists in continental source areas because of their larger size. Second, islands have less diverse biotic communities and underutilized resources (ecological space), which are available for arriving colonists. Finally, greater species richness on continents selects increased competitive ability in continental populations, raising the probability that colonists will become established on islands. Loss of competitive ability and dispersal ability by island populations further exaggerates the advantage of continental populations as colonists.

MacArthur and Wilson considered the dispersal of populations across stepping-stone islands, which allowed two-way colonization traffic, but dispersal was influenced mostly by distance. Island biogeography theory has been extended to describe the persistence of single-species metapopulations (i.e. a set of partially isolated local populations in a fragmented landscape) [53]. In contrast to the island biogeography theory, metapopulation theory focuses on population turnover (the extinction and reestablishment of each population on patches), but both theories adopt the premise that colonization flows from larger to smaller sites.

Empirical studies have shown that species diversity generally decreases with increasing distance from the mainland [54,55], which reinforces the asymmetry of colonization. However, this provides no information about the relative propensity of continental and island populations to become colonists.

Although the notion of 'unidirectional colonization' has found support both theoretically and empirically for more than 40 years, molecular phylogenies showing evidence for island-to-mainland colonization open exciting possibilities for studying colonization from the standpoint of individual populations rather than as a statistical property of mainland and island biotas.

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future research directions concerning the issue of reverse colonization.

Which factors influence the direction of colonization between continents and islands?

The direction and probability of colonization between islands and continents depend on dispersal ability, population size and productivity, the relative diversity of source and receiving communities, and environmental conditions in each area.

Many island populations, including birds and insects, lose the ability to disperse long distances, most conspicuously through the evolution of flightlessness, particularly where long-range mobility is not integral to foraging or social interactions, or required for escaping predators [13–15]. MacArthur and Wilson [3] stated that 'several characteristics of adaptation to insular environment can be generalized and documented. The most conspicuous is the tendency to lose dispersal power.' Nevertheless, many species clearly retain the ability to move between islands. This is particularly evident in species that have spread over long distances by island hopping across the western Pacific Ocean to Polynesia and even as far as the Hawaiian Islands [15–17]. Comparisons of indices of dispersal ability (e.g. wing size or flight muscle mass) in sister groups inhabiting islands and continents might reveal potential loss of dispersal ability of species colonizing islands from the continent [14].

Because of the restricted area, island populations produce fewer potentially dispersing individuals than larger continental landmasses, thereby favoring continent-to-island dispersal. This bias is diminished somewhat by the typically higher densities of island populations, which could produce more pressure for dispersal, and larger proportions of individuals living closer to the edges of islands owing to perimeter–area allometry. Indeed, large continental populations might produce relatively few potential over-water colonists. Little is known about the factors that motivate individuals to undertake dispersal movements, and so the numerical argument against island-to-continent colonization is difficult to evaluate.

More diverse communities (i.e. continents compared to islands) are generally thought to be more difficult to invade [6,18,19], particularly for species adapted to the low levels of interspecific competition on islands. Much has been said about the difficulty of invading diverse communities, especially in the context of 'invasive' species becoming established in 'natural' habitats [20,21]. For example, one study identified a set of 'supertramp' bird species in the western Pacific that readily colonize across great distances, yet are unable to invade forested habitats or larger islands with high species richness [22]. However, theory does not preclude specialists from invading diverse communities; the proportional relationship between local and regional diversity in many systems [23,24] and the inverse relationship between island diversity and distance illustrate the importance of colonization pressure in augmenting local diversity [25,26]. Indeed, the overwhelming volume of species traffic to islands might simply reflect the high diversity of continental biotas relative to those of islands as sources for colonization, and not different probabilities of colonization and establishment of individual populations.

The lower diversity of islands might also apply to predators and pathogens. Insular populations that lose natural defenses against such antagonists might be less suited to more dangerous continental environments. Cases of island populations losing their fear of predators or their defenses against introduced diseases (e.g. malaria in the Hawaiian avifauna [27,28]) have been well documented. As in the case of reduced dispersal ability, if defenses diminish over evolutionary time, the window of opportunity for island-to-continent colonization might be narrow.

In conclusion, several factors might place roadblocks in the way of island populations becoming established on the

continent. However, island-to-mainland colonization events are possible and might be more frequent than commonly assumed (Box 2).

Evidence for reverse colonization

The arrival of new species on islands has been attributed to four main processes (see Ref. [29] for a review): vicariance, colonization across land bridges (e.g. during low sea-level stands associated with glacial maxima), translocation by humans and over-water dispersal. Although most previous work on island biotas has assumed that species derive from continental source areas, phylogenetic analysis provides a method for assigning the origin of individual lineages. Indeed, it is difficult to unambiguously identify cases of reverse colonization without phylogenetic reconstruction of the ancestry of populations and species. In general, when an island lineage is imbedded within a clade otherwise restricted to a continental region, one can infer that colonization occurred from continent to island. When continental lineages are imbedded within clades restricted to islands or archipelagos, one can infer reverse colonization as the most likely scenario.

To estimate the prevalence of reverse colonization, we searched the literature for molecular phylogenies of non-human terrestrial animals that included a clade of species inhabiting both continental landmasses and islands, focusing on over-water dispersal. We disregarded large island fragments of continental crusts, such as Madagascar, Australia, New Caledonia, New Zealand and New Guinea, which could be regarded as 'mini-continents,' and thereby create ambiguity concerning reverse colonization. Thus, our survey focused on both continental and oceanic islands that are small relative to continental source areas and that have presented the same dispersal barrier in both directions (barring directional bias from ocean or wind currents) over the entire histories of the species of concern.

Thirty-seven studies published between 1988 and 2008 fit the above criteria (Table 1; Figure 1). More than a third of the studies show evidence of reverse colonization, revealing continental lineages nested within island clades (shown in bold in Table 1). The clearest examples included birds (bananaquit [30], flycatchers [31], monarch flycatchers [10], parrots [32], Darwin's finches [33], catbirds [34] and orioles [35]), lizards [11,36], frogs [9,37], short-faced bats [38], drosophilid flies [39] and turtles [40]. Only a few of these studies explicitly discussed the phenomenon of reverse colonization [10,11,39].

In all of the cases of reverse colonization, the lineages had crossed water barriers at least once to establish the island populations. However, not all of these species disperse easily across open ocean. For example, frogs and lizards relocate by rafting [41,42]. Colonization of the West Indies by reptiles and amphibians from continental areas of the Caribbean Basin has been infrequent, at intervals of perhaps 0.75 My judging from age distributions of island lineages [43,44]. Many of the recolonizers, including some birds, have not dispersed further within island archipelagos, even though a member of the clade was able to colonize a continental landmass. For example, the three species of orioles (*Icterus*) in the Lesser Antilles are highly endemic to individual islands (Montserrat, Martinique, St. Lucia),

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Box 2. Reverse colonization is poorly known but can be detected by phylogenetic reconstruction

Reverse colonization has been underappreciated because of a widespread prejudice against it and a lack of the phylogenetic data required for identifying these events. Recent studies suggest that the phenomenon probably is more common than previously assumed. In our literature survey of clades with suitable molecular phylogenies, about one-third of those involving terrestrial animals provide evidence of over-water dispersal from islands to continental regions. Based on morphological and molecular observations, several cases of reverse colonization have also been found in Macaronesia flora [49], and the author of this study considers that such events might be 'far more frequent than presently considered' (J. Caujapé-Castells, pers. comm.).

Identification of reverse colonization requires appropriate sampling of taxa and DNA sequences. The well-established assumption of unidirectional colonization (see Box 1) might fail to motivate investigators to sample continental and island taxa sufficiently. Reverse colonization is apparent only when continental lineages are nested within island radiations, and nesting can be identified readily only with large samples of taxa. When lineages have not diversified on islands, reverse colonization produces an ambiguous sister relationship between island and mainland taxa, and thorough sampling of both island and continental taxa is needed to estimate how many of these cases might involve reverse colonization.

Identification of reverse colonization also requires well-supported phylogenetic relationships among island and continental taxa. Because many island-to-continent colonization events might have occurred recently in evolutionary time, relationships among these continental and island taxa might not be well resolved. Thus, lack of polymorphism in genetic markers could hinder the discovery of reverse colonization. Newly developed sequencing techniques, such as the high parallel sequencing systems [56] that allow a 100-fold increase in throughput over current Sanger sequencing technology, will probably help to solve this problem.

Finally, extinction of lineages that arise from ancestral splitting events can erase the evidence of phylogenetic nestedness needed to identify the direction of colonization. Because extinction rates are thought to be higher on islands than in continental regions, extinction might obscure more cases of reverse colonization than continent-to-island colonization. In principle, this bias might be evaluated by constructing models of evolutionary diversification, extinction and forward and reverse colonization that allow one to estimate each of these rates from empirical data [57]. However, estimating multiple variables probably will require many phylogenies from several taxa, permitting only generalized results that obscure heterogeneity in rates among taxa and islands.

Our compilation of studies from the literature (Table 1) suggests variation in the proportion of reverse colonization events between island groups and between organisms. First, island-to-continent colonization accounted for less than 10% of colonization events reported for the endemic Macaronesian flora [49], compared to ~38% for animal taxa. Relative frequency of reverse colonizations also differed between animal groups, being lower in insects and mammals compared to birds, reptiles and amphibians. Second, reverse colonizations were more frequent in the West Indies compared to other island groups or archipelagos. Determining whether these discrepancies reflect actual patterns or biases in data collection must await further sampling. However, reasonable assumptions are that reverse colonizations will be more frequently detected from archipelagoes than from single islands because of the higher potential for diversification in archipelagos. Large islands or island groups might also produce more reverse colonists because the retained diversity resulting from lower extinction rates facilitates the identification of unambiguous reverse colonization and also might select higher interspecific competitive ability for successful establishment in diverse continental communities. Dispersal distances, favorable winds and currents, and ecological similarities between continental and island environments might also favor reverse colonization more in some island groups than others. In the end, further ecological and biogeographic studies of reverse colonization might have to rely on a few well-supported cases.

Table 1. Examples of studies of molecular phylogenies of terrestrial animal species inhabiting both continental landmasses and islands, showing evidence of over-water dispersal (see the main text for selection criteria). Examples of reverse colonizations are in bold)

Taxon	Organism	Colonization route	Refs
Birds	Bananaquits	**From the West Indies to South-Central America**	[29]
	Hummingbirds	From South America to the West Indies	[58]
	Mockingbirds (*Mimidae*)	From South America to the Galápagos Islands	[59]
	Grey parrot (*Psittacus erithacus*)	From Gabon to the Island of Principe (Gulf of Guinea)	[60]
	Galápagos hawks (*Buteo galapagoensis* and *B. swainsoni*)	From Argentina to the Galápagos Islands	[61]
	Bush-warbler (*Cettia*)	From Southeast Asia to Bougainville Island (New Guinea)	[62]
	Vitelline warbler (*Dendroica vitellina*)	From North America to the Cayman Islands	[63]
	Pacific monarchs (*Monarcha*)	From Australia/New Guinea to Micronesia, Sulawesi, Polynesia, Solomon Islands	[9]
		And from Solomon islands to New Guinea/Australia	
	Myiarchus tyrant-flycatchers	From South America to northern Central America and the Caribbean	[30]
		And from the West Indies to northern South America	
	Psittacula parakeets	From India across the Indian Ocean to Mauritius	[64]
	Amazona parrots	**From the West Indies to South-Central America**	[31]
	Kestrels	From Africa via Madagascar toward Mauritius and the Seychelles	[65]
	Thrashers, tremblers and mockingbirds (*Mimidae*)	From South and Central America to the West Indies (three cases)	[33]
		And from the West Indies to North America (weak evidence)	
	Orioles (*Icterius*)	From Central America to the West Indies	[34]
	Gray-crowned babbler (*Pomatostomus temporalis*)	From Northern Territory, Australia to Melville Island	[66]
		And from Melville Island to Northern Territory, Australia	
	White eyes (*Zosterops*)	From Australia to the Heron Islands	[67]
	Darwin's finches	From Central and South America to the Caribbean, Cocos Island and the Galápagos archipelago	[32]
		And from the Caribbean to South America	
Insects	Coleopters (*Carabidae*)	From the Iberian Peninsula to the Balearic Islands	[68]
	Butterflies	From South and Central America to the West Indies	[69]
	Scaptomyza	**From Hawaii to Africa either through Asia or through North/South America**	[38]
	Drosophila	From Florida to the West Indies	[70]
	Drosophila	From Cameroon to Sao Tomé (Gulf of Guinea)	[71]
	Coleopters (*Calathus*)	From North Africa to the Canary Islands (four colonizations) and from the Canary Islands to Madeira	[72]
	Spiders in Hawaii (different genera)	From South-Central America to Hawaii	[73]
Mammals	Mouse (*Mus cypriacus* and *M. macedonicus*)	From the eastern Mediterranean area to Cyprus	[74]
	Philippine endemic rodents (*Murinae*)	From the mainland to the Philippine Islands followed by a colonization between islands and a diversification within the archipelago	[75]
	Nyctalus bats	From Europe to Madeira and from North Africa to the Canary Islands (*N. leisleri*), and from Europe to the Azores (*N. azoreum*)	[76]
	Short-faced bats (*Stenodermatina*)	From South America to the West Indies	[37]
		And from the West Indies to Central America	
Reptiles	Anoles (*Norops*)	**From the West Indies to Central and South America**	[10]
	Lizards (*Anolis carolinensis*)	**From Cuba to other islands and the southeastern United States**	[35]
	Snakes (Bothrops jararaca complex)	From the Brazilian Atlantic forest to near islands (Alcatraz and Queimada Grande)	[77]
	Geckos (*Hemidactylus*)	From Africa to Sao Tomé, Principe, Bioko (Gulf of Guinea)	[78]
	Gekkonid lizards (*Tarentola*)	From North Africa to Cuba, the Canary Islands and from Gomera/Tenerife to Cape Verde	[79]
	Turtles	From North America to the West Indies	[39]
		And from Cuba to Central America	
	Galápagos tortoise	From South America (Chile) to the Galápagos	[80]
Amphibians	Frog Eleutherodactylus	From South America to the West Indies	[8]
		And from the West Indies to northern Central America	
	Frog Eleutherodactylus	From South America to the West Indies	[36]
		And from the Greater Antilles to Central America	

separated by unoccupied islands with suitable habitat (e.g. Guadeloupe, Dominica) [45]. Apparently, colonization of the South American continent was part of the original spread of the clade from the Greater Antilles through the Lesser Antilles and on to the mainland (Figure 2). Additional taxa and model-based phylogenetic analysis lend further support for this reverse colonization route (R. Sturge and K. Omland, pers. comm.). Evidently, this

was followed by a shutting down of over-water dispersal within the archipelago, judging from the endemism of the contemporary Lesser Antillean populations and the absence of orioles from several large islands.

The frequency of reverse colonization seems to be influenced both by distance to the continent and by the geographic localization of islands. Most of the cases of island-to-continent colonization that we detected (11 of
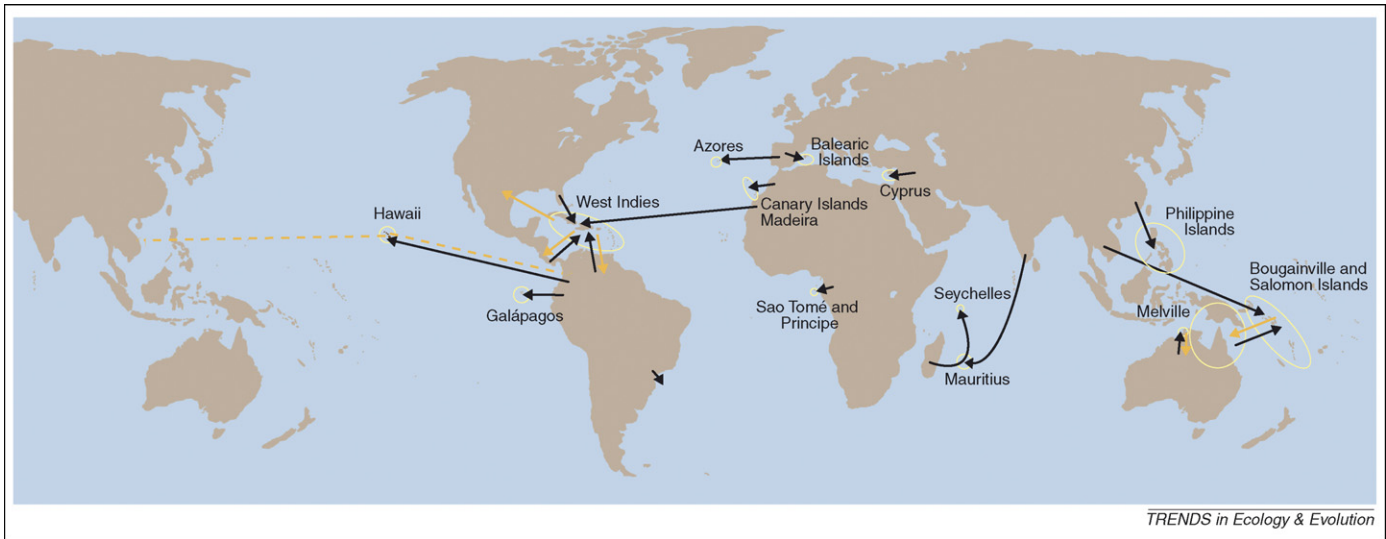
Figure 1. World map showing cases of over-water colonizations (dark arrows) and over-water reverse colonizations (orange arrows) from studies of molecular phylogenies of terrestrial animal clades inhabiting both continents and islands (as described in Table 1). Dashed arrows indicate alternative potential routes of colonizations for drosophilid flies (P. O'Grady, pers. comm.).

14 cases) were confined to the well-known fauna of the West Indies region, with colonizations from the West Indies to South, Central or North America (Figure 1), involving water gaps of less than 800 km. The West Indian archipelago is probably favorable for reverse colonization because it is sufficiently close to mainland America to produce a dynamic interaction between continents and islands (but see Box 2). However, two of the examples of

reverse colonizations [10,39], which involve crossing water gaps of between 2000 and 4000 km, demonstrate that long-distance reverse colonizations are also possible. One of these studies [39] showed that two species of *Scaptomyza* (Drosophilidae) from Gough Island in the south Atlantic Ocean are nested phylogenetically within a clade of Hawaiian species, and suggested that their ancestors dispersed out of the Hawaiian Islands to continental regions as eggs
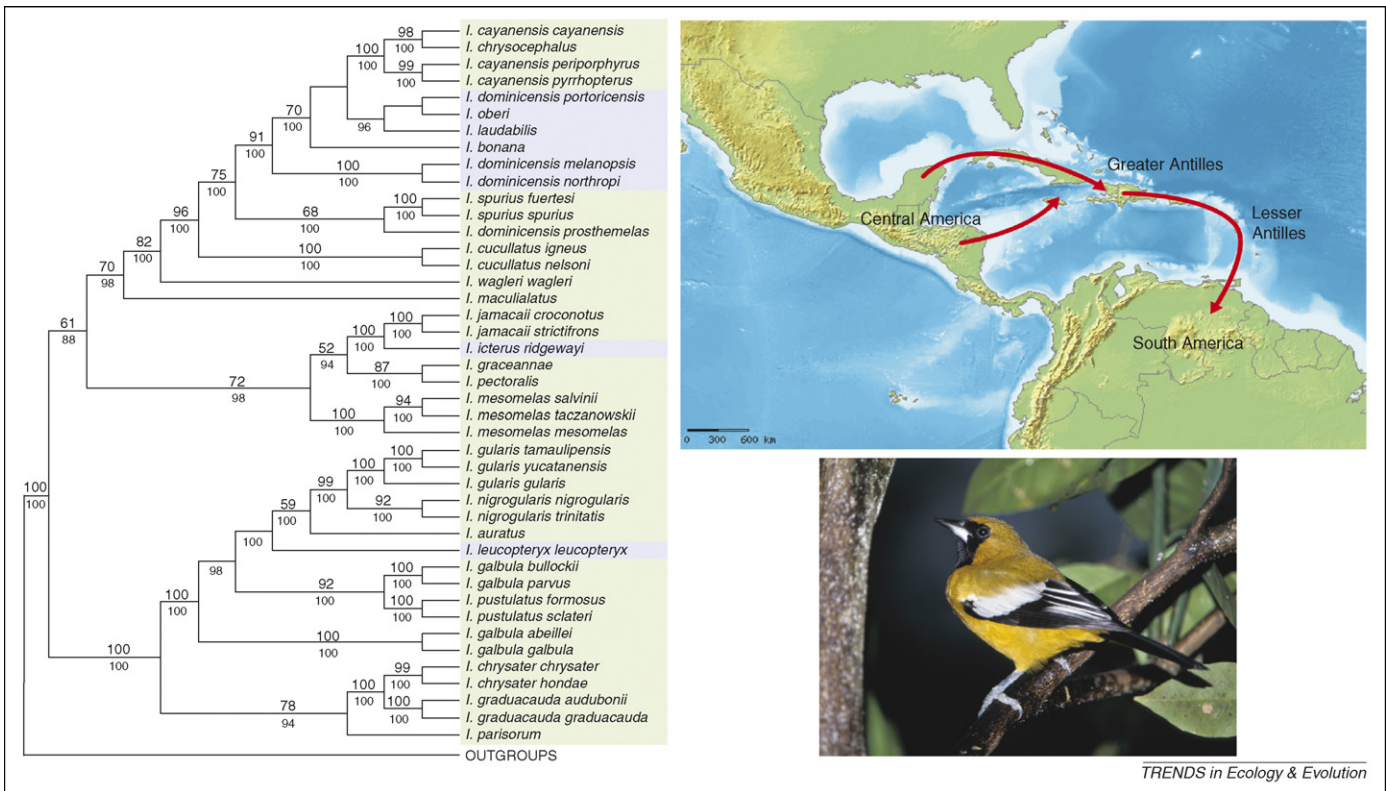

Figure 2. Reverse colonization in orioles (*Icterus*) from the Lesser Antilles. The phylogenetic tree is based on combined mitochondrial data for CytB and ND2. Bootstrap values are shown above branches (100 replications), and jackknife values are shown below branches. Names in blue represent island species and those in green represent continental species. The tree shows that the South American *I. cayanensis* group (top of the tree) is nested with island taxa (birds from the Bahamas, Cuba, Puerto Rico, Montserrat, Martinique, St. Lucia), which indicates colonization from the Greater Antilles through the Lesser Antilles and on to South America. The arrows on the map show the directions of colonizations of the orioles. Adapted, with permission by Elsevier, from Ref. [35].

or larvae in sticky fruits (genus *Pisonia*) carried by birds. This hypothesis implies that one or more lineages of *Pisonia* host plants also colonized the mainland from Hawaii. This has not yet been documented by phylogenetic reconstructions within the genus. Avian transport might have included migrants, such as bristle-thighed curlews (*Numenius tahitiensis*), which regularly fly between North America and Hawaii. Many species of plants and insects might have arrived in Hawaii by island hopping from Micronesia [46] suggesting that populations from small, remote islands are still able to disperse to other places. Long-distance mainland-to-island colonizations have been reported in plants (e.g. [47,48]) and we predict that further phylogeographic studies, involving far islands or archipelagos as well as continents, might shed light on the pattern and frequency of long-distance colonization in both directions.

Although we chose to focus our literature search on terrestrial animals, reverse colonizations have been reported for plants as well, including three cases in Macaronesia. *Convolvulus fernandesii*, a Portuguese neo-endemic of recent origin, represents colonization of the continent from Macaronesia (a minimum distance of 1200 km) [49]. A lineage of the perennial *Androcymbium* (Colchicaceae) is postulated to have colonized the Canary Islands during the Pliocene and later to have recolonized the mainland of Africa [50], although the African *A. wyssianum* is sister to, rather than nested within, the Canarian clade. A more convincing case for colonization from island to continent can be made for the East African *Aeonium leucoblepharum*, which is nested within an endemic Macaronesian radiation [51]. Considering the various mechanisms allowing for long-distance and chance dispersal of plants (e.g. wind, floating in ocean currents, rafting, or movements by birds), such two-way founder events (the 'boomerang effect' [50]) could operate in other species and other geographic contexts.

Conclusion and perspectives

Oceanic islands are not merely sinks for biodiversity but also contribute to continental biotas. Biogeographers have largely failed to appreciate reverse colonization (Box 2), but this neglected phenomenon is important because it alters our perception of the dynamic interaction between islands and continental areas and challenges preconceptions about factors influencing invasion success. Because of the rapidly increasing number of phylogenetic analyses of clades inhabiting both continents and islands, we expect that reverse colonization will soon receive more systematic attention in biogeographic and ecological analyses. Although colonization traffic will be dominated by continental species, island colonists to the mainland might contribute unique variation to mainland communities because of the evolutionary potential of taxa in low-diversity island settings. Indeed, some island-derived clades, such as the *Norops* anoles, have diversified in the continental setting.

The phenomenon of reverse colonization provides a foundation for novel and potentially fruitful avenues of research (Box 2). The 'island–continent' conceptual model of MacArthur and Wilson [3] should be expanded to incorporate reverse colonization, particularly incorporating the impact of evolution in island populations on probabilities of extinction and dispersal. Islands provide unique environments with strong selective pressures on new colonists, considering the rapid evolution and diversification of some island taxa. Empirically, we can evaluate the frequency of reverse colonizations (i.e. colonizations resulting in successful establishment of populations in continental regions) compared to continent–island colonizations and, using molecular dating, whether the probability of reverse colonization of an island population declines with time. Much can be learned about the ecology of invasions from island-to-continent colonists. Conventional wisdom suggests that more diverse continental communities are difficult to invade. Accordingly, one might expect 'reverse colonists' to occupy ecologically peripheral or specialized positions in continental communities, perhaps with little potential for further diversification. Thus, much could be learned from the ecological and geographic distributions, as well as the evolutionary fates, of reverse colonists. How are they differentiated ecologically from species in continental communities? What ecological and genetic traits characterize island populations that have become reverse colonists? How important is genetic diversity to colonization success? What characteristics of reverse colonist lineages are associated with further diversification in continental settings? Answering these questions will require, as an initial step, a large sample of reverse colonization events that can be used to test clearly stated predictions from hypotheses concerning colonization potential, invasion success and community assembly.

Reverse colonization is important, perhaps above all for refining our concepts of colonization, community assembly and evolution on islands. We hope that the cases of reverse colonization highlighted here will stimulate new work, with respect to both phylogenetic and ecological analyses, on the phenomenon of reverse colonization, contributing more generally to the role of dispersal and establishment in biogeographic distributions.

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