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Carlquist revisited: history, success, and applicability of a natural history model

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Abstract In 1966, island biogeographer Sherwin Carlquist published a list of 24 principles governing long-distance dispersal and evolution on islands. The 24 principles describe many aspects of island biology, from long-distance dispersal and establishment to community change and assemblage. Although this was an active period for island biogeography, other models and research garnered much more attention than did Carlquist's. In this review, over 40 years of support for or against Carlquist's principles is presented. Recent work has supported most of the 24 principles, and improved methodologies have generally substantiated his initial claims. However, Carlquist's original work and ideas remain relatively underrepresented in the biogeographic literature. Use of philosophical model domains provides one explanation as to why Carlquist's work has received little attention. Carlquist's principles are largely natural history tests, and don't translate well into the theoretical, design of preserves, or the experimental domains—whereas other competing models do well in such domains.

Keywords Sherwin Carlquist · Long-distance dispersal · Island biogeography · Model domains · Natural history · Oceanic islands

Introduction

Oceanic islands have long been of high value and interest to biogeographers. The idea that islands offer discrete windows into evolutionary processes gained momentum during the Darwin-Wallace era (Carlquist 1966). Even before Darwin and Wallace, however, travelers made many of their observations about the

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distribution of species on the basis of islands. More recently, islands became prominent in studies on the distribution of biodiversity (Diamond 1975) as well as ecological rules, histories of species, and evolutionary rules (Carlquist 1966). Amid the heated debate between vicariance and dispersal biogeographers during the 1960s, MacArthur and Wilson (1963, 1967) published their equilibrium theory of island biogeography (ETIB). Concurrently, new ideas about plate tectonics contributed to the debate by both answering long-standing conundrums and positing new questions regarding geographic distributions of organisms. Work on island biogeography has been steady since the 1960's (Diamond 1975; Simberloff and Wilson 1970; Whittaker 1998), but work on the rules governing the evolution and history of island species has been more diffuse—perhaps in part because of a lack of tools to address historical questions.

Contemporaneously with the development of ETIB, a separate body of theory developed among dispersal biogeographers, which focused not on a general model of biogeography, but rather suites of evolutionary predictions or principles regarding the traits and processes associated with species on oceanic islands. Sherwin Carlquist (1966) presented 24 principles that he believed governed long distance dispersal, natural history, and evolution on islands. Although arguably more testable and diverse than the headlining ETIB model, Carlquist's principles did not receive the same lasting attention as ETIB. For example, although there have been many tests of individual aspects of Carlquist's predictions and Carlquist's work is regarded as a "classic" in biogeography, his body of predictions was never reviewed in a comprehensive manner. His work represented an attempt to more fully explain the mechanisms and limitations of long distance dispersal than did ETIB; while MacArthur and Wilson strove to predict the end of the story, Carlquist set forth to explain the plot. Currently, a broader review of Carlquist's principles—including their perceived success or failure—does not exist.

If Carlquist presented detailed and thoughtful predictions during a period of activity in the development of biogeography, why do his ideas about evolutionary trends on islands tend to be less known than others from the same time? To answer this, we propose a two-dimensional analysis for assessing the legacy of Sherwin Carlquist. First, we will review 40 years of literature that support or refute each of his 24 individual principles in order to judge not only how specific ideas have survived, but to understand the general success of his body of work. Second, we present a philosophical argument—using Carlquist as a case study—as to why some models do not become mainstream in ecology. We have adopted Sismondo's (2000) four philosophical model domains for this analysis, but structure them in a unique way.

In building a framework for our analyses and discussion, it is important to understand the differences between Carlquist's principles and ETIB. Several of the key distinctions between ETIB and Carlquist's principles are: (1) the relative difficulty of testing Carlquist's predictions; (2) the breadth of their apparent applicability; and (3) perhaps as a consequence, the relative amount of attention paid to them in the literature. MacArthur and Wilson's ETIB was revolutionary, partly due to the simplicity of its model. While the model's success remains debated (Gilbert 1980), there is little doubt that in the past 40 years it has successfully infused the scientific—and most notably the biogeographic—communities. The theory of island biogeography has elicited numerous responses, ranging from the philosophical (Sismondo 2000) to the experimental (Cairns et al. 1969; Rey and Strong 1983; Simberloff and Wilson 1970). In contrast, Carlquist's principles relate to the specifics of island faunas, their histories and tendencies—specifics that rely not only on statistical tests, but on historical data as well. This approach has resulted in fewer publications explicitly responding to either Carlquist's individual principles or his larger theory. Subsequently, in over four decades since publication, the body of ensuing research is significantly smaller and less organized than that which followed ETIB. However, new technologies, an increased understanding of global biodiversity patterns, and recent phylogenetic refinements have all helped to add to the body of literature that has tested Carlquist's principles in subsequent decades.

This paper will present a review of biogeographic literature, serving to support or question—individually as well as holistically—Carlquist's 24 principles of dispersal and evolution (1966). The 24 principles have been partitioned into smaller, logical groups to investigate. Along with this assessment, we will highlight where the predictions fall in a structure of model domains, and use this to explore reasons why Carlquist's ecological contribution—while large and diverse in its coverage—has been relatively small in legacy. We hypothesize that a partial explanation as to the lack of recognition of Carlquist comes from the nature of the model domains; i.e., it is likely that Carlquist only operates in a specific domain(s) and that other, more popular models can be categorized in other domains. Finally, the future of Carlquist's contributions will be discussed.

(Throughout the paper ordinal values will refer to individual principles (Table 1), unless otherwise suggested. Likewise, the term 'island' will refer to oceanic islands unless otherwise stated.)

Model domains

We have adopted the four model domains proposed by Sismondo (2000) and will describe them here. The first domain is naïve realism, the realm in which natural history studies operate. This domain is rooted in the idea of perception or observation; e.g., a prediction might fall into the naïve realism domain if it derives a pattern from an observed natural phenomenon. The second domain is instrumentalism, the category in which a testable model and its predictions would fall. For example, if an ecological principle identified an area that was expected to contain more species or was otherwise a candidate for conservation (and this outcome could be tested against the expectation), we would consider this instrumentalism. The third domain Sismondo (2000) outlines is metaphysical realism—the idea that science can be a window to reality. This domain is realized through experimentation, and candidate principles for this domain would include those in which control and manipulation can take place. Often, metaphysical realism is the domain in which individual pieces of a larger principle can be deconstructed and explicitly tested. Finally, the last domain we will use is rationalism. Rationalism generally is characterized by intellect and deduction over perception, and the principles

Table 1 Carlquist's 24 principles of long-distance dispersal and evolution (1966)

Our grouping	Principle no.	Principle
A1	1	Disharmony in species composition is evidence of long-distance dispersal
A1	2	Positive adaptations for LDD are key to disharmony, meaning disharmony is not a negative concept
A2	3	LDD is more successful with repeated or simultaneous introductions
A2	4	Among organisms for which LDD is possible, eventual introduction is more probable than non-introduction.
A2	5	Elements are present not only in proportion to dissemination Ability, but also establishment ability
A3	6	Migration is governed by chance and probability
A3	7	Now-vanished islands may have aided dispersal in the past by serving as "stepping-stones" to remote islands
A4	8	Size and systematic composition of insular biotas between islands are determined by factors which differ in relative importance
A4	9	Relicts in the strictest sense are few or absent on oceanic islands, but "recent relicts" represent more primitive island autochthones
A4	10	Immigrant species must overcome the restriction of genetic material related to the very small size of the initial population
B1	11	Rapid evolution of island immigrants is possible and frequent
B1	12	Adaptive radiation is the inevitable result on a small landmass where species face a broad array of ecological opportunities
B1	13	An immigrant group that is not confronted with a broad spectrum of available niches may evolve into one or a few niches
B2	14	New growth forms evolve among plants on islands, with a trend towards increased stature
B2	15	Changes in form, size, and color of animals often occur on islands, such as gigantism and dwarfism
B2	16	Dispersal mechanisms and dispersal ability may be lost during evolution of plants following establishment
B2	17	Flightlessness may evolve in volant groups of animals in response to insular conditions such as wind and lack of predators
B2	18	Competitive ability is often decreased among island endemics
B2	21	Pollination relationships correspond to and change with respect to availability of pollinating agents
B3	19	Means for out-crossing become highly developed in waif floras
B3	20	Natural hybridization acquires a positive value in evolution of waif biota
B3	22	Some otherwise disadvantageous mutations may have a more neutral value in the less competitive environment of an island
B4	24	Evolutionarily plastic groups will be indicators of evolutionary direction in biota after LDD
B4	23	Endemism is not itself a criterion for identification of an island as oceanic, but the nature of the endemism may be

The Group column corresponds to the treatment of principles in this review, while the Principle no. and Principle columns represent Carlquist's original classification considered rationalist are those that work toward theoretical elaborations without intent for explicit testing.

We have elected to use this model framework because we think it is appropriate in classifying Carlquist's principles and an existing investigation (Sismondo 2000) has already been conducted using these same model domains to explore MacArthur and Wilson's ETIB (1963). We acknowledge that other domains as well as variations on these domains exist.

Review of principles

Carlquist's principles tend to fall into two natural groups that we will consider in turn (Table 1). The first 10 predictions represent a group that addresses species arrival via long distance dispersal (LDD) and ideas governing establishment. The final 14 predictions represent the second group, which addresses the mechanisms behind the changes that take place after establishment and works toward predicting general trends on varying levels, from species to community. Within these two groups we identified clusters of predictions (e.g., disharmony, routes of dispersal, morphological changes) that were sufficiently related as to make them useful to consider together. Along with each principle's literature review, we suggest the domain in which the principle would most logically operate.

Group A: Arrival and establishment

To successfully establish a persistent population on an island (or continent, in the context of species invasions) a species must overcome several obstacles. Although dispersal filters (i.e., obstacles) work against the immigration of many species, understanding these filters helps to distinguish the characteristics that are favorable for dispersal. Disharmony—a phenomenon that results in different patterns of mainland and insular fauna—can offer evidence for dispersal and filters, and the ideas surrounding rates of establishment, routes of dispersal, and island-species lineages help to articulate and interpret dispersal successes.

Disharmony as support of filters and LDD (Principles 1, 2)

Carlquist cites disharmony—the disproportionate presence of species with an ability to disperse over long distances—as evidence of long distance dispersal. Many studies have supported the idea that island biota can be disharmonic, though whether such disharmony is the rule or not remains unclear. The expectation of Carlquist's disharmony principle states that island biota should be biased toward representation of lineages and traits associated with good dispersal relative to a random draw from mainland species of the same taxa. As such, major taxa thought to be better dispersers, such as plants (seeds), flying insects, birds, and bats should be better represented on island than non-volant mammals, amphibians, and flightless birds and insects (De Queiroz 2005). Lomolino (2010) makes the point that the limited dispersal ability of many predators—such as terrestrial carnivores—can allow "super-generalist" species to expand their niche breadth and undergo adaptive radiation into new ecological roles, creating a further faunal disparity relative to ancestral mainland communities. Van der Geer et al. (2010) note that regionally disharmonic mainland fauna can indicate that some areas, such as the Gargano peninsula of Italy, were isolated islands at some point in the past.

Recently, studies of disharmony have begun to look at asymmetrical influences—dispersal tending in a certain direction based on wind, ocean currents, and other processes independent from a species' ability to simply disperse (Cook and Crisp 2005). Geiger et al. (2007) used molecular phylogenies to analyze the distribution of ferns and lycophytes of the Hawaiian archipelago, and found strong evidence to support hypotheses of specific dispersal routes (e.g., via the northern subtropical jet stream) for specific genera. Hoekstra and Fagan (1998) found that climactic factors and unfavorable ocean currents act as filters to dispersal for small mammals in the Kuril Islands, creating communities in which mammal diversity is proportionally dominated by large carnivores, an unusual occurrence on oceanic islands.

Principles 1 and 2 tend to fall into the naïve realism domain, as disharmony can be generally thought of as an observation of dispersal. Some instrumentalism is possible, because taxonomic predictions can be made based on dispersal abilities. Carlquist, however, does not propose a specific model or prediction and therefore we consider these principles to be naïve realism.

Establishment is difficult to achieve and to test (Principles 3, 4, 5)

Once an organism arrives, success may depend on a separate set of traits that favor another non-random (disharmonic) subset of species. (Carlquist 1966; Egler 1942). As Carlquist (1966) states, "Difficulties of establishment seem much greater than those of transport." Two kinds of evidence serve as appropriate tests of this principle. First, one can test whether molecular data suggest single or multiple colonization events. Phylogenetic analyses of Macaronesian woody shrubs (Kim et al. 1996), Jamaican crabs (Schubart et al. 1998), Canary Island skinks (Brown and Pestano 1998) and Madagascan tortoises (Caccone et al. 1999) all suggest single colonization events. Gillespie et al. (2008) note that Hawaiian flora and fauna appear to have resulted from far fewer colonization events than there are species, making the point that adaptive radiation can create abundant diversity from relatively few successful establishments, although this does not necessarily imply that single event colonization is common. Although Carlquist views single colonization events as unlikely, he did not discount the possibility, and he failed to specify what defines a multiple-colonization event. This leads to unresolved questions such as whether the simultaneous arrival of multiple individuals could be considered a single event.

A second approach to the issue of establishment is to consider biological invasions. Perhaps the best support for Carlquist's prediction that successful taxa are often those that are introduced multiple times comes from studies of introduced and invasive species. Data from cheatgrass (Novak and Mack 2001), non-native ants (Suarez et al. 2005) and birds (Green 1997) all follow Carlquist's prediction that successful establishment is a function of repeated introductions. In many cases of modern biological invasion, LDD was facilitated by anthropogenic activity, although these cases are still useful for insight into principles of establishment. Support has been generated for this prediction from the study of orchids, which tend to be good dispersers yet poor establishers (McGlone et al. 2001; Bernardello et al. 2006).

Additional studies have supported Carlquist's argument by showing that multiple events are correlated with increased genetic diversity (Dlugosch and Parker 2008), providing evidence for multiple colonization routes for a given taxa (Jones and Kennedy 2008), and demonstrating multiple haplotypes within a given morphotypes among island fauna (Percy et al. 2008).

Much like disharmony, Principles 3, 4, and 5, as Carlquist describes them, all fall into the naïve realism domain; what we have are a series of observations or perceptions, and the specifics that Carlquist provides are often not what was actually tested in subsequent studies. Numerous researchers have studied colonization and establishment, but the studies are varied and do not focus on one instrumentalist prediction.

Dispersal routes speak to historical debate (Principles 6, 7)

Several aspects of Carlquist's model touch on issues that continued to be debated within the scientific community for decades after his paper was published. For example, Principles 6 and 7 are historical insofar as they address the long-standing debate of biological provinces and land bridges. These debates trace their history nearly as far back as the field of biogeography itself, and, prior to 1966, it had been proposed that the ability of provinces and land bridges to govern species distributions were ineffective as applied to islands (Mayr 1944).

Carlquist predicted that chance might play a larger role than predetermined provincial borders in shaping faunal communities. In subsequent decades, researchers have repeatedly concluded that chance plays a large role in species dispersal and distribution (Connor and Simberloff 1979; Martin 1981; Terborgh 1971; Turner et al. 1998), although in some cases random models have shown to be weak predictors of species distributions (Stone and Roberts 1990), such as for the Galapagos finches (Alatalo 1982), spiders inhabiting a group of lake islands (Ulrich et al. 2010), and mammals of the Sundaland islands in Southeast Asia (Cardillo and Meijaard 2010).

Likewise, Carlquist's argument for the significance of stepping-stones to dispersal has been supported in subsequent studies, and it appears that this mechanism can occur in a variety of ways. For example, Díaz-Pérez et al. (2008) found that the genetic structure of red fescue plants in the Macaronesian islands suggests multiple stepping stone patterns taken by different fescue species: a bi-directional centripetal dispersal sequence of dispersal for *Festuca agustinii*, an east–west pattern associated with volcanism for *F. francoi*, and an opposite west-east pattern for the more evolutionarily recent *F. petraea*. It has even been suggested that artificially constructing stepping-stones between coral reefs may be a promising conservation strategy for maintaining gene flow across disturbed or destroyed reef areas (Hellberg 2006).

Similarly, studies have demonstrated high rates of endemism along certain stepping-stone routes (de Forges et al. 2000). While endemism and mechanisms associated with loss of dispersal ability will be discussed in later principles, these patterns would be expected if species colonize via movement across adjacent islands, thus supporting the stepping-stone hypothesis. When utilizing oceanic and atmospheric patterns and processes as predictive mechanisms for dispersal events, it is prudent to consider phylogenetic patterns within a set of islands. This allows the mapping of genetic isolation and diversification over time, which may act as an indicator of larger historical biogeographic processes (Morrone 2010).

Principles 6 and 7 fit easily into naïve realism, because they describe natural history. Carlquist (1966) makes a point to describe how difficult it is to come up with any specific prediction, noting that previous attempts to do so have been hampered by the inherent complexity of dispersal and the wide ranges of priorities held by biogeographers and biologists.

'Relict' offers various interpretations and mixed support (Principles 9, 10)

Perhaps some of the most striking evidence against Carlquist's model involves species ancestry, although some of the controversy can be expressed as a debate over the definition of the term 'relict.' Carlquist (1966) posited that although ancestral forms of many endemic species with low dispersal ability could travel between islands, specific examples are sparse. In the event that these ancestral mainland relatives go extinct, the island forms become relict species. He suggests that the true trend is for speciation to render "recent relicts" of those species that have increased the frequency of speciation upon arrival. Cronk (1987, 1992) has been a major proponent of the idea of "true relicts" on oceanic islands. The main distinction between the definitions used by Carlquist and Cronk are that Carlquist's "recent relicts" have significantly diverged from their mainland ancestors, due to the rapid cycles of extinction and speciation facilitated by the shuffle to obtain and expand into open niches after colonization of an island. Cronk (1987) cites that up to one-third of the St. Helena flora could be classified as extreme relict endemics, and later coined the term "paleoendemic" to describe those species with a founding lineage from a continental source that has not left any descendents (Cronk 1992). Other studies—such as work with *Argyranthemum* spp. (Francisco-Ortega et al. 1995), eyeless arthropods (Peck 1990), and ferns on islands surrounding southern Africa (Aldasoro et al. 2004)—also suggest a stronger meaning for the term relict than Carlquist uses, by demonstrating that relict species may not be strongly divergent from ancestral mainland populations. In light of these patterns, it has been suggested that paleoendemics be targeted as conservation priorities (Kier et al. 2009). Support for Carlquist's less stringent definition of relict exists in studies involving eyeless subterranean fauna (Howarth 1987) and work with the genus *Pericallis*, which is shown to be woodier than its mainland ancestors (Panero et al. 1999). As with any attempt to package natural entities into human-created categories (e.g., neoendemic vs. paleoendemic relicts), some of this disagreement is likely an artifact of trying to dichotomize organisms that exist along a spectrum of degrees of divergence from mainland predecessors. At best we can conclude that both sides will have strong arguments until the definition is standardized and further genetic work clarifies questionable phylogenies.

It is commonly asserted that the smaller the initial gene pool, the lower the chance of establishing a healthy descendant population, a view reflected in Carlquist's tenth principle. For example, McDowall (2003) has shown that all four of Hawaii's endemic freshwater gobies have overcome inbreeding depression through the use of ephemeral streams and the varying ecological opportunities those streams present.

A complete consensus has not been reached on the issue; however, MacArthur and Wilson (1967) dismiss the issue of small founding gene pools as "one reduced to relative in significance" through changes in life history factors involving offspring number and development, immigration rates, and novel environmental conditions. Clegg (2010) points out that bottlenecks in an initial founding population may be more easily overcome than those resulting from population crashes, due to a host of ecological factors and selection pressures. Studies have suggested that reduced genetic diversity may not always be as significant as expected in colonizing populations, especially for asexual organisms (Roman and Darling 2007) and sexual organisms which reach maturity relatively quickly (Neigel 2010). Research has also shown that the correlation between diversity at markers such as mtDNA and microsatellites with quantitative trait loci is not as strong as is often assumed (Reed and Frankham 2001). An additional mechanism of overcoming genetic bottlenecking appears to be resource partitioning (Bernatchez et al. 1999), given that enough heterozygosity remains to facilitate adaptation to open niches (Holt and Gaines 1992).

Carlquist's presentation of Principle 9 could be considered instrumentalism, in simplistic form, as it describes the testable prediction that relicts are absent on oceanic islands. Indeed, recent studies benefitting from newer genetic techniques have tested these predictions, but with mixed results. Principle 10, although also linked to many recent studies examining immigrant populations, lacks a clear expectation or prediction and should be considered naïve realism.

Arrival and establishment predictions accumulate evidence (Principle 8)

Overall, the first part of the model regarding arrival and establishment has been supported by published studies. Carlquist's eighth principle is general and functions almost as a summary of the first ten principles. Its broadness, however, opens up debate as to which of the many factors in determining community composition is of greatest importance.

Determining the relative importance of factors affecting arrival and establishment are of specific concern in the context of predicting and managing biological invasions, whether natural or anthropogenic (Herborg et al. 2007). Dispersing species must overcome 3 main barriers: (1) finding a mechanism of travel to a new site, (2) surviving the transition, and (3) establishing self-sustaining populations at their new site. Non-invasive species will stop the process at that point, but invasive organisms will continue to spread across both physical area and niche space within the community, to the detriment of sympatric species (Kolar and Lodge 2001).

As Carlquist (1966) points out, the relative significance of the given factors involved in overcoming any of these barriers depends upon the specific characteristics of the island in question. While some ambiguity exists surrounding interpretations or relative importance of certain principles—most notably those involving repeated introductions and relict species—Carlquist's wording is broad enough to accommodate a diverse array of situations and studies. Also, evidence contrary to Carlquist's assertions may suffer from lack of developed and standardized experimental methods rather than inherent falsehood of a principle. Regardless, ideas of arrival and establishment will continue to be studied and—if the trend persists—continue to provide support.

Drawing from parts of many of the first 10 principles, Carlquist comes close to the rationalism domain as he begins to identify a conceptual framework and abstract model to describe insular biotas. However, he largely cites criteria (area, altitude, climate, etc.) presented by other biogeographers as possible factors in dispersal and establishment and avoids making a commitment to any specifics. Although Principle 8 could arguably fall into the domain of rationalism, we think there is an absence of specificity to confidently call this an abstract theory. Placing this principle in the domain of naïve realism is also questionable (as this principle is largely comprised of previous predictions), but somewhat safer than labeling this rationalist and therefore we consider this to fall into the domain of naïve realism, but it is perhaps not the clearest example.

Overall, from the first group of predictions we see a strong tendency for the principles to fall into our philosophical domain of naïve realism; Carlquist has coupled his observations of patterns and trends with ideas of natural history to describe tendencies of dispersal. Although these principles have generally been accepted, their lack of predictive power (or the inherent complexity of the phenomenon they describe) has prevented explicit testing and has stifled any movement outside of the domain of naïve realism.

Group B: Change

While numerous factors work against organisms dispersing to and establishing populations on an oceanic island, once a species is established there exist conditions and processes—chiefly evolution—that can often allow species to diversify (Carlquist 1965). There is mild but notable overlap; Principles 9 and 10 are relevant to the themes of both A and B, and provide a bridge between the complex and intertwined factors that influence species dispersal and distribution (Group A) and the processes that take place after an organism has successfully dispersed (Group B). This second group of Carlquist's principles deals with the mechanisms behind the changes that take place after establishment and work toward predicting general trends and outcomes on varying levels, from species to community.

Initial evolution upon establishment (Principles 9, 10, 11, 12, 13)

Evolution, adaptive radiation, and niche partitioning are some of the most substantive developments after establishment, and are treated thoroughly in Carlquist's work. Evidence exists to support the idea of rapid evolution following the founding of a new population; quantifying this process, however, can become difficult when compounded with accounting for other factors such as genetic drift, limited historical genetic material and differing interpretations of 'rapid.'

Allender et al. (2003) outlines several different models for adaptive radiation involving the divergence of color pattern in a radiation of cichlids: (1) a "colonization model" in which each color evolves once and genetic distance correlates to geographic distance; (2) a "character displacement model" in which a given color may evolve multiple times, and sister species are spread between different geographic regions, and (3) a "divergent selection model", in which colors may evolve repeatedly, with genetic distance correlating to geographic distance but not phenotypic similarity.

Adaptive radiation is a process consisting of two components: speciation and the adaptation of existing species to new ecological niches (Gavrilets and Losos 2009). In the case of islands, adaptive radiation suggests "genus-and-family-poor but species-rich" assemblages (Carlquist 1966). This pattern is seen in cases such as Hawaiian lobeliads (Givnish et al. 2009) and Rift Lake cichlids, such as the genus *Tropheops* (Seehausen 2006). Some adaptive radiations consist of relatively few species, which cover a broad range of ecological niches (Ribera and Balke 2007). Carlquist (1966) was able to cite several examples of adaptive radiation, including Darwin's finches and Hawaiian honeycreepers, and subsequent studies have uncovered many more cases of adaptive radiation following colonization. Irschick et al. (1997) suggested that the selective forces—some as-yet to be determined—driving evolution on islands are different than those in mainland communities in *Anolis* lizards. Work with *Tetragnatha* spiders in Hawaii (Gillespie 2004) has shown radiation in the form of divergence of prey-capture techniques as well as diversification of web shape, with convergence occurring between species on differing islands (Blackledge and Gillespie 2004). While ecological factors on islands are various and complex (adaptive radiation in mainland ecosystems is also various and complex, but driven by different factors), adaptive radiation is widely accepted as a common process among insular fauna.

One debatable point about adaptive radiation is defining what qualifies as "rapid evolution." This greatly depends upon the scale of observation: small genotypic changes can accumulate quite rapidly, allowing for the development of disease resistant microbes (Holden et al. 2004) and artificial selection of domestic species has shown that dramatic phenotypic changes can accumulate within the space of a few generations (Lendvai and Levin 2003). Neither of these, however, may be directly comparable to the natural selection pressures affecting ecologically significant traits of colonizing species, which are concomitantly interacting with other evolving species. How fast can evolution happen?

Competing species of *Drosophila* have been shown to evolve to the point of altering competitive outcomes within the span of only 60 years (Krebs and Barker 1993). Slikas et al. (2002) were able to narrow certain Pacific flightless bird speciation down to a window of 500,000 years, suggesting rapid evolution relative to mainland populations.

Perhaps the least supported of the principles in Group B addresses "incomplete" or "lop-sided" adaptive radiation (Carlquist 1966). This seems to be an ill-defined concept that tries to categorize circumstances in which some species within a clade are more successful in radiating into new niches and undergoing correlative speciation than their congeners. While not disproven, little recent evidence has worked to promote the idea of incomplete radiation. To clarify this issue, it is necessary to further delineate the types of evolutionary changes island populations can be expected to demonstrate.

Carlquist (1966) cites examples of niche partitioning on islands, and many studies have demonstrated this phenomenon amongst a wide variety of species ranging from dinoflagellates (Sampayo et al. 2007) and insects (Ishil et al. 2008) to sea birds (Young et al. 2010) and even between recently introduced and native mammalian carnivores (Phillips et al. 2007). By and large, studies have shown that when confronted with a new suite of resources and reduced or altered competition structures, dispersed organisms tend to fill vacant niches and subsequently broaden their ecological repertoire. These radiations have been shown to be replicative between different clades faced with similar ecological circumstances (Schluter and McPhail 1993, Siepielski and Benkman 2004).

Principles 11, 12, and 13 are best classified as naïve realism, as they lack the specifics and predictive power of instrumentalism, the nearest possible domain. Principle 11 doesn't appear to offer much new insight to the rapid evolution debate and the adaptation discussed in Principles 12 and 13 cover ideas that have been widely studied. Without a specific expectation presented by Carlquist, researchers have generally not returned to Principle 11 to make comparisons.

Predicted morphological and structural changes (Principles 14, 15, 16, 17, 18, 21)

Carlquist believed that island biotas tend to draw non-randomly from mainland biotas, but also that once having arrived, their evolutionary trajectories differ from those of mainland assemblages. In particular, Carlquist suggested—on the basis of earlier work—that a suite of traits has consistently and repeatedly evolved in island biotas (Johnson 1953; Mertens 1934). In general, those traits fall into two groups: traits associated with size and feeding, and traits associated with dispersal.

Specific, predicted functional changes include increase or decrease in stature and/or body mass, flightlessness, and loss of dispersal and competitive abilities (Lomolino 2005; Roff 1990). Increase in plant stature is predicted (after the initial selection of smaller seeds to disperse better) by lack of herbivores, intra- and inter-specific plant competition, and extended growing season. Studies have provided support for trends towards increasing size, but tend to disagree on the underlying theory. Böhle et al. (1996) used DNA analysis of insular and continental *Echium* spp. to conclude that insular species evolved "woodiness" from more herbaceous ancestors. Although this is an example of Carlquist's idea of insular change, that study noted that all species were from a similar climate and cited inbreeding depression as the causal agent in this evolutionary trend. The confounding effect of the genetic dynamics found in small populations weakens Carlquist's theory of climatic differences as the driving factor. On the other hand, Baldwin's (2007) work with the rDNA of a group of tarweeds, *Deinandra*, found on Guadalupe Island has demonstrated in situ radiation, to which they draw parallels with Carlquist's predictions regarding Hawaiian silverswords. Subsequent work on silverswords has shown that the common ancestor of insular and continental populations was even younger than previously thought, and insular populations of these plants have diversified at much higher rates than those of continental radiations (Baldwin and Sanderson 1998). This work has supported the hypothesis that plants may change significantly after their initial colonization.

In Carlquist's time, evidence for body size patterns was limited by available data. Since then, however, many more datasets on body size variation both within and among animal species have become available. Studies on island gigantism and dwarfism have provided evidence for predictable patterns in body size discrepancies between island and mainland populations (Case 1978, Lomolino 2005). In a phenomenon known as the "Island Rule," smaller mammals tend to increase in size while larger mammals tend to decrease in size (Burness et al. 2001; Foster 1964; Van Valen 1973). This rule does not always hold, however. For example, studies have shown, that carnivore body size does not seem to follow the general trend seen in other mammals (Meiri et al. 2004; Meiri et al. 2006), small mammals on Finnish islands show an increase in offspring size yet not adult size relative to their mainland counterparts (Mappes et al. 2008), and birds did not appear to show significant size differences between insular and continental populations (Gaston and Blackburn 1995). These differences could be, in part, a reflection of differences among study methods. For example, Burness et al. (2001) investigated known and projected body masses of fossils, while Meiri et al. (2004) used skull and teeth measurements of Carnivoran species. Although the Island Rule will likely remain an oft-cited phenomenon, we can expect to see further data challenging it.

Mainland and insular populations can show a variety of morphological distinctions beyond body size. Pinto et al. (2008) show that although insular and mainland populations of Caribbean *Anolis* lizards appear to have speciated at similar rates, island *Anolis* have evolved shorter limbs and wider toe pads. In this case, the rate of change between the two groups is not significantly different, yet they have moved into different morphological directions over time.

The expectation of trends in selection for dispersal traits among insular populations—similar to that for body-size trends—is that selection should be so strong that convergent traits emerge among evolutionarily unrelated taxa. Here, the predicted convergent trait is the loss of dispersal ability (Carlquist 1966). In both plants and animals, the traditional idea has been that once species establish themselves on islands, the loss of dispersal ability would be favored by the poor fitness (e.g., high mortality) of organisms that dispersed off the island. Such a dispersal-loss theory has also been empirically supported. The most striking of such studies could be that of Cody and Overton (1996) who were able to show that older populations of island plants demonstrated increasingly reduced dispersal potentials. Other work by Roff (1990), Frankham (1998), and Takayama et al. (2005) also document insular loss of dispersal mechanisms.

The evolution of flightlessness is perhaps only an expansion or caveat of the previous principle; however, it remains an extremely illustrative example of insular change. Flightnessness has evolved in at least 8 orders of birds, with multiple independent origins within some of those lineages (Boyer and Jetz 2010). Two lineages of flightless birds found on the Hawaiian islands, the moa-nalos (*Thambetochen* spp.) and flightless geese, have independent origins. The moa-nalos lost their flight so early that they were unable to colonize the youngest island in the chain, Hawaii (Sorenson et al. 1999). Another species of Hawaiian goose, the Nene-nui, (*Branta hylobadistes*) appears to have been at an intermediate stage of flight loss at the time of its extinction, with fossil evidence suggesting that it was, "at best, a weak flier" (Paxino et al. 2002). The factors driving flightlessness have been studied and have produced a rich mix of explanations. Roff (1990) identified five variables associated with loss of flight in insects: environmental heterogeneity, geographic variables, gender, alternate modes of migration and taxonomic variation. In addition, McNab (1994) suggested that the reduced muscle mass associated with loss of flying ability in birds significant lowers energy expenditure amongst island rails.

To round out the predictions associated with functional changes, overall competitive ability was the last issue to be addressed by Carlquist. He cites rapid destruction of native assemblages by invasive species to support his claim of decreased competitive ability in insular populations. Some research (Wittenberg and Cock 2001) refutes Carlquist's claim, suggesting that invasions are not particular to island populations. Callaway and Aschehoug (2000) have also suggested that invasive species may be more competitive than island species—rather than island species being reduced competitors relative to mainland counterparts—simply because they have escaped their natural predators. Competitive ability of island endemics may not be low so much as that of the invasive species is relatively high.

Environmental factors may also correlate to success in establishment and invasion by alien species (Ehrenfield 2008). Studies of niche pre-emption (Herben et al. 2005; Rejmanek and Richardson 1996) have documented immigrant species which were unable to out-compete island endemics and subsequently establish. Research on failed invasions is sparsely reported; however, this is in part due to negative publication bias that favors studies of invasions with significant impact on native fauna (Gurevitch and Hedges 1993). Carlquist's original call for more evidence regarding loss of competitive ability remains valid.

In Principle 21, Carlquist predicts that the pollination syndrome and morphology of plant species will vary relative to the type and diversity of pollinator species available. Feinsinger et al. (1982) compared the hummingbirds of Trinidad and Tobago, and showed that on Tobago, which has fewer pollinators relative to Trinidad, hummingbirds carried more multi-specific pollens than hummingbirds found on the neighboring island. Further work with wind pollination conducted by Anderson et al. (2001) on the Juan Fernandez Islands provided evidence that on a largely wind-pollinated island, ancestral pollination structures were retained by endemic species, a reversal of the "loss of dispersal ability" trend predicted in Principle 16. This suggests that the relative pressure exerted by selection for dispersal versus reproductive features may vary according to local environmental factors, meaning that not all of Carlquist's predictions are compatible to an equivalent degree in every case.

This cluster of predictions can be considered—at least in part—to be instrumentalist. Carlquist lays out some specifics regarding insular plant and animal changes and these specific predications could be considered as testable. In fact, many have observed these exact patterns that Carlquist listed. Many studies conducted prior to Carlquist's publication of his 24 principles also noted these changes, however, and therefore Carlquist becomes less the originator of these predictive forms and more a member in the line of biogeographers having dealt with these questions. Surely there are parts of Principles14–18 and Principle 21 that are naïve realism, and combined with the lack of originality, one could argue against instrumentalism. Although we acknowledge this position, we are more inclined to classify these principles as instrumentalism due to their predictive nature when compared with the other principles. Certainly either domain has a viable claim to these principles and if anything, the principles are illustrative of the lack of strong movement away from the naïve realism domain.

Classic genetics questions have modern answers (Principles 19, 20, 22)

Insular changes in form and function have long been researched and repeatedly supported as the tools and knowledge have been refined; conversely, questions involving genetics and phylogenies have had to wait for advances in genetic analysis techniques to produce quantitative answers. Studies involving out-crossing, hybridization, pollination and mutations have only recently been able to obtain the volume of methodological resources that have long been available to other branches of biogeography. Initial applications of such answers to Carlquist's model have proven generally successful. In the field of genetics, as demonstrated before, certain observable environmental factors found on islands can be used to invoke and possibly explain different trends. Carlquist's prediction involving the necessity of out-crossing stemmed largely as a rebuttal to Baker's (1955) claim that self-pollination is advantageous on islands. Carlquist quickly asserted that while monoecious organisms may be viable, their populations would ultimately suffer the disadvantages of inbreeding. While monoecious species remain more widely spread than dioecious species (in both island and continental habitats), advantages of out-crossing have been confirmed (Anderson et al. 2001; Baker and Cox 1984; Barrett 1996). Anderson et al. (2001) also showed that dioecism can have autochthonous origins from a monoecious ancestry, and Venkatasamy et al. (2007) suggest that "leaky dioecy"—in which some self-fertilization is possible in a largely dioecious species—may facilitate establishment after colonization.

Carlquist's principles regarding hybridization (Principles 19 and 20) state that out-crossing and "natural hybridization" abilities are selected for amongst waif organisms. Both of these assertions rest upon the assumption that variable species have an advantage. Hybridization as a mechanism for speciation on islands was once a largely theoretical idea that was seen as a fitness detriment by early population geneticists (Dobzhansky 1937; Mayr 1963). Recently, however, historical hybridization events have been detected using genetic markers among groups of island plants (Barrett 1996; Mayer 1991; Smith et al. 1996), in addition to animals such as frogs (Christiansen and Reyer 2010), butterflies (Abbott et al. 2010), and bats (Larsen et al. 2010). Genetic introgression and reticulation between species has been shown to occur between continental species as well, although hybridization on mainlands appears more often as a form of genetic out-crossing than distinct speciation. In both continental and insular contexts, these cases can result in ambiguous species delimitations (Petit and Exocoffier 2009), with challenging implications for conservation policy (Allendorf et al. 2001).

A final genetic prediction was made in Principle 22, in which Carlquist proposed that certain negative mutations might diminish in importance within a less competitive, insular environment. In addition to mutation compensation—having lethal mutations counteracted by other mutations (Kulathinal et al. 2004)—Wang et al. (1999) has proposed that lethal mutations in small populations can diminish in frequency and thus, impact. Further work in the realm of gene duplication and subsequent non-functionality has also gone toward supporting the negative-neutral idea (Leigh 2007; Nei and Roychoudhury 1973).

This cluster of principles has benefitted greatly from recent genetic innovations and in a sense many of the expectations previously set forth by Carlquist and others have been addressed in ways formerly unknowable. While some of the recent research has tended to put the "instrumentalism sheen" on these principles, in returning to Carlquist's original language, we see that the domain of naïve realism is more appropriate. Carquist's original principles were generated from his observations and perceptions; however, there existed (and still exists) plenty of complexity in these principles for specific, testable models to be created.

Endemism provides final evidence of long distance dispersal (Principles 23, 24)

Despite its limited availability at the time Carlquist first set forth his principles, genetic evidence serves as a final component to his concluding "rules" leading to the ultimate principle regarding endemism. Of relevance to both basic biology and to conservation, one of Carlquist's final predictions was that endemism should be more common on islands than on mainlands. This concept has received so little criticism as to now seem a default conclusion, yet it was not as readily accepted in Carlquist's day. Higher rates of endemism on oceanic islands than on continental areas have been repeatedly demonstrated (Greenslade 1968; Kier et al. 2009; Vuilleumier 1970). Such a finding would be expected if older oceanic islands have consistently shown higher rates of endemism than younger islands (Heaney 1986; Hesse et al. 1951; Weller et al. 1990). Cronk (1992, 1997) addresses the presence of endemism in species and genera compared to families, and concluded that the more oceanic an island is (the greater its isolation from other land masses), the more likely it will be to experience species and genera-rich endemism. While evidence for a species-rich outcome of island specialization could be analyzed by examining phylogenies of labile groups and rates of endemism, an investigation at the global scale has yet to take place. Carlquist likely included this idea to be a more general and futuristic statement—one concerned less with historical explanation and more abstract theory.

Just as Principle 8 served as a summary of concepts for the first group of principles, so do Principles 23 and 24 for the second group. Here, we consider these principles to fall into naïve realism, both for lack of a better classification and because they are generally built upon a subset of naïve realism principles. And similarly to the first group of principles, we see a strong tendency for the principles in Group B to be rooted in naïve realism. Even for the principles we have decided to classify as instrumentalism, we acknowledge that the predictive power is not as high or explicit as it could be, and that some might consider them more naïve realism than we do. Overall, it is clear that Carlquist's principles are strongly observational in nature and his work occupies the domain of naïve realism.

Conclusions

Since initial publication in 1966, few of Carlquist's 24 Principles of Long Distance Dispersal have been rejected. Some studies have questioned aspects of individual principles, and there has certainly been a demonstrated need for more research to fully backup some hypotheses, yet his hypotheses have largely been supported. Some of Carlquist's work is original, and in other parts he is simply contributing to an ongoing biogeographic debate. Regardless of the exact level of contribution, it is clear that on the whole, his work in the 1960s is comprehensive and provides an excellent basis for the study of the natural history of long distance dispersal to ocean islands.

Yet if his set of principles is successful, why is Carlquist typically given much less attention in ecology curricula, whereas island biogeographic models—although often not supported in their particulars—are a mainstay of ecology? We proposed the use of model domains to answer this question. After outlining four model domains (Sismondo 2000) that we would adhere to, we categorized each principle based on these philosophical domains. It is clear that the vast majority of principles are classified as naïve realism, meaning they are observations and perceptions of ecology, but that they lack a testable model (instrumentalism), components to experiment (metaphysical realism), or an abstract theory (rationalism). Although few principles can be argued as instrumentalism, the tone of the predictions as a whole is that of naïve realism, and it is possible that for those instrumentalist principles we are seeing specific predictions that Carlquist did not originally intend.

Simply because most of the principles fit into one domain doesn't mean the work is any less successful, however. Again, we ask: where is the disconnect between this work and popular ecological appeal? To address this, we have created a structured version of the model domains that provides one hypothesis as to the disconnect (Fig. 1). In this conceptual model, we propose that there is a hierarchical structure to the model domains, where all principles must first be perceived and observed (naïve realism) before they can be understood, developed, and pass on to subsequent domains. For example, a pattern in nature is first observed and initially classified as naïve realism. After one or more scientists digest this pattern, it has the opportunity to evolve into something that could provide a testable model (instrumentalism), components to experiment (metaphysical realism), or contribute to an abstract theory (rationalism). Although not impossible for a principle to skip the naïve realism stage, we suspect that few scientific ideas are initially discovered as belonging to any of the three lower domains. We see a corollary in the general attitude of science to our domain structure. That is, much of the early work in

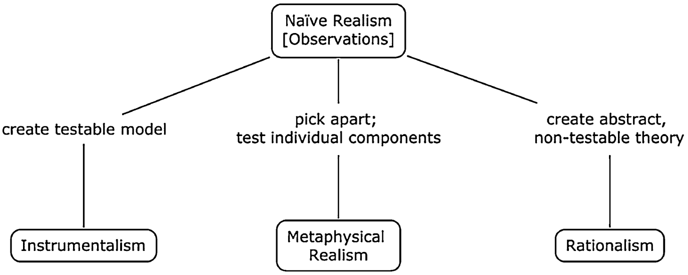

Fig. 1 Structured, hierarchical model using four model domains. Model domains are taken from Sismondo (2000); however, we suggest a unique structure that reflects both the chronology of science and the connections between domains

biogeography was based purely on naïve realism—models were harder to test and experiments were not widely used, and composite, abstract theories were likely harder to come by. Therefore, observation and perception—naïve realism—was all that was needed to conduct science. By the 1960's, however, we see a fundamental change in this model. Biogeography is rising in activity, as is the demand (across ecology) for more than naïve realism. At this time, ecology was growing, as was the suite of methodological advances available to ecologists. The result was that biogeography and ecology (and science as a whole) began to demand more than just observations. The scientific community wanted testable models, explicit experiments, and more theories. Although Carlquist provides a comprehensive package of observations on island biogeography, we see the need for more detail and prediction for his work to have entered mainstream biogeography. While this paper only examines the fate of Carlquist's ideas, this model domain framework could be a starting point for asking why other ideas and models—often perfectly good ones—fail to become popularized in science and ecology.

Counter to the independent, investigative fate of Carlquist's numerous principles was the neat equilibrium formula of ETIB—readily illustrated in a single figure—put forth by MacArthur and Wilson (1963). Sismondo (2000) provides an excellent overview of ETIB with respect to model domains and his findings can be used to further demonstrate the differences between ETIB and Carlquist with respect to use in science. Table 2 shows the translation and applicability of both ETIB and Carlquist into four domains. We define translation similar to the way in which we have used it throughout this paper; translation is the natural tendency of an idea, principle, etc. to fall into a domain. For example, Carlquist's principles fall naturally

Table 2 Model translation and applicability using Sismondo (2000) model domains

Model domain	Translation		Application	
	Carlquist	ETIB	Carlquist	ETIB
"Naïve" realism	Yes	Yes	Yes	No
Instrumentalism	No	Yes	No	No
Metaphysical realism	No	Yes	No	No
Rationalism	No	Yes	No	Yes

into the naïve realism domain (Table 2) and can only be addressed through natural history tests. Carlquist's model often has little instrumental value; it is somewhat difficult to test comprehensively and quantitatively, and due to its diversity of specific assertions, it has diminishing theoretical elaborations. On the other hand, ETIB has been translated into all four domains (Sismondo 2000).

We define application as the success of the idea, principle, etc. within the translated domain. Because Carlquist's set of principles only translated into the naïve realism domain, its only possible application is in naïve realism (Table 2). Through an extensive literature review (present study), we have found the vast majority of Carlquist's principles to be validated and therefore we conclude that the application is successful. While ETIB can be translated into all four domains, the application is less successful. It has been shown that the success of ETIB within each domain is limited and that the model's greatest success lies in the rationalism domain (Sismondo 2000). Although the application of ETIB is limited or unsuccessful in most domains, the fact that science has been addressing this model and testing it means that it has infiltrated mainstream ecology. Despite the fact that both Carlquist and ETIB are only applicable in one domain, the difference lies in the translation—ETIB is widely translatable while Carlquist is not. Further debate will find fertile ground in the relative merits of specific domain applicability and whether it is more desirable to be strongly theoretical or have cache in articulating natural history.

So what is the next logical step for examining the collective ideas of Carlquist? Many tools Carlquist initially lacked (developed genetic methods, more complete phylogenies, increased understanding of atmospheric and oceanic patterns and process) have been and will continue to be made available. Should we, with recent and future tools, continue to prod at the nuance of the principles? Some advocate a new paradigm comprised of older dispersal and vicariance themes (Heaney 2007). Or is it simply time to accept the individual principles as largely valid, understand they have limited predictive and experimentation value, and focus on other, pioneering questions of island biogeography?

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