

RESEARCH
PAPER



PACT in practice: comparative historical biogeographic patterns and species–area relationships of the Greater Antillean and Hawaiian Island terrestrial biotas

Mallory E. Eckstut^{1,2*}, Caleb D. McMahan^{1,3}, Brian I. Crother¹,
Justin M. Ancheta⁴, Deborah A. McLennan⁴ and Daniel R. Brooks⁴

¹Department of Biological Sciences, Southeastern Louisiana University, Hammond, LA 70402, USA, ²School of Life Sciences, University of Nevada, Las Vegas, 4505 Maryland Parkway, Las Vegas, NV 89154, USA, ³Division of Ichthyology, LSU Museum of Natural Science, Baton Rouge, LA 70803, USA, ⁴Department of Ecology & Evolutionary Biology, University of Toronto, Toronto, Ontario, Canada, M5S 3G5

ABSTRACT

Aim To compare the evolutionary and ecological patterns of two extensively studied island biotas with differing geological histories (the Hawaiian Islands and the Greater Antilles). We evaluated the results from PACT (phylogenetic analysis for comparing trees), an innovative approach that has been proposed to reveal general patterns of biotic expansion (between regions) and *in situ* (within a region) diversification, as well as species–area relationships (SAR) and the taxon pulse dynamic.

Location The Hawaiian Islands and Greater Antilles.

Methods We used the PACT algorithm to construct general area cladograms and identified biotic expansion and *in situ* nodes. We analysed the power-law SAR and relative contribution of biotic expansion and *in situ* diversification events using power-law and linear regression analyses.

Results Both biotic expansion and *in situ* nodes were prevalent throughout the PACT general area cladograms (Greater Antilles, 55.9% biotic expansion, 44.1% *in situ*; Hawaiian Islands, 40.6% biotic expansion, 59.4% *in situ*). Of the biotic expansion events, both forward and backward events occurred in both regions (Greater Antilles, 85.1% forward, 14.9% backward; Hawaiian Islands, 65% forward, 35% backward). Additionally, there is a power-law SAR for the Greater Antilles but not for the Hawaiian Islands. However, exclusion of Hawai'i (the youngest, largest Hawaiian Island) produced a power-law SAR for the Hawaiian Islands.

Main conclusions The prevalence of *in situ* events as well as forward and backward biotic expansion events reveals that both Hawaiian and Greater Antillean biotas have evolved through alternating episodes of biotic expansion and *in situ* diversification. These patterns are characteristic of the taxon pulse dynamic, for which few data have previously been recorded on islands. Additionally, our analysis revealed that historical influences on the power-law SARs are pronounced in both assemblages: old, small islands are relatively species rich and young, large islands are relatively species poor. Thus, our PACT results are consistent with hypotheses of geological influence on the evolution of island biotas and also provide greater insight into the role of the taxon pulse dynamic in the formation of island equilibria.

Keywords

Dispersal, equilibrium theory, Greater Antilles, Hawaiian Islands, Hennig's progression rule, *in situ* diversification, island biogeography, taxon pulse dynamic, vicariance.

*Correspondence: Mallory E. Eckstut, School of Life Sciences, University of Nevada, Las Vegas, 4505 Maryland Parkway, Las Vegas, NV 89154, USA.
E-mail: eckstutm@unlv.nevada.edu

INTRODUCTION

The evolution of island biotas has long been considered a linchpin of modern biogeographic studies, beginning with Wallace (1855) and Darwin (1859) and continuing into modern biogeography (e.g. MacArthur & Wilson, 1963, 1967; Funk & Wagner, 1995a; Heaney, 2000; Whittaker, 2000, 2004a,b,c).

With the advent of vicariance biogeography, the focus of historical biogeography has been on mainland rather than island biotas, and on the isolation events producing species (see Brooks & McLennan, 2002, for a review). Dispersal and isolation events resulting from active dispersal across pre-existing barriers (peripheral isolates speciation) were considered poor descriptors of historical biogeography because these events are assumed to be clade specific and do not produce general patterns. Therefore, isolation resulting from the formation of physical barriers (vicariance) has often been seen as the null hypothesis for historical biogeographic analysis of general patterns (Nelson & Platnick, 1981), including island biotas in the Caribbean (Rosen, 1975; Crother & Guyer, 1996) and even in the Hawaiian Islands (Melville, 1981).

However, other models for general patterns of insular biotas produced by biotic expansion have been suggested, including Hennig's progression rule, where the oldest species occur on the oldest islands and the youngest species on the youngest islands (Hennig, 1950, 1966; Wiley, 1981; Cowie & Holland, 2008). This pattern is produced only by dispersal for islands that have never been connected. Lieberman & Eldredge (1996) presented insights about an alternative process for producing general patterns: geodispersal, where geographic barriers fall and subsequent biotic expansion can produce congruent patterns among clades.

Brooks & van Veller (2008) proposed that if non-vicariant mechanisms are a contributing factor to a region's biotic history, then analysis is required where all species and their distributions are analysed without modification, i.e. no branches from the input trees are removed, moved to different nodes or duplicated, so each original input tree can be superimposed in its original form onto the resulting general area cladogram (GAC; see Table 1 for a complete list of abbreviations used in this paper). Using multi-clade analysis, recent studies on mainland biotas have found alternating nodes of expansion, where lineages are produced between regions, and isolation, where lineages are

produced within a region (e.g. Bouchard *et al.*, 2004; Brooks & Folinsbee, 2005; Halas *et al.*, 2005; Lim, 2008). These events are not in accordance with maximum vicariance (optimizing the number of possible vicariant events in a dataset). Rather, this supports another model of non-vicariance-driven general patterns: the taxon pulse dynamic. The taxon pulse dynamic predicts that historical biogeographic patterns result from alternating waves of geographic isolation (with *in situ* speciation, i.e. speciation that occurs at the site of a lineage's origin) punctuated by episodes of colonization into any available areas, regardless of the area's age (Erwin, 1981). However, despite the recent work on mainland biota taxon pulse dynamics, few data are available regarding island biotas.

The importance of using a phylogenetic perspective (thus evolutionary diversification, including non-vicariant mechanisms) in the study of island biotas has been emphasized (e.g. Heaney & Rickart, 1990; Pregill & Crother, 1999; Heaney, 2000). However, as noted by Heaney (2000), these studies usually focus upon one clade, although there are exceptions (e.g. Crother & Guyer, 1996).

Further, the species–area relationship (SAR; see MacArthur & Wilson, 1963, 1967) is a well-known and studied aspect of island biogeography that is proposed to have a linear log–log relationship between species richness and area size (Rosenzweig, 1995). Biotic history in the form of process affects the linearity of the SAR in a variety of ways: through *in situ* speciation, speciation resulting from biotic expansion and niche diversification accompanied by 'back-colonization' into the ancestral region, which is part of the source of the 'pulses' outlined in the taxon pulse hypothesis (e.g. MacArthur & Wilson, 1963, 1967; Ross, 1972; Heaney, 2000; Whittaker, 2000; Ackermann & Doebeli, 2004). As a result, we expect taxon pulse-driven biotic diversification to be associated with significant phylogenetic influences on the SAR (Halas *et al.*, 2005). We propose to test this hypothesis using two extensively studied archipelagos with differing histories: the Hawaiian Islands and the Greater Antilles.

Geology, biogeography and history of the Hawaiian Islands

The north-west Hawaiian Islands date back as far as 29 million years ago (Ma), but the main Hawaiian Islands are relatively young in origin (Ziegler, 2002). The majority of systematic analyses have been conducted on the main islands, hence those will be addressed in this paper. The oldest main island is Ni'ihau, estimated to have arisen through volcanic activity up to 5.5 Ma, whereas the youngest island, Hawai'i, arose less than 1 Ma and is still being formed (MacDonald *et al.*, 1983; Ziegler, 2002; Cowie & Holland, 2008). The islands in the Hawaiian Archipelago arose both sequentially and linearly in the Pacific Ocean (Fig. 1a). The Hawaiian Archipelago is also one of the most isolated island chains, and is over 4000 km from the nearest mainland source, although the islands themselves are in relatively close proximity to one another, with the farthest distance, between Kauai and Oahu, slightly more than 130 km (Fig. 1a).

Table 1 Abbreviations used throughout this study.

Abbreviation	Term
BE	Biotic expansion
DELTRAN	Delayed transformation optimization
ETIB	Equilibrium theory of island biogeography
IS	<i>in situ</i>
GAC	General area cladogram
OTU	Operational taxonomic unit
PACT	Phylogenetic analysis for comparing trees
SAR	Species–area relationship

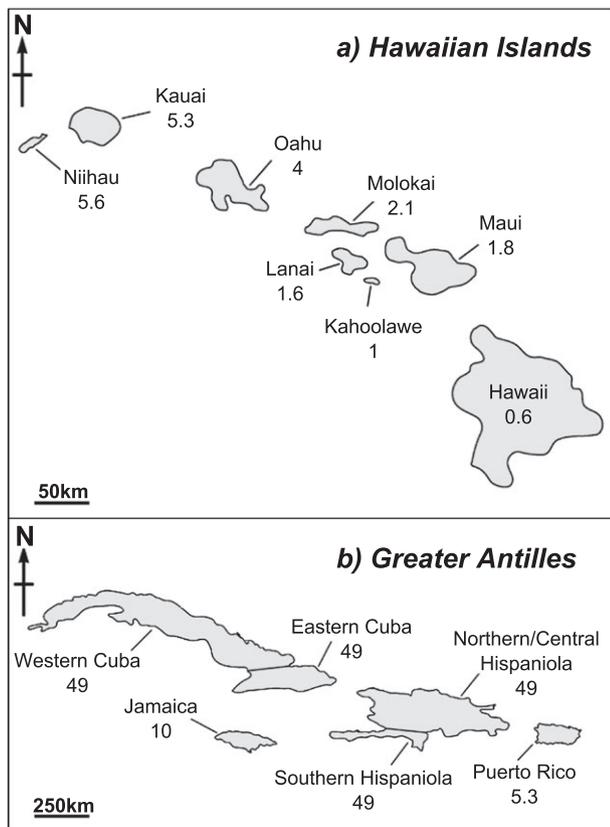


Figure 1 Maps and ages of the Hawaiian Islands and Greater Antilles, with oldest estimated dates (in millions of years) of sustained emergence depicted (Hawaiian Islands, Ziegler, 2002; Greater Antilles, Graham, 2003): (a) Hawaiian Islands, (b) Greater Antilles. Lines depict geologically and historically separate geological regions.

Funk & Wagner (1995a) produced the most comprehensive collection of historical biogeographic studies of the Hawaiian Islands, including analyses of 19 clades of insects, plants and birds. Funk & Wagner (1995b) suggested that the most common pattern of inter-island relationships conformed to the progression rule, namely inter-island dispersal from older to younger islands. Recently, Cowie & Holland (2008) provided an updated review of Hawaiian biogeography, and suggested that the progression rule may still hold for many Hawaiian endemics, but there are many instances of alternative patterns occurring (e.g. original colonization of younger Hawaiian islands from a non-Hawaiian source, followed by dispersal to older islands). Both reviews, however, focused on examining potential general historical biogeographic patterns by examining individual clades (Funk & Wagner, 1995b).

Geology, biogeography and history of the Greater Antilles

The Greater Antilles is an archipelago in the Caribbean Sea of the Atlantic Ocean encompassing the islands of Cuba, Hispaniola (Haiti, Dominican Republic), Puerto Rico and Jamaica. This

archipelago is older than the Hawaiian Islands, and its origin is more complex as not all of the islands share a common geological history (Iturralde-Vinent & MacPhee, 1999; Fig. 1b). The proto-Greater Antillean Arc originated an estimated 130 Ma (early Cretaceous) in the present Isthmian region. This arc subsequently began moving eastward during the Tertiary (estimated 65 Ma), and remained mostly submerged until about 49 Ma during the Middle Eocene (Graham, 2002, and references within). Jamaica was then resubmerged from the middle Eocene to late Miocene (42–10 Ma). Puerto Rico was mostly submerged between the late Oligocene and the Pliocene (23.7–5.3 Ma). The Greater Antilles had numerous episodes of fragmentation and accretion, further complicating its geological and biotic histories (Rosen, 1985), and there is substantial debate about the connectivity of the Greater Antillean Arc (continuous or with subsequently fragmented series) as well as connectivity to North and South America (Graham, 2002, and references within). Additionally, the islands of the Greater Antilles are larger and farther apart from each other than the Hawaiian Islands, with the largest island in the Greater Antilles, Cuba, having a surface area of 110,861 km², and the greatest distance being between Jamaica and Hispaniola (226 km; Fig. 1b). However, the Greater Antilles are closer to the mainland than are the Hawaiian Islands, with Puerto Rico the most distant (734 km from Venezuela in South America).

The biogeographic history of the Greater Antilles has been an issue of much controversy and debate among scientists (Crother & Guyer, 1996; Hedges, 2001; Chakrabarty, 2006; Vázquez-Miranda *et al.*, 2007; and references within each). Heinicke *et al.* (2007) provide a summary of the two major hypotheses explaining biotic presence in the Greater Antilles: (1) a vicariance model of fragmentation of the proto-Antillean arc and the biota between North and South America being carried eastward, or (2) a dispersal model where biota arrived on flotsam from mainland sources. Researchers have argued on behalf of both sets of hypotheses, and both have limitations (Heinicke *et al.*, 2007); however, Crother & Guyer (1996) proposed that a combination of dispersal and vicariant events explain the occurrence of biota given the complex geological history of the archipelago.

Comparative analysis of the Hawaiian Islands and the Greater Antilles

PACT (phylogenetic analysis for comparing trees) is a novel method for biogeographic analysis that builds upon secondary Brooks parsimony analysis (BPA) (Wojcicki & Brooks, 2004, 2005; Brooks & van Veller, 2008) that has previously been used for analysis of species and areas (Folinsbee & Brooks, 2007; Lim, 2008) and also for assessment of historically reticulated and non-reticulated relationships among parasites and hosts (Brooks & Ferrao, 2005).

In this paper we assess the utility of PACT analysis in island systems by comparing analyses conducted on the Hawaiian Islands and the Greater Antilles. These two island series differ substantially in geological history, origin and connectivity to mainland sources, and thus have been proposed to have differ-

ing speciation patterns between these island biotas and mainland biotas (Ricklefs & Bermingham, 2008). By assessing GACs generated by PACT analyses (e.g. using analyses of SAR and speciation types) with geographic and geological parameters, we propose to further illuminate the use of this novel method for biogeographic inference.

MATERIALS AND METHODS

Our study comprised three steps: (1) creation of a GAC using the PACT algorithm (Wojcicki & Brooks, 2004, 2005), (2) differentiating *in situ* and biotic expansion (which is either active, via dispersal and subsequent peripheral isolates speciation, or passive, via vicariant isolation. We note that at present these mechanisms are indistinguishable using PACT), and (3) examine the *in situ* and biotic expansion influences on the SAR for these islands. These protocols follow Halas *et al.* (2005).

We acknowledge that area cladograms built using assumptions of cladograms and congruence are often criticized for a number of reasons. Methodologies producing these area cladograms rely on available data, which may be relatively few, and thus they cannot be tested if the distributions observed correspond to a more general pattern (Hausdorf & Hennig, 2004). Additionally, there are limitations on what can be inferred from patterns alone. For example, pseudo-congruence of temporally and spatially discordant events can result in identical cladogram patterns and be misidentified as vicariant events, and pseudo-incongruence can result in differing responses to similar vicariant events (Donoghue & Moore, 2003; Riddle & Hafner, 2006). For these issues, molecular clocks and fossil information are needed, although there is no current way to incorporate these techniques into PACT analysis. However, while there is no way at present to incorporate a temporal component, PACT analysis is not restricted to vicariant event analysis and incorporates dispersal and *in situ* events as well, thus many of these issues with vicariance biogeography have reduced applicability (Wojcicki & Brooks, 2004, 2005).

Step 1: generating the GACs

For the Greater Antilles, 18 phylogenies were first arbitrarily selected based on available datasets at the time of analysis. These clades consisted of six plant, two insect, one amphipod, one fish, one amphibian, five reptile, one bird and one mammal, totalling 292 species (see Appendix S1 in Supporting Information for a summary of all 18 clades considered; taxon–area cladograms are available upon request from M.E.E.).

Using a variety of organisms can result in different area cladograms that reflect their own dispersal and speciation mechanisms that often differ between clades. To control for variation between clades, we attempted to use a similar variety of clades when possible (including a variety of plants and invertebrates, and, when possible, vertebrates). We acknowledge that the available data for endemic taxa differ, and this is in part due to geological histories and associated differences in community assembly based on characteristics such as age and proximity to

mainland sources. We argue that the differing lineages are essential characteristics of the archipelagos because they contribute to the biotic disparities, and these characteristics are reflected in the PACT analyses.

The dataset for the Hawaiian Island meta-analysis included a total of 787 species: fifteen plant, one bird, seven insect, four arachnid and two terrestrial mollusc clades (see Appendix S2 for a summary of all 29 clades considered; taxon–area cladograms are available upon request from D.R.B. or from <http://labs.eeb.utoronto.ca/brooks/>).

In the Hawaiian analysis, taxon–area cladograms including non-Hawaiian lineages were not included in the analysis. However, in the Greater Antillean analysis, area cladograms comprising only organisms in the Greater Antilles were difficult to obtain and thus cladograms including mainland and Lesser Antillean lineages were still included in the analysis. This would affect the overall structure of the GAC, resulting in a monophyletic Hawaiian GAC comprising only the Hawaiian Islands, and a more cosmopolitan Greater Antillean GAC, including other regions, such as mainland (e.g. North, South and Central America) and other island systems (e.g. the Lesser Antilles and Bahamas). However, this does not alter subsequent analysis utilizing the protocols proposed by Halas *et al.* (2005).

The phylogenetic tree for each clade was converted into a taxon–area cladogram by replacing the names of each of the terminal species with their respective areas. The taxon–area cladograms were combined by hand to form a GAC using the PACT algorithm as described by Wojcicki & Brooks (2004, 2005). A software program for GAC construction using the PACT algorithm is not yet available, although one is currently in development.

Step 2: distinguishing between *in situ* and biotic expansion

The GAC and each taxon–area cladogram were then analysed using Delayed Transformation (DELTRAN) optimization with MACCLADE 4.08 (Maddison & Maddison, 2000) to infer ancestral areas. In cases where strict parsimony optimization cannot distinguish between two character states at a node, DELTRAN optimization retains the pre-existing state and transformation occurs at the last possible moment. Accordingly, it favours biotic expansion while minimizing *in situ* speciation with extinction, thus avoiding situations in which a species could be interpreted as having gone extinct and subsequently having ‘re-evolved’ (Wiley, 1986, 1988a,b). There have been criticisms of the use of parsimony methods for ancestral character-state reconstructions, particularly for *in situ* situations where there are stochastic evolutionary processes and fast rates of evolutionary change (Schluter *et al.*, 1997), as well as regarding the cladistic assumption of irreversibility (Cunningham, 1999). This is only the second time that the PACT protocol has been used experimentally (Halas *et al.*, 2005), and the third time that PACT has been used for biogeographic analysis (Halas *et al.*, 2005; Folinsbee & Brooks, 2007; Lim, 2008). Thus, we favoured a parsimony optimization method because it is a conservative optimization pro-

cedure (Brooks & McLennan, 2002; Kluge, 2002). Because this is a conservative method, it will produce ambiguity with respect to unique events but will not affect our assessment of general nodes (which we are maximizing). At the moment we are unaware of any appropriate model-based (likelihood and Bayesian) optimization routines for taxon pulses.

In situ speciation nodes were defined as those that comprise the same areas or a subset of those areas encompassed by the previous node (these processes can include within-area vicariance, peripheral isolates speciation and sympatric speciation); biotic expansion nodes are those that comprise more areas than those encompassed by the previous node. While dispersal is understood to be the predominant mechanism of biotic expansion for the Hawaiian clades, both vicariance and dispersal are prevalent biotic expansion mechanisms for the Greater Antillean clades (Crother & Guyer, 1996). Thus, all instances of either dispersal or vicariant speciation in this paper are referred to as biotic expansion.

On the GAC and each taxon–area cladogram we counted the nodes that resulted in lineages developing via biotic expansion, *in situ* and both biotic expansion and *in situ*. We further analysed the biotic expansion nodes to assess the degree to which the GAC supported the progression rule. We followed Funk & Wagner (1995b, Figs 17.1, 17.2 and 17.4) in distinguishing two classes of biotic expansion: ‘forward biotic expansion’, corroborating the progression rule (Hawaiian Islands, from older to younger islands; Greater Antilles, from previously inhabited islands to new, uninhabited islands), and ‘back biotic expansion’ (Hawaiian Islands, from younger to older islands; Greater Antilles, return to previously occupied islands).

We discarded Kahoolawe and Ni‘ihau from the Hawaiian analysis. Few data come from Kahoolawe, because it has a history of use as a military weapons testing range and has been modified by grazing ungulates (Carlquist, 1970; Peck *et al.*, 1999). Alternatively, Ni‘ihau has few data because it is privately owned and generally inaccessible to researchers (Peck *et al.*, 1999).

Step 3: GAC influences on SARs

We generated the power-law SAR for each island series using the species in our datasets (Preston, 1962; MacArthur & Wilson, 1967; Halas *et al.*, 2005). Hawai‘i is a statistical outlier, although it is biologically relevant to the Hawaiian Islands, so Hawaiian analyses were conducted both including and excluding Hawai‘i. We plotted the number of area operational taxonomic units (OTUs) on each GAC and the surface area (in km²) of each island.

We constructed species–area plots distinguishing species arising through biotic expansion from those arising *in situ* to assess the effects of the GAC on the SAR. We examined the relationship between the total number of species on each island and island size, between the number of *in situ* species on each island and island size, and between the number of species arising through biotic expansion and island size. Finally, we plotted the relationship between species produced by biotic expansion and

those produced by *in situ* speciation for each island. We assessed the direction and strength of the relationships for these plots using linear regression analysis. Preliminary analysis of residuals depicted non-uniformity of variables, thus all variables were log-transformed for analysis. Statistical analyses were run using SPSS 16.0.1 (SPSS, Inc., 2007).

Additionally, we acknowledge that statistical artefact may be an issue with our low sample sizes. However, for our study we strictly applied previously described protocols to examine how these methods perform in the context of archipelagos that have been thoroughly studied but have substantially divergent histories. As in all island biogeographic analyses, we are limited by the number of islands that exist (the Greater Antilles has four islands and the Hawaiian Islands has six islands). Thus, to minimize over-prediction of issues in our datasets, we remained conservative in our interpretation of the statistical analyses.

RESULTS

Step 1: the GACs

The Hawaiian Island analysis yielded a GAC with 858 OTUs (see Appendix S3), whereas the Greater Antillean analysis produced a GAC with 250 OTUs (see Appendix S4). When taking into account the differing number of clades in each analysis, the proportion of clades to number of OTUs differ between island series (Hawaiian Islands, 0.03; Greater Antilles, 0.07). Further, the majority of Hawaiian clades entered the GAC at different points throughout the tree, whereas the majority of the Greater Antillean clades entered at the same region in the GAC and generally toward the base of the tree (see Appendices S3 and S4).

Step 2: residents and colonizers

The Greater Antillean GAC comprises 178 nodes, of which 82 (44%) are *in situ* nodes and 104 (56%) are biotic expansion nodes. The Hawaiian Island GAC comprises 276 nodes, of which 164 (59%) are *in situ* nodes and 112 (41%) are biotic expansion nodes (Table 2). *In situ* speciation occurs throughout both GACs; however, the Greater Antilles had more forward biotic expansion than the Hawaiian Islands (85% and 65%, respectively; Table 2).

Independent analysis of each clade revealed that all of the Greater Antillean clades favour biotic expansion (Table 3). The highest proportion of *in situ* speciation events was 47% (for the plant genera *Erithalis* and *Ernodea*; Table 3). However, several clades have few or no instances of *in situ* speciation events, including clades such as the fish genus *Rivulus* (none), the plant genus *Sabal* (one) and the reptile genus *Epicrates* (one) (Table 3).

Alternatively, many Hawaiian clades predominantly show *in situ* speciation. For the Hawaiian insects, five clades heavily favour *in situ* speciation, while one has a roughly equal number of species arising *in situ* and through biotic expansion, and only one shows predominantly biotic expansion (Table 3). All terrestrial molluscs, two arachnid clades and six of the 15 plant clades

Island series	Node category	Total	Percentage	Percentage (of total)
Greater Antilles	Total nodes	186		
	Total nodes (<i>IS</i>)	82		44.1
	Total nodes (BE)	104		55.9
	Total nodes (Full BE)	9	8.7	4.8
	Total nodes (BE/ <i>IS</i>)	92	88.5	49.5
	Total nodes (BE Amb.)	3	2.8	1.6
	BE – Forward	86	85.1	
	BE – Back	15	14.9	
Hawaiian Islands	Total nodes	276		
	Total nodes (<i>IS</i>)	164		59.4
	Total nodes (BE)	112		40.6
	Total nodes (Full BE)	25	22.3	9
	Total nodes (BE/ <i>IS</i>)	78	69.6	28.3
	Total nodes (BE Amb.)	9	8.1	3.3
	BE – Forward	67	65	
	BE – Back	36	35	

IS, *in situ*; BE, biotic expansion; BE Amb, ambiguous biotic expansion; BE – Forward, forward biotic expansion; BE – Back, back biotic expansion. Percentage (of total) indicates percentage of each event throughout the entire GAC, whereas Percentage indicates the percentage of BE events attributed to the subsets of events (Full BE, BE/*IS*, and BE Amb, BE – Forward, and BE – Back).

show a preponderance of *in situ* speciation. The avian clade studied displayed more speciation events resulting from biotic expansion (Table 3).

Step 3: GAC influences on the SAR

Table 4 depicts the number of species produced from *in situ* and biotic expansion events for both island groups. The power-law SAR, $S = cA^z$ (MacArthur & Wilson, 1967) for the Greater Antilles ($c = 0.134, z = 1.585$) yielded an r^2 of 0.999 ($P = 0.001$, Fig. 2a), the Hawaiian Islands including Hawai'i ($c = 1.706, z = 0.209$) yielded an r^2 of 0.404 ($P = 0.175$, Fig. 2b) and the Hawaiian Islands excluding Hawai'i ($c = 1.157, z = 0.63$) yielded an r^2 of 0.969 ($P = 0.002$, Fig. 2c). This indicates power-law SARs for the Greater Antilles and the Hawaiian Islands excluding Hawai'i, but no power-law SAR for the Hawaiian Islands including Hawai'i.

Species arising from biotic expansion had a strong relationship with area for the Greater Antilles ($r^2 = 0.927, P = 0.037$, Fig. 3a) but not for the Hawaiian Islands (Hawaiian Islands including Hawai'i, $r^2 = 0.189, P = 0.389$, Fig. 3b; Hawaiian Islands excluding Hawai'i, $r^2 = 0.533, P = 0.161$, Fig. 3c). *In situ* species showed no significant relationship with area for the Greater Antilles ($r^2 = 0.875, P = 0.065$, Fig. 3d) or the Hawaiian Islands including Hawai'i ($r^2 = 0.305, P = 0.256$, Fig. 3e). However, exclusion of Hawai'i resulted in a strong relationship for the remaining Hawaiian Islands ($r^2 = 0.97, P = 0.002$, Fig. 3f).

Biotic expansion species showed strong relationships with total number of species per island for both the Greater Antilles ($r^2 = 0.918, P = 0.042$, Fig. 4a) and the Hawaiian Islands ($r^2 = 0.701, P = 0.038$, Fig. 4b), whereas exclusion of Hawai'i resulted in an insignificant relationship for the Hawaiian Islands ($r^2 =$

Table 2 Node analyses of resulting Greater Antillean and Hawaiian Island general area cladograms (GACs).

0.694, $P = 0.08$, Fig. 4c). *In situ* speciation yielded an insignificant relationship for the Greater Antilles ($r^2 = 0.888, P = 0.058$, Fig. 4d), and significant relationships with total number of species for the Hawaiian Islands (Hawaiian Islands including Hawai'i, $r^2 = 0.898, P = 0.014$, Fig. 4e; Hawaiian Islands excluding Hawai'i, $r^2 = 0.901, P = 0.004$, Fig. 4f). No analysis yielded relationships between species produced *in situ* and via biotic expansion (Greater Antilles, $r^2 = 0.653, P = 0.192$, Fig. 4g; Hawaiian Islands including Hawai'i, $r^2 = 0.377, P = 0.27$, Fig. 4h; Hawaiian Islands excluding Hawai'i, $r^2 = 0.389, P = 0.186$, Fig. 4i).

DISCUSSION

Comparative analyses and attributable geographic and geological characteristics

Both Hawaiian and Greater Antillean analyses yielded large, complex GACs (858 OTUs and 250 OTUs, respectively). However, the island systems differed when comparing the number of clades analysed with the number of OTUs (Hawaiian Islands, 0.03; Greater Antilles, 0.07). This disparity may result from the differing mechanisms of biotic expansion in the island systems: while the Hawaiian Islands with the exception of the Maui Nui complex are limited to dispersal (Price & Elliott-Fisk, 2004), the Greater Antilles have been proposed to exhibit both vicariant and dispersal events (Crother & Guyer, 1996; Heinicke *et al.*, 2007). Following PACT procedures involves combining common elements, Y, where $Y + Y = Y$, and retaining novel elements, N, where $Y + N = YN$. Thus, congruence in vicariant events between several lineages would result in fewer OTUs than in a dispersal-dominant system.

Table 3 Type of speciation events associated with each clade used in Greater Antillean and Hawaiian Island PACT (phylogenetic analysis for comparing trees) analyses.

Clade	Group	Total	IS	BE	Fwd BE	Bkwd BE	Amb.
Greater Antilles							
<i>Exostema</i>	Plants	20	5	5	0	0	10
<i>Pictetia</i>	Plants	22	4	14	2	2	0
<i>Sabal</i>	Plants	7	1	1	5	0	0
Lythraceae	Plants	17	6	8	2	0	1
<i>Poitea</i>	Plants	13	5	7	0	1	0
<i>Erithalis</i> and <i>Ernodea</i>	Plants	17	8	7	0	1	1
<i>Platynus</i>	Insects	22	9	3	4	0	6
<i>Polycentropus</i>	Insects	10	2	7	1	0	0
<i>Carbitroides</i>	Amphipods	6	1	0	4	0	1
<i>Rivulus</i>	Fishes	6	0	2	3	0	1
Bufonidae	Amphibians	14	5	7	1	1	0
<i>Sphaerodactylus</i>	Reptiles	39	15	20	3	1	0
Iguanidae	Reptiles	17	4	6	1	4	2
Xenodontine	Reptiles	23	9	10	1	3	0
<i>Epicrates</i>	Reptiles	11	1	7	1	0	2
Typhlopidae	Reptiles	14	5	4	0	0	5
Mimidae	Birds	14	5	4	3	2	0
Capromyidae	Mammals	20	2	12	1	0	5
Hawaiian Islands							
<i>Prognathogryllus</i>	Insects	28	24	4	2	2	0
<i>Laupalla</i>	Insects	33	31	2	0	2	0
<i>Megalagrion</i>	Insects	34	15	19	14	5	0
<i>Sarona</i>	Insects	69	62	7	2	5	0
<i>Drosophila</i>	Insects	44	35	7	1	6	2
Platynini	Insects	69	46	23	12	11	0
<i>Hylaeus</i>	Insects	83	25	51	9	42	8
<i>Kokia</i>	Plants	5	0	0	0	0	5
<i>Hesperomannia</i>	Plants	6	2	3	3	0	1
<i>Remya</i>	Plants	3	2	1	1	0	0
<i>Neurophyllodes</i>	Plants	7	5	2	1	1	0
<i>Hibiscadelphus</i>	Plants	11	11	0	0	0	0
Silversword alliance	Plants	53	36	17	9	6	0
<i>Schiedea</i>	Plants	37	22	15	6	9	0
<i>Cyanea</i>	Plants	52	50	2	2	0	0
<i>Scaevola</i>	Plants	5	2	1	1	0	2
<i>Clearmontia</i>	Plants	29	20	7	3	4	2
<i>Tetramolopium</i>	Plants	20	6	12	3	9	2
<i>Platydesma</i>	Plants	9	0	0	0	0	9
<i>Adenophorus</i>	Plants	10	6	3	1	2	1
Lamiaceae	Plants	30	24	6	0	6	0
<i>Psychotria</i>	Plants	22	15	3	2	1	4
<i>Tetragnatha</i> elongate	Arachnids	14	9	4	2	2	1
<i>Tetragnatha</i> spiny leg-1	Arachnids	7	3	3	1	2	1
<i>Tetragnatha</i> spiny leg -2	Arachnids	10	3	5	2	3	2
<i>Orsonwelles</i>	Arachnids	24	24	0	0	0	0
Succineidae	Molluscs	14	13	1	1	0	0
Achatinellidae	Molluscs	32	24	8	3	5	0
Drepanidinae	Birds	27	9	15	11	4	3

IS, *in situ* speciation events; BE, biotic expansion; Fwd BE, forward biotic expansion; Bkwd BE, backward biotic expansion; Amb., ambiguous biotic expansion events

Further, the relatively close inter-island proximities in the Hawaiian Islands seem to have facilitated inter-island dispersal, producing lineages that occur on multiple islands. In our analysis, these were represented by polytomies, increasing the total

number of OTUs counted. Moreover, the two GACs depict different patterns of speciation. The Hawaiian Islands are one of the most isolated island series in the world, and thus dispersal to other regions is fairly restricted. A few Hawaiian clades dispersed

Island group	Island	Total sp.	IS sp.	BE sp.	% IS sp.	% BE sp.	Area
Greater Antilles	Hispaniola	46	21	25	45.7	54.3	76,480
	Jamaica	17	11	6	64.7	35.3	11,100
	Cuba	53	22	31	41.5	58.5	110,860
	Puerto Rico	15	6	9	40	60	9104
	Total	131	60	72	45	55	
Hawaiian Islands	Kauai	143	90	53	63	37	552
	Oahu	149	75	74	50	50	597
	Molokai	124	44	80	35.5	64.5	260
	Lanai	88	29	59	33	67	141
	Maui	207	89	118	43	57	727
	Hawai'i	145	72	73	50	50	10,432
	Total	858	399	459	46.5	53.5	

Table 4 Summary proportions for species (sp.) arising through *in situ* (IS) or biotic expansion (BE) for both individual islands and for the whole of each island group (Greater Antilles and Hawaiian Islands). Area is in km².

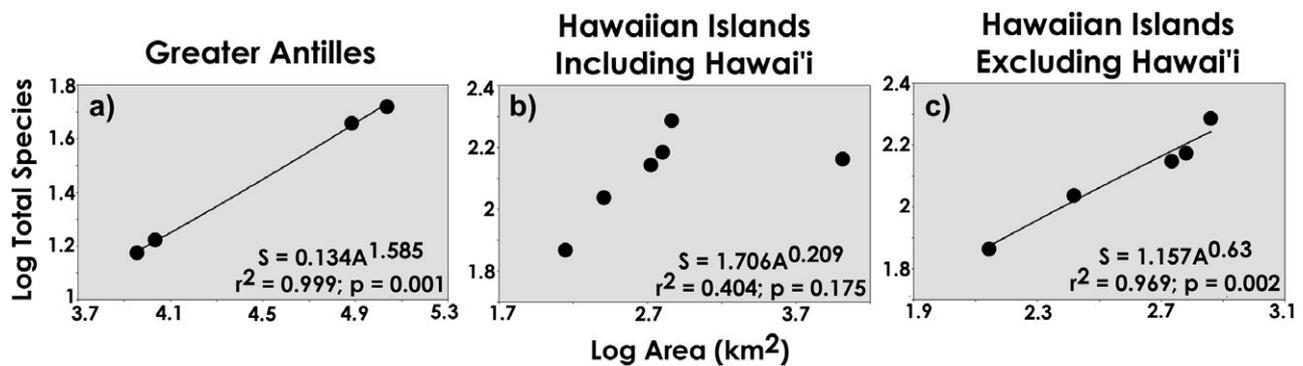


Figure 2 Log-log power-law species–area relationships (SAR) of the Greater Antilles and Hawaiian Islands. The number of species represents the number of nodes representing each region in the general area cladograms. (a) The Greater Antilles yielded a strong linear SAR. (b) The Hawaiian Islands yield no SAR. (c) The removal of Hawai'i (a statistical outlier) resulted in a strong linear SAR for the Hawaiian Islands. Trendlines are only present for significant relationships.

to outside sources, including the land snail *Succinea* to Tahiti and Samoa (Cowie & Holland, 2008), the fruit fly *Scaptomyza* to other continental and island regions (O'Grady & DeSalle, 2008) and the plant *Meliocope* to Polynesia (Harbaugh *et al.*, 2009). However, at present these instances still appear to be the exception rather than the rule. Alternatively, the Greater Antilles are exceptionally close to another island series, the Lesser Antilles, and mainland sources (e.g. North, Central and South America), and back colonization to those sources has occurred regularly. The proportion of species resulting from *in situ* and biotic expansion events in each island series is similar for each island assemblage (Table 4), even though individual Hawaiian clades exhibited more *in situ* than biotic expansion events (Table 3).

Our results show the evolutionary histories of the Greater Antilles and Hawaiian Islands conform more to a taxon pulse than a progression rule dynamic, because they show alternating phases of species arising *in situ* and through biotic expansion. This is in accordance with other recent studies of historical biogeography for both island (Spironello & Brooks, 2003) and mainland biotas (Bouchard *et al.*, 2004; Halas *et al.*, 2005; Folinsbee & Brooks, 2007; Lim, 2008). Both island groups show a preponderance of forward colonization in their biotic expan-

sion events (85.1% for the Greater Antilles, 65% for the Hawaiian Islands), suggesting that most inter-island relationships have been produced in a manner consistent with the progression rule. However, both island groups also show evidence of back colonization. In our analysis of the Hawaiian Islands, the back colonization is restricted to older islands within the assemblage, because none of our analysed lineages have mainland or other island sources nested within the area cladograms. However, the Greater Antillean analysis depicted some back colonization to original mainland source areas because most lineages had back colonizations nested within the area cladograms. Forward colonization events occur slightly more often than back colonization events in Hawaiian taxa (65% forward, 35% back), whereas there is a higher percentage of Greater Antillean forward colonization events (85.1% forward, 14.1% back). However, some of the Greater Antillean speciation events can be attributed to inter-island vicariance (Crother & Guyer, 1996), thus there is more pattern congruence between taxa that speciated at the time of island formation (e.g. islands colliding and subsequently diverging). However, the only biotic expansion events possible between the Hawaiian Islands are dispersal based and may lack distinct directionality. This is probably further enhanced by the

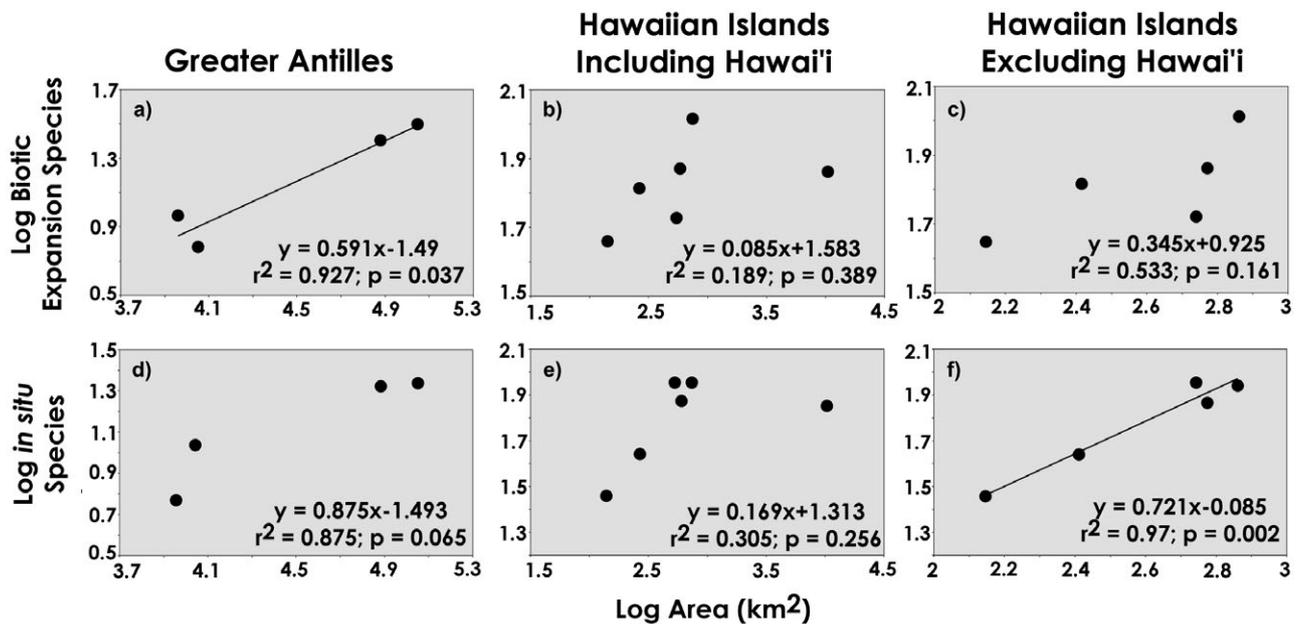


Figure 3 Influence of area on types of speciation events. Speciation event type was determined based on optimized nodes in the general area cladograms that showed diversification events between regions (biotic expansion) and within regions (*in situ*). Log–log relationships between area and species produced via biotic expansion were (a) significant for the Greater Antilles and insignificant for the Hawaiian Islands both including (b) and excluding Hawai'i (c). Log–log relationships for species produced *in situ* and area are insignificant for both the Greater Antilles (d) and the Hawaiian Islands when Hawai'i is included (e). Exclusion of Hawai'i from the Hawaiian analysis resulted in a strongly linear relationship (f). Trendlines are only present for significant relationships.

increased proximity of islands to one another in the Hawaiian Islands (Fig. 1).

The use of geological events as calibration points for molecular clocks has previously been perceived as problematic because of the assumption that the event produced the divergence (e.g. Renner, 2005). However, despite this limitation, using geological calibrations in the absence of a fossil record has still been perceived as better than nothing (Scheen *et al.*, 2004). Our results underscore the strength of the taxon pulse in the Hawaiian Islands and Greater Antilles, and we further emphasize that caution should be used when calibrating molecular clock estimates of speciation events based on the ages of the islands or other areas inhabited, because the taxon pulse signal indicates speciation events that do not necessarily correspond to the age of an area.

PACT analysis of SARs

Assuming all other island attributes to be equal (e.g. distance from mainland source, habitat variability and age of islands), the equilibrium theory of island biogeography (ETIB; MacArthur & Wilson, 1963, 1967) suggests that the SAR should be linear when species richness is perfectly correlated with island area. In our analyses we examined the information extracted from PACT regarding ecological biogeographic processes; our results are not inconsistent with some recent work that has suggested that modifications of the ETIB are necessary to incorporate complex patterns of immigration, extinction and diversification (e.g.

Heaney, 2000; Whittaker, 2000) and modifications to the power-law SAR algorithm are needed to reduce inherent errors of over-generalization (e.g. Garcia Martín & Goldenfeld, 2006; Triantis *et al.*, 2008).

MacArthur and Wilson's ETIB predicts that islands with fewer than the expected number of species are presumed to be young islands or islands with increased distance from a 'mainland' (i.e. the area serving as the species source for dispersal, which itself may be an island) or islands experiencing species loss. We see this pattern in the Hawaiian Islands, because there is no significant SAR unless Hawai'i, being both the youngest and the largest island (Fig. 1a), is removed from analysis. Alternatively, the Greater Antilles yielded a strong SAR, which is consistent with the ETIB hypothesis and previous analyses (Ricklefs & Bermingham, 2008, and references within).

In their original discussion of the ETIB, MacArthur & Wilson (1963) summarized the dynamics of the SAR and suggested that in most cases, it would be permissible to disregard the number of species generated by *in situ* speciation, referred to as 'autochthonous' or 'local' speciation, since it would be significant only in large, old archipelagos such as the Greater Antilles in our analysis. Otherwise, this variable would potentially confound and complicate the linear SAR (see Heaney, 2000, for an argument for the importance of studying this confounding effect).

MacArthur & Wilson (1963) did not provide an explicit reason for the confounding effect in *in situ* speciation events; however, the complication could occur in two ways: (1) if *in situ* speciation and speciation by colonization are not causally

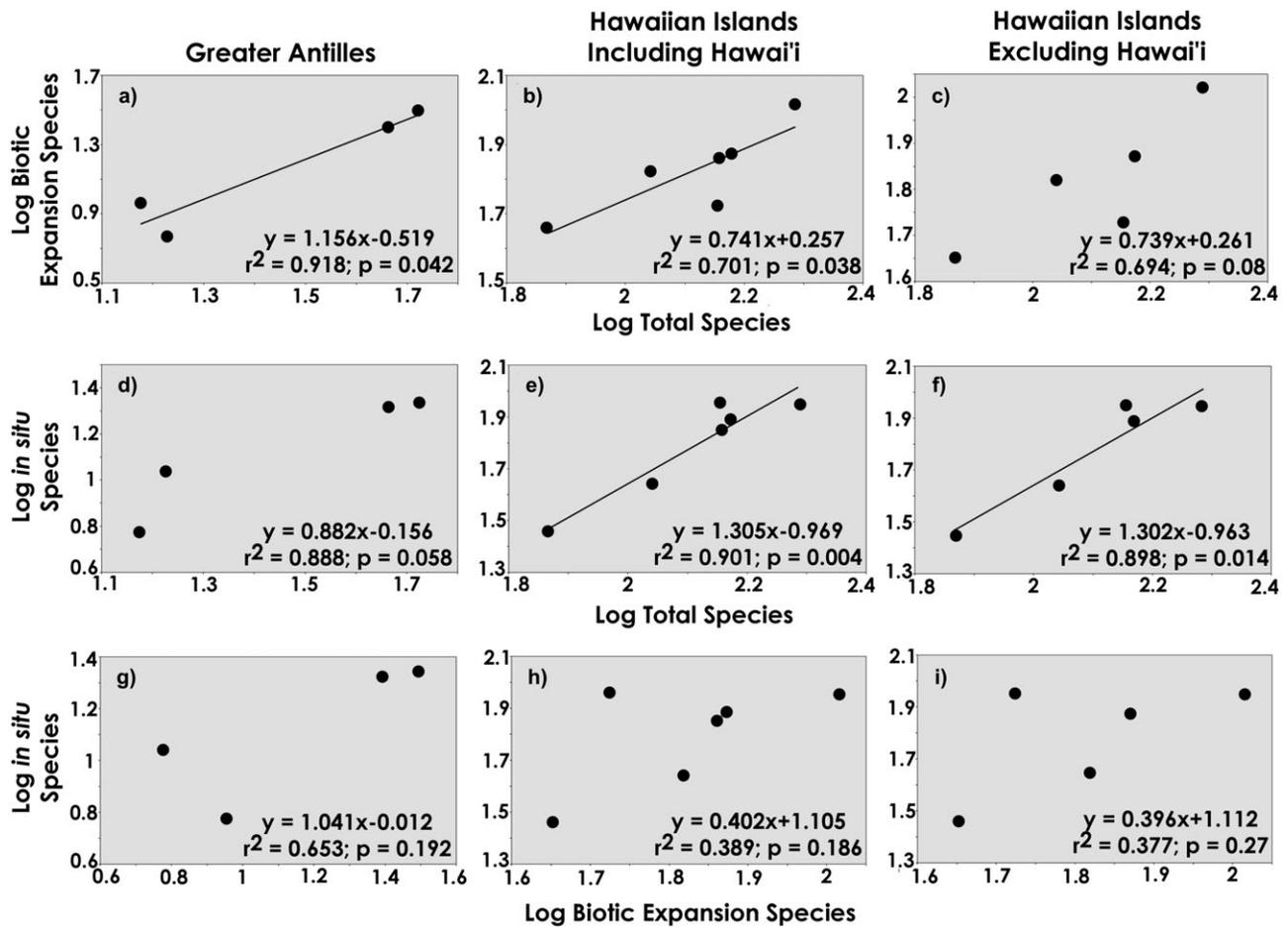


Figure 4 Contribution of speciation types to total species production. Speciation event type was determined based on optimized nodes in the general area cladograms that showed diversification events between regions (biotic expansion) and within regions (*in situ*). Log–log relationships for species produced via biotic expansion and total number of species produced was significant for the Greater Antilles (a) and the Hawaiian Islands including Hawai'i (b), but was insignificant when Hawai'i was removed from analysis (c). Log–log relationships for species produced *in situ* and total number of species produced was insignificant for the Greater Antilles (d) but significant for the Hawaiian Islands, both including (e) and excluding (f) Hawai'i. There was no log–log relationship between species produced via biotic expansion and produced *in situ* for the Greater Antilles (g), Hawaiian Islands including Hawai'i (h), or Hawaiian Islands excluding Hawai'i (i). Trendlines are only present for significant relationships.

coupled, and (2) if back-dispersal occurs. In the case of the former, if *in situ* speciation is a process independent of colonization that may influence the shape of the species–area curve to a considerable extent, depending on the age and size of the island (Heaney, 2000; Halas *et al.*, 2005; Brooks & van Veller, 2008). In the latter case, back-dispersal permits islands serving as sinks ('evolutionary dead ends') for incoming species to become sources of species to other islands, violating the underlying assumption of a unidirectional source–sink relationship between islands and the 'mainland', which is a species source outside the archipelago of concern and may be a continent or another island series. Thus, a nonlinear SAR (defined in our study as one with either a weak r^2 or a statistically insignificant r^2) suggests that islands may have capacity to serve as both sources and sinks, irrespective of size. However, both of these scenarios are plausible in our analysis of the Hawaiian Islands,

because we observe no coupling of *in situ* speciation and colonization, and 34.5% of biotic expansion events were back dispersal.

Our data suggest that the contribution of *in situ* speciation events is independent of area for the Greater Antilles (Fig. 3d) and the Hawaiian Islands (Fig. 3e). However, exclusion of Hawai'i resulted in a significant relationship for the remaining islands of the Hawaiian Archipelago (Fig. 3f). Removal of Hawai'i from the analysis yielded a strong relationship between species produced *in situ* and area (Fig. 3f), and both Hawaiian analyses showed strong relationships between species produced *in situ* and total number of species (Fig. 4e–f). In this case, Hawai'i distorts the *in situ*–area relationship because it is both the largest and youngest Hawaiian island, indicating that it may not have reached species equilibrium yet. This has been previously observed by Gillespie (2004), where Hawai'i did not

exhibit the spider diversification that is seen throughout the rest of the archipelago. Gillespie (2004) suggested that, given more time, the clades on Hawai'i are likely to further diversify.

Our results may lend more credence to this possible explanation of how *in situ* speciation confounds the classical SAR, involving species sinks as species sources, and strongly reinforces the notion that any island, regardless of its size, can act as a dynamic source–sink area – such roles would not be necessarily limited to larger islands. Therefore, more islands would be acting as source–sink areas because of the presence of *in situ* speciation events across the entirety of these archipelagos. This is further supported by the weak relationship between species produced *in situ* and by biotic expansion (Fig. 4g–i), denoting that the number of *in situ* events across all of the islands is relatively independent of the number of biotic expansion events. This suggests that speciation through *in situ* and biotic expansion may be acting independently, an expected observation in a situation where areas have the potential to serve as both species sources and sinks.

The results we find with PACT analyses are relatively novel and unexplored, and as a consequence we currently have no means to apply statistical tests of node robustness. Even though statistical tests may show a falsification of maximum vicariance models, we do not yet have taxon pulse models to test. We acknowledge that the assessment of unique and general nodes may be affected by this. This is why we must be conservative about inferences of unique events in the absence of models. At the moment, any node supported by more than one taxon–area cladogram is considered a general node. As a result, PACT may underestimate the general nodes, but should not overestimate them. However, we emphasize that the development of a general taxon pulse model and associated confidence intervals for variations on that theme would be valuable for future inferences (e.g. how close to a 1:1 alternation of expansion/isolation nodes must there be for a taxon pulse? Are there different kinds of taxon pulses?).

ACKNOWLEDGEMENTS

Genevieve Toutain provided aid with statistical analyses and Smitty Smith assisted with data collection. Funding for this project was provided by Southeastern Louisiana University and the University of Nevada, Las Vegas (to M.E.E.), and by a Discovery grant from the Natural Sciences and Engineering Research Council (NSERC) of Canada (to D.R.B.). We thank Tereza Jezkova, Matthew Lattanzio and Brian T. Smith for helpful discussions regarding this study, and this paper was improved with comments and suggestions from the University of Nevada, Las Vegas Systematics Discussion Group.

REFERENCES

- Ackermann, M. & Doebeli, M. (2004) Evolution of niche width and adaptive diversification. *Evolution*, **58**, 2599–2612.
- Bouchard, P., Brooks, D.R. & Yeates, D.K. (2004) Mosaic macroevolution in Australian wet tropics arthropods: community assemblage by taxon pulses. *Rainforest: past, present, future* (ed. by C. Moritz and E. Bermingham), pp. 425–469. University of Chicago Press, Chicago, IL.
- Brooks, D.R. & Ferrao, A.L. (2005) The historical biogeography of co-evolution: emerging infectious diseases are evolutionary accidents waiting to happen. *Journal of Biogeography*, **32**, 1291–1299.
- Brooks, D.R. & Folinsbee, K.E. (2005) Paleobiogeography: documenting the ebb and flow of evolutionary diversification. *Paleontological Society Papers*, **11**, 15–43.
- Brooks, D.R. & McLennan, D.A. (2002) *The nature of diversity: an evolutionary voyage of discovery*. University of Chicago Press, Chicago, IL.
- Brooks, D.R. & van Veller, M.P.G. (2008) Assumption 0 analysis: comparative evolutionary biology in the age of complexity. *Annals of the Missouri Botanical Garden*, **95**, 201–223.
- Carlquist, S. (1970) *Hawaii: a natural history*. Natural History Press, New York.
- Chakrabarty, P. (2006) Systematics and historical biogeography of Greater Antillean Cichlidae. *Molecular Phylogenetics and Evolution*, **39**, 619–627.
- Cowie, R.H. & Holland, B.S. (2008) Molecular biogeography and diversification of the endemic terrestrial fauna of the Hawaiian Islands. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **363**, 3363–3376.
- Crother, B.I. & Guyer, C. (1996) Caribbean historical biogeography: was the dispersal–vicariance debate eliminated by an extraterrestrial bolide? *Herpetologica*, **52**, 440–465.
- Cunningham, C.W. (1999) Some limitations of ancestral character-state reconstruction when testing evolutionary hypotheses. *Systematic Biology*, **48**, 665–674.
- Darwin, C. (1859) *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life*, 2nd edn. Oxford University Press, New York.
- Donoghue, M.J. & Moore, B.R. (2003) Toward an integrative historical biogeography. *Integrative and Comparative Biology*, **43**, 261–270.
- Erwin, T.C. (1981) Taxon pulses, vicariance, and dispersal: an evolutionary synthesis illustrated by carabid beetles. *Vicariance biogeography: a critique* (ed. by G. Nelson and D.E. Rosen), pp. 159–196. Columbia University Press, New York.
- Folinsbee, K.E. & Brooks, D.R. (2007) Miocene hominid biogeography: pulses of dispersal and differentiation. *Journal of Biogeography*, **34**, 383–397.
- Funk, V.A. & Wagner, W.L. (ed.) (1995a) *Hawaiian biogeography: evolution on a hot-spot archipelago*. Smithsonian Institution Press, Washington, DC.
- Funk, V.A. & Wagner, W.L. (1995b) Biogeographic patterns in the Hawaiian Islands. *Hawaiian biogeography: evolution on a hot-spot archipelago* (ed. by V.A. Funk and W.L. Wagner), pp. 379–420. Smithsonian Institution Press, Washington, DC.
- Garcia Martin, H. & Goldenfeld, N. (2006) On the origin and robustness of power-law species–area relationships in ecology. *Proceedings of the National Academy of Sciences USA*, **103**, 10310–10315.

- Gillespie, R. (2004) Community assembly through adaptive radiation in Hawaiian spiders. *Science*, **303**, 356–359.
- Graham, S.A. (2002) Phylogenetic relationships and biogeography of the endemic Caribbean genera *Crenea*, *Ginoria*, and *Haitia* (Lythraceae). *Caribbean Journal of Science*, **38**, 195–204.
- Graham, A. (2003) Geohistory models and Cenozoic paleoenvironments of the Caribbean region. *Systematic Botany*, **28**, 378–386.
- Halas, D., Zamparo, D. & Brooks, D.R. (2005) A historical biogeographical protocol for studying biotic diversification by taxon pulses. *Journal of Biogeography*, **32**, 249–260.
- Harbaugh, D.T., Wagner, W.L., Allan, G.J. & Zimmer, E.A. (2009) The Hawaiian Archipelago is a stepping stone for dispersal in the Pacific: an example from the plant genus *Melicope* (Rutaceae). *Journal of Biogeography*, **36**, 230–241.
- Hausdorf, B. & Hennig, C. (2004) Does vicariance shape biotas? Biogeographical tests of the vicariance model in the north-west European land snail fauna. *Journal of Biogeography*, **31**, 1751–1757.
- Heaney, L.R. (2000) Dynamic disequilibrium: a long-term, large-scale perspective on the equilibrium model of island biogeography. *Global Ecology and Biogeography*, **9**, 59–74.
- Heaney, L.R. & Rickart, E.A. (1990) Correlations of clades and clines: geographic, elevational, and phylogenetic distribution patterns among Philippine mammals. *Vertebrates in the tropics* (ed. by G. Peters and R. Hutterer), pp. 321–322. Museum Alexander Koenig, Bonn.
- Hedges, S.B. (2001) Afrotheria: plate tectonics meets genomics. *Proceedings of the National Academy of Sciences USA*, **98**, 1–2.
- Heinicke, M.P., Duellman, W.E. & Hedges, S.B. (2007) Major Caribbean and Central American frog faunas originated by ancient oceanic dispersal. *Proceedings of the National Academy of Sciences USA*, **104**, 10092–10097.
- Hennig, W. (1950) *Grundzüge einer Theorie der phylogenetischen Systematik*. Deutscher Zentralverlag, Berlin.
- Hennig, W. (1966) *Phylogenetic systematics*. University of Illinois Press, Urbana, IL.
- Iturralde-Vinent, M.A. & MacPhee, R.D.E. (1999) Paleogeography of the Caribbean region: implications for Cenozoic biogeography. *Bulletin of the American Museum of Natural History*, **238**, 1–95.
- Kluge, A.G. (2002) Distinguishing ‘or’ from ‘and’ and the case for historical identification. *Cladistics*, **18**, 585–593.
- Lieberman, B.S. & Eldredge, N. (1996) Trilobite biogeography in the Middle Devonian: geological processes and analytical methods. *Paleobiology*, **22**, 66–79.
- Lim, B.K. (2008) Historical biogeography of New World emballonurid bats (tribe Diclidurini): taxon pulse diversification. *Journal of Biogeography*, **35**, 1385–1401.
- MacArthur, R.H. & Wilson, E.O. (1963) An equilibrium theory of insular zoogeography. *Evolution*, **17**, 373–387.
- MacArthur, R.H. & Wilson, E.O. (1967) *The theory of island biogeography*. Princeton University Press, Princeton, NJ.
- MacDonald, G.A., Abbott, A.T. & Peterson, F.L. (1983) *Volcanoes in the sea: the geology of Hawaii*. University of Hawaii Press, Honolulu, HI.
- Maddison, D.R. & Maddison, W. (2000) *MacClade analysis of phylogeny and character evolution, version 4.08*. Sinauer Association, Inc., Sunderland, MA.
- Melville, R. (1981) Vicarious plant distributions and paleogeography of the Pacific region. *Vicariance biogeography: a critique* (ed. by G. Nelson and D.E. Rosen), pp. 238–274. Columbia University Press, New York.
- Nelson, G. & Platnick, N. (1981) *Systematics and biogeography: cladistics and vicariance*. Columbia University Press, New York.
- O’Grady, P. & DeSalle, R. (2008) Out of Hawaii: the origin and biogeography of the genus *Scaptomyza* (Diptera: Drosophilidae). *Biology Letters*, **4**, 195–199.
- Peck, S.B., Wigfull, P. & Nishida, G. (1999) Physical correlates of insular species diversity: the insects of the Hawaiian Islands. *Annals of the Entomological Society of America*, **92**, 529–536.
- Pregill, G.K. & Crother, B.I. (1999) Ecological and historical biogeography of the Caribbean. *Caribbean amphibians and reptiles* (ed. by B.I. Crother), pp. 335–356. Academic Press, San Diego, CA.
- Preston, F.W. (1962) The canonical distribution of commonness and rarity, part I. *Ecology*, **43**, 185–215.
- Price, J.P. & Elliott-Fisk, D. (2004) Topographic history of the Maui Nui complex, Hawaii, and its implications for biogeography. *Pacific Science*, **58**, 27–45.
- Renner, S.S. (2005) Relaxed molecular clocks for dating historical plant dispersal events. *Trends in Plant Science*, **10**, 550–558.
- Ricklefs, R.E. & Bermingham, E. (2008) The West Indies as a laboratory of biogeography and evolution. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **1502**, 2393–2413.
- Riddle, B.R. & Hafner, D.J. (2006) A step-wise approach to integrating phylogeographic and phylogenetic biogeographic perspectives on the history of a core North American warm deserts biota. *Journal of Arid Environments*, **66**, 435–461.
- Rosen, D.E. (1975) A vicariance model of Caribbean biogeography. *Systematic Zoology*, **24**, 431–464.
- Rosen, D.E. (1985) Geological hierarchies and biogeographic congruence in the Caribbean. *Annals of the Missouri Botanical Garden*, **72**, 636–659.
- Rosenzweig, M.L. (1995) *Species diversity in space and time*. Cambridge University Press, Cambridge.
- Ross, H.H. (1972) The origin of species diversity in ecological communities. *Taxon*, **21**, 253–259.
- Scheen, A.-C., Brochman, C., Brysting, A.K., Elven, R., Morris, A., Soltis, D.E., Soltis, P.S. & Albert, V.A. (2004) Northern Hemisphere biogeography of *Cerastium* (Caryophyllaceae): insights from phylogenetic analysis of noncoding plastid nucleotide sequences. *American Journal of Botany*, **91**, 943–952.
- Schluter, D., Price, T.D., Mooers, A.Ø. & Ludwig, D. (1997) Likelihood of ancestor states in adaptive radiation. *Evolution*, **51**, 1699–1711.
- Spironello, M. & Brooks, D.R. (2003) Dispersal and diversification: macroevolutionary implications of the MacArthur–

- Wilson model, illustrated by *Simulium (Inseliellum)* Rubstov (Diptera: Simuliidae). *Journal of Biogeography*, **30**, 1563–1573.
- SPSS, Inc. (2007) *SPSS, version 16.0.1*. SPSS, Inc., Chicago, IL.
- Triantis, K.A., Nogués-Bravo, D., Hortal, J., Borges, A.V.P., Adersen, H., Fernandez-Palacios, M., Araújo, M.B. & Whittaker, R.J. (2008) Measurements of area and the (island) species–area relationship: new directions for an old pattern. *Oikos*, **117**, 1555–1559.
- Vázquez-Miranda, H., Navarro-Sigüenza, N.G. & Morrone, J.J. (2007) Biogeographical patterns of the avifaunas of the Caribbean Basin islands: a parsimony perspective. *Cladistics*, **23**, 180–200.
- Wallace, A.R. (1855) On the law which has regulated the introduction of new species. *Annals and Magazine of Natural History*, **16**, 184–196.
- Whittaker, R.J. (2000) Scale, succession, and complexity in island biogeography: are we asking the right questions? *Global Ecology and Biogeography*, **9**, 75–85.
- Whittaker, R.J. (2004a) The island biogeography of a long-running natural experiment: Krakatau, Indonesia. *Ecología insular/Island ecology* (ed. by J.M. Fernández-Palacios and C. Morici), pp. 57–59. Asociación Española de Ecología Terrestre (AEET), Cabildo Insular de la Palma, Santa Cruz de la Palma.
- Whittaker, R.J. (2004b) The importance of islands. *Foundations of biogeography* (ed. by J.H. Brown, M.V. Lomolino and D. Sax), pp. 931–1026. Chicago University Press, Chicago, IL.
- Whittaker, R.J. (2004c) Dynamic hypotheses of richness on islands and continents. *Frontiers of biogeography: new directions in the geography of nature* (ed. by M.V. Lomolino and L.R. Heaney), pp. 211–231. Sinauer Associates, Inc, Sunderland, MA.
- Wiley, E.O. (1981) *Phylogenetics: the theory and practice of phylogenetic systematics*. John Wiley and Sons, New York.
- Wiley, E.O. (1986) Phylogenetic systematics. *McGraw-Hill yearbook of science and technology*, pp. 343–346. McGraw-Hill, New York.
- Wiley, E.O. (1988a) Parsimony analysis and vicariance biogeography. *Systematic Zoology*, **37**, 271–290.
- Wiley, E.O. (1998b) Vicariance biogeography. *Annual Review of Ecology and Systematics*, **19**, 513–542.
- Wojcicki, M. & Brooks, D.R. (2004) Escaping the matrix: a new algorithm for phylogenetic comparative studies of coevolution. *Cladistics*, **20**, 341–361.
- Wojcicki, M. & Brooks, D.R. (2005) PACT: a efficient and powerful algorithm for generating area cladograms. *Journal of Biogeography*, **32**, 755–774.
- Ziegler, A.C. (2002) *Hawaiian natural history, ecology, and evolution*. University of Hawaii Press, Honolulu, HI.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Clades utilized and studies referenced for Greater Antillean PACT analysis.

Appendix S2 Clades utilized and studies referenced for Hawaiian Islands PACT analysis.

Appendix S3 General area cladogram generated from the 29 Hawaiian clades studied.

Appendix S4 General area cladogram generated from the 18 Greater Antillean clades studied.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials are peer-reviewed and may be reorganized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.

BIOSKETCH

Mallory E. Eckstut is a Doctoral candidate in the lab of Dr Brett Riddle at University of Nevada, Las Vegas. Her research interests include historical biogeographic analysis and methodological development, reptile and amphibian evolutionary ecology, and the evolution of vertebrate reproductive strategies.

Author contributions: M.E.E., B.I.C. and D.R.B. conceived the ideas; M.E.E., C.D.M. and B.I.C. gathered and analysed the Greater Antillean data; J.M.A., D.A.M. and D.R.B. gathered and analysed the Hawaiian Island data; M.E.E., C.D.M. and D.R.B. led the writing.

Editor: Jack Lennon