

## A PHYLOGENETIC BASIS FOR SPECIES–AREA RELATIONSHIPS AMONG THREE PACIFIC ISLAND FLORAS<sup>1</sup>

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- *Premise of the study:* The angiosperm floras of the Hawaiian, Society, and Marquesas archipelagoes are remarkably comparable ecologically and evolutionarily, a result of similar geologic history, climate, and isolation.
- *Methods:* We characterized variation in species richness among islands and whole archipelagoes by analyzing species–area relationships (SARs). By partitioning each flora into putative phylogenetic lineages each derived from a given colonization event, we explored several ways in which speciation contributes to SARs.
- *Key results:* Specifically, these groups exhibit expected island SARs and a whole archipelago SAR characterized by a steep slope. The number of species added by net cladogenesis increases with area much more quickly than the number contributed by net colonization from outside. In each of the three archipelagoes, most colonists do not speciate, while many species occur in a few diverse colonist lineages. Colonization events that are unique to a given archipelago are in more prone to speciation than lineages with close relatives in the other archipelagoes. Most lineages with relatives in all three archipelagoes have one species in each, suggesting a similar tendency not to diversify. On the other hand, a correlation between lineage size in one archipelago and that of related lineages in other archipelagoes suggests a consistent tendency among diverse groups to speciate extensively. Lineages with multiple species in each archipelago also tend to have far more species in the largest archipelago, the Hawaiian Islands.
- *Conclusions:* The most diverse lineages exhibit a strong response to archipelago area. These diverse, area-sensitive lineages contribute substantially to the slope of the inter-archipelago SAR. Regional species pools elsewhere may exhibit similar steep-sloped SARs; thus, these findings may inform how the behavior of lineages with different responses to increasing shapes these patterns.

**Key words:** biodiversity; flora; Hawaiian Islands; Marquesas Islands; phylogeny; Society Islands; species–area relations.

A major goal in biology is the reconciliation of regional and local processes in determining diversity patterns (Ricklefs and Schluter, 1993) and community structure (Webb et al., 2002), with considerable progress being achieved as phylogenies become available for more groups of organisms. In particular, species–area relationships (henceforth SARs) have received continuing attention due to their consistency (Connor and McCoy, 1979; Rosenzweig, 1995; Lomolino, 2000b; Whittaker and Fernández-Palacios, 2007) to the point of being considered the equivalent of a law in ecology and biogeography (Schoener, 1976). MacArthur and Wilson (1967) expounded the ecological processes regulating species number ( $S$ ) in varying areas, namely immigration and extinction, but critics cite the omission of speciation as a shortcoming of the equilibrium model (reviewed by Lomolino and Brown, 2009). Since then, evolutionary underpinnings of SARs have been examined theoretically and empirically.

Rosenzweig’s (1995) provincial theory proposed a nested model that includes a steep slope for a SAR between evolutionary provinces (regions of locally evolved endemism with different evolutionary histories) and modest slopes for SARs of islands or mainland samples within provinces. This model asserts that the modest slopes of SARs within evolutionary provinces are driven largely by ecological processes, while the steep

slope of the interprovincial SAR is driven by differences in evolutionary history. Some alternative models of immigration–extinction–speciation dynamics treat speciation as a form of immigration whose contribution increases with isolation (Heaney, 2000; Lomolino, 2000a). The model of Whittaker et al. (2007; 2008) characterizes variation in speciation rates, along with immigration and extinction rates, through the lifespan of a typical volcanic oceanic island. Hubbell’s (2001) neutral theory considers speciation as an essentially random process influencing relative abundance distributions. Gavrillets and Vose (2005) developed a spatially explicit, individual-based model of adaptive radiation; by varying the area available, they found theoretical support for the “area rule” whereby a clade speciates to a greater degree on islands or archipelagoes with greater areas.

Several empirical studies have demonstrated that the degree to which related clades speciate within different islands (or lakes) increases with available area: *Anolis* lizards in the Caribbean (Losos and Schluter 2000), *Bulimulus* land snails in the Galapagos Islands (Parent and Crespi 2006), and cichlid fishes in African lakes (Seehausen 2006). In evaluating these studies, Gavrillets and Losos (2009) indicated that the area effect is partly due to the fact that islands below a certain area threshold do not support intra-island speciation, even when they contain a diversity of habitats. Studies such as these examine colonist-lineages for which phylogenetic relationships are resolved; however, they tend to focus on the most species-rich lineages in a given archipelago and may not consider the context of these within the overall pool of lineages.

Other studies examine the full set of species endemic to a range of islands or archipelagoes to assess the role of area or

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habitat heterogeneity in promoting cladogenesis. Coyne and Price (2000) found that among single-island endemic birds, only the very largest islands appeared capable of supporting intra-island speciation, suggesting a lower sensitivity of speciation to area compared with adaptive radiations summarized by Gavrillets and Losos (2009). In an exhaustive examination of island endemic taxa, Kisel and Barraclough (2010) estimated the minimum island size necessary for intra-island speciation in various taxonomic groups and showed that taxa able to speciate in smaller areas had the lowest rates of intraspecific gene flow. Stuessy et al. (2006) analyzed the floras of 13 archipelagoes to assess the importance anagenetic speciation (between an external ancestor and an endemic island species) compared with cladogenetic speciation (divergence of island taxa within an archipelago), showing that larger archipelagoes had lower proportions of anagenetic speciation and complementarily higher rates of cladogenetic speciation. In light of the fact that larger islands have more endemic species, Givnish (2010) interprets the higher proportions of cladogenetic speciation there as evidence that island plants follow the “area rule” demonstrated for individual clades. Triantis et al. (2008) calculated SARs for single-island endemic species in different taxonomic groups within several archipelagoes and found very steep  $z$ -values, similar to those predicted by Rosenzweig (1995) to occur between regions, pointing toward the speciation-area rule playing a role in shaping SARs. In these cases, counts and proportions of different kinds of endemic species are intended to represent the behavior of “average lineages” of a given taxonomic group when confronted with different physical environments, while variation among lineages is downplayed. Additionally, studies comparing archipelagoes are often confounded by differences in regional climate, source biota, degree of isolation, and geologic age (for example, see Domínguez-Lozano et al. (2010) for a comparison of the Hawaiian and Canary Island floras).

Here we compare the angiosperm floras of the Hawaiian, Society, and Marquesas Islands with the specific goal of assessing the degree to which different kinds of lineages adhere to the “area rule” and contribute to large-scale species–area relationships. These three Pacific archipelagoes make excellent subjects for comprehensive biogeographic analysis because they represent self-contained evolutionary provinces that are nonetheless highly comparable and that can be examined in considerable detail. All three are hot-spot volcanic archipelagoes that have tropical climates dominated by trade winds, including a range of moisture regimes and elevations. They include comparable numbers of high islands, which we define here as being over 500 m a.s.l.; lower elevation islands do not sufficiently generate mesic to wet upland climates and typically contain mostly widespread nonendemic coastal taxa (Mueller-Dombois and Fosberg, 1998; Price, 2004). All are isolated from continents and islands with analogous habitats, although the Society Islands are somewhat closer to biotic source areas such as the Austral Islands and Fiji.

Parallel geologic histories further suggest similar evolutionary histories: All consist of hot-spot volcanoes increasing in age to the northwest as a function of the movement of the Pacific tectonic plate (so-called “conveyor belts”; Wilson, 1963) and spanning very similar ranges of age (Fig. 1). While the Hawaiian chain also includes older formerly high islands (Clague, 1996), these had largely diminished by the time the present high islands from Kaua‘i to Hawai‘i formed, constraining most colonization and diversification to the last 5 Ma as confirmed by multiple molecular clock studies of Hawaiian organisms (Price

and Clague, 2002). The oldest dated rock in the Society Islands is 4.5 Ma from Maupiti (Blais et al., 2002). However, several atolls to the northwest were formed by the Societies hot-spot, and presumably formed high islands; while no radiometric dates are available, Craig et al. (2001) used the estimated rate of tectonic plate movement to project the ages of these to be between 5.9 and 7.2 Ma. In the Marquesas Islands, the oldest rocks are about 5.8 Ma old from Eiao (Brousse et al., 1990) with no known potentially older islands. Therefore, the geologic ages of the oldest high islands constrain the time available for colonization and speciation similarly in each of these archipelagoes. One difference in geologic histories is that the Hawaiian chain is dominated by the island of Hawai‘i, which makes up 63% of the archipelago’s area yet is younger than 1 Ma (Moore and Clague, 1992; Wagner 1991), in contrast to the other archipelagoes, which have no comparably large young island.

Because the climate, geology, isolation, and source biotas are remarkably comparable, we can explore how the behavior of phylogenetic groups shapes variation in species richness among archipelagoes. Due to the isolation and geologic history of these archipelagoes, species can be grouped into lineages descended from a limited number of colonist ancestors (Fosberg, 1948; Wagner et al., 1990, 1999; Wagner, 1991; Sakai et al., 1995). These colonist lineages thus comprise monophyletic groups that have evolved under similar spatial and temporal constraints.

Colonization history often underlies major disparities in biodiversity among oceanic islands. Assuming a target area effect resulting in higher colonization rates (Lomolino, 1990) and a lower extinction rate (MacArthur and Wilson, 1967) for greater areas, regional species number may simply be a function of the ability of larger archipelagoes to receive and maintain a higher number of colonist lineages. Colonization rates should also be higher on archipelagoes that are less isolated (MacArthur and Wilson, 1967) or that lie in strategic positions with respect to migrating birds (Vargas et al., 1998; Ballard and Sytsma, 2000; Baldwin and Wagner, 2010), the primary vectors of plant colonization on remote islands (Carlquist, 1974; Price and Wagner, 2004). It is therefore possible that a given archipelago has been colonized far more than the others and that this process outweighs any differences in diversification rates. For example, despite having similar total species numbers, the Canary Islands have been colonized far more than the Hawaiian Islands (Domínguez-Lozano et al., 2010). There is also considerable variation in species number among colonist lineages as reported in the Hawaiian and the Canary Islands, with a few strongly divergent lineages contributing disproportionately (Domínguez-Lozano et al., 2010). If by chance a given archipelago received colonists predisposed to adaptive radiation, then the intrinsic characteristics of those lineages may underlie major differences in diversity among archipelagoes. For example, the well-known adaptive radiations of the silversword alliance (Asteraceae; Baldwin et al., 1991) and *Schiedea* (Caryophyllaceae; Nepokroeff et al., 2005), among others, resulted from chance colonizations of the Hawaiian Islands, yet there are no close relatives in other Pacific archipelagoes. It could thus be argued that the species richness of the Hawaiian Islands has been enhanced by unique colonization events that were not replicated in the other archipelagoes.

Alternatively, the increasingly recognized speciation–area effect may contribute to differences among whole regional biotas. Given the possibility of viewing SARs through the lens of phylogeny, we pursue here several central questions. What kinds of SARs exist within and between archipelagoes? What are the roles of colonization, extinction, and speciation within

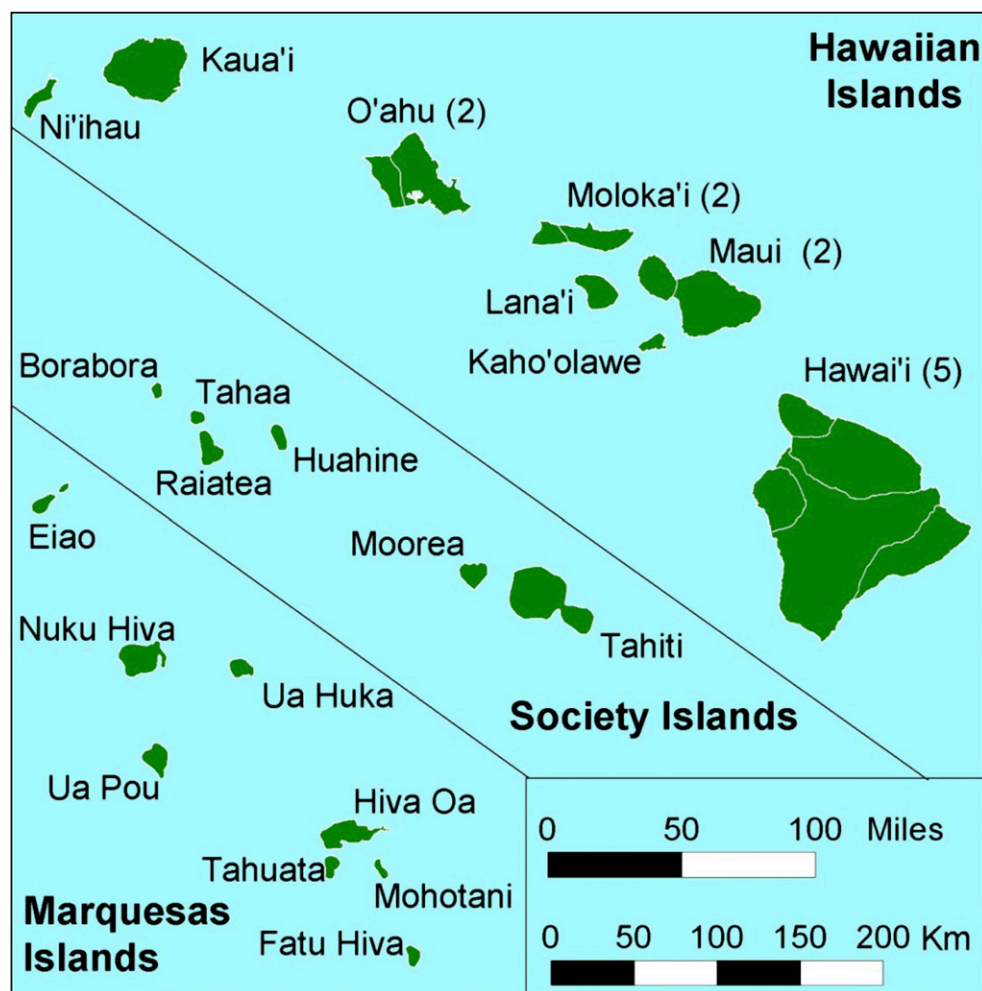


Fig. 1. Map of major islands. For Hawaiian Islands, the number of volcanic mountains comprising each island is shown in parentheses.

archipelagoes with different areas? How comparable is the nature of diversification in evolutionary lineages between these archipelagoes? How does variation among lineages contribute to large-scale SARs?

## MATERIALS AND METHODS

**Assessment of species–area relationships**—Thanks to the modest size of their floras, species distributions can be compiled with reasonable effort, permitting good assessments of species numbers for the islands of these archipelagoes. Data for the Hawaiian angiosperm flora build on data from Price (2004), including a few range extensions and newly described species (Wagner et al., 2005). For this analysis, we recognize 1001 species with 902 (90%) endemic (these numbers differ somewhat from Price (2004) because we have excluded the Northwest Hawaiian Islands and the small islands of Ni'ihau and Kaho'olawe in this study). Data for the Marquesan angiosperm flora were built from the ongoing Marquesas flora project (Wagner and Lorence, 2002), with supplemental data from Florence (1997, 2004). As presently delimited, the Marquesan angiosperm flora includes 229 species of which 128 (56%) are endemic. Assessment of the Society Islands flora was somewhat more tentative due to the lack of a comprehensive flora. We began with a checklist by Fosberg (1997) and the flora by Welsh (1998). For some families, more recent and thorough treatments by Florence (1997, 2004) resolved various taxonomic questions. Examination of specimens at the Bishop Museum herbarium in Honolulu (BISH), the U. S. National Herbarium in Washington, D.C. (US), and the National Tropical Botanic Garden on Kaua'i (PTBG) further improved species lists for the three

archipelagoes. Our present assessment recognizes 370 species in the Society Islands Flora with 192 (52%) being endemic. Because many genera have been studied by the same researchers in different archipelagoes, differences in taxonomic delimitation and species concept presumably have been minimized. While there are undoubtedly taxonomic issues remaining, and while there are certainly unrecorded occurrences of species on islands beyond those included in our assessments, these data are likely sufficient to characterize SARs.

All SARs were determined as a power function following the equation derived by Arrhenius (1921):  $\log S = \log c + z \log A$ , where  $S$  is the number of species,  $A$  is the area of an island group,  $c$  is the intercept of the regression function, and  $z$  is the slope of the regression function. Two types of SARs were considered. Island SARs (henceforth ISARs) consider islands individually, while the whole archipelago SAR (henceforth ASAR) considers total numbers of species in each archipelago and the area of all islands combined. While the ISARs include sufficient numbers of islands to assess a regression function, we concede that the ASAR, with only three points, lacks statistical power; however, it is not possible to include more archipelagoes with comparable geologic, climatic, and isolation characteristics. We therefore assert that the ASAR is a rough estimate of a theoretical relationship among distinct regions. Furthermore, due to the exceedingly large area of the island of Hawai'i despite its containing a modest number of total species and single island endemics, we calculated the ISAR for the Hawaiian Islands and the ASAR both including and excluding the island of Hawai'i; when excluding the island of Hawai'i from the ASAR, its area and single island endemic species were not counted toward the archipelago totals. The regression equations for all SARs were calculated using Minitab 16.1.0 (Minitab, 2010).

**Circumscription of phylogenetic groups**—Many Hawaiian lineages have been confirmed to represent monophyletic groups in phylogenetic studies using



molecular data, with the degree of diversification relating to various biogeographic and ecological traits (Wagner and Funk, 1995; Price and Wagner, 2004). For the Hawaiian Islands, species were grouped into colonist lineages following Price and Wagner (2004), which built on previous works (Fosberg, 1948; Carlquist, 1974; Wagner et al., 1990, 1999; Sakai et al., 1995) and established 31 lineages as monophyletic groups from phylogenetic studies. Subsequent phylogenetic work in various groups has largely confirmed assertions about monophyly, while slightly altering the circumscription of some phylogenetic groups such as *Cyrtandra* (Cronk et al., 2005) and *Silene* (Eggens et al., 2007).

The Marquesas and Society Islands have been the subject of far fewer phylogenetic studies, presenting challenges to lineage circumscription. Island taxa may diverge remarkably to the point that a single adaptive radiation may be mistaken for several separate lineages (Givnish, 1998). In fact, several taxa in the Hawaiian islands formerly considered to originate from separate introductions by Wagner et al. (1990), were subsequently recognized as single, large lineages: lobelioids (Givnish et al., 2009), *Cyrtandra* (Cronk et al., 2005), *Melicope* (Harbaugh et al., 2008), and *Silene* (Eggens et al., 2007). This problem may be less likely to occur in the smaller archipelagoes, because even the plant families with the most species (i.e., those capable of containing large radiations) tend to have few species compared with the most species-rich families in the Hawaiian Islands (where such problems have arisen). On the other hand, the presence of multiple endemic species within a genus may be mistakenly interpreted as a single colonist lineage, when in reality it is the result of multiple colonization events (e.g., *Rubus*; Howarth et al., 1997). However, in many cases, multiple species in a genus are nonendemic (and therefore have presumably separate origins outside the archipelago).

For the Marquesas Islands, species were grouped into putative colonist lineages following Wagner (1991) with modifications including recent phylogenetic treatments (Clark et al., 2008, 2009) and ongoing unpublished work for the Marquesas flora project (Wagner and Lorence, 2002). There are very few phylogenetic studies that include plants from the Society Islands; however, by incorporating these (e.g., Mouly et al., 2009) along with a taxonomic and morphological examination of known species, we divided the flora into colonist lineages with reasonable accuracy in the same way that we did for all presumed lineages for the Marquesas and Hawaiian islands for which molecular phylogenies are not available. Despite the potential pitfalls of delineating lineages based on morphology, our assumptions are similar to those of other studies (Coyne and Price, 2000; Stuessy et al., 2006; Kisel and Barraclough, 2010), with additional refinements made after close taxonomic and morphological scrutiny.

**Relative contributions of colonization, extinction, and cladogenesis**—To understand how whole archipelago area may relate to external colonization and internal extinction and cladogenesis, we assessed the relative contributions of these processes on each archipelago's flora. The number of species contributed to a given flora by net colonization (total number of colonization events minus the number of lineage extinctions) is effectively the number of colonist lineages in that archipelago. Cladogenesis adds species to a biota without adding colonist lineages, and therefore the number of species subsequently added by net cladogenesis equals the total number of species minus the number of colonization events. Again, an unknown number of extinctions influence the amount of net cladogenesis in an archipelago, although only those species extinctions that remove the last member of a colonist lineage influence our measure of net colonization. We then generated ASARs examining the relationship between the areas of archipelagoes and the numbers of species contributed by each process. Each of these ASARs was considered both including and excluding the contribution of the area and endemic species for the island of Hawai'i from archipelago totals. Given that there are only three archipelagoes considered, we calculated  $z$ -values as a way to quantify general trends rather than test statistical significance. Comparison of the  $z$ -value of colonization and cladogenesis ASARs indicates how sensitive the two processes are to increasing area: steeper slopes (higher  $z$ -values) indicate a greater increase in  $S$  with a given increase in  $A$ .

**Comparing lineages among archipelagoes**—We characterized the distribution of lineage size within and among archipelagoes to identify which lineages were strongly contributing to net cladogenesis. Within each archipelago, we classified lineages into four types: (1) nonendemic, (2) endemic single-species (anagenetic), (3) small cladogenetic, and (4) large cladogenetic. Cladogenetic lineages contain more than one species within a given archipelago and range in size from two to the largest lineage in that archipelago, with a strong right-skew (Fig. 3). We expect that the most diverse lineages in each archipelago should have the most sensitivity to area, since the scale of speciation in these is expected to be small (Kisel and Barraclough, 2010). Within each archipelago, lineages were classified as "large" or "small" lineages by ranking lineages by size and

partitioning them into two equal groups. Therefore, rather than being based on a set number, this division specifically accommodates the distribution of lineage size in each archipelago. Numbers of cladogenetic lineages vary among archipelago; however, we also expect that the mean species number ( $S$ ) of lineages in each archipelago should increase with area. We also posit that if larger lineages are more responsive to area, comparison of the large lineages should indicate a greater disparity in mean  $S$  than small lineages. We therefore performed one-way ANOVA to compare the mean size of large lineages across archipelagoes and a separate analysis to compare small cladogenetic lineages. Values were log-transformed to reduce skewness.

To determine whether an archipelago has enhanced diversity as a function of exceptional colonization events, we assessed the phylogenetic relationships among lineages on different archipelagoes. Drawing from phylogenetic relationships established by molecular sequence data or presumed from taxonomic/morphological examination, we classified some lineages in different archipelagoes as being relatively closely related. In many cases, these are simply widespread species shared between two or three archipelagoes, including many pantropical strand taxa; however, some taxa, such as *Ilex anomala* (Aquifoliaceae), are endemic to this collective trio of archipelagoes. In other cases, archipelagoes contain species that are clearly closely related, typically members of the same genus or section of a genus. In a smaller number of cases, typically in diverse lineages, phylogenetic analyses establish close relationships among taxa in different archipelagoes: lobelioids (Givnish et al., 2009), *Cyrtandra* (Cronk et al., 2005; Clark et al., 2009), *Melicope* (Harbaugh et al., 2008), *Bidens* (Ganders et al., 2000), *Labordia/Geniostoma* (Motley and Carr, 1998), *Pittosporum* (Gemmell et al., 2002), and Araliaceae (Costello and Motley, 2001; Plunkett and Lowry, 2010). A complete listing of all lineages and presumed relationships, including numbers of species represented in each archipelago can be found in Appendix S1 (see Supplemental Data with online version of this article).

For each archipelago, we produced contingency tables of the numbers of single vs. multispecies lineages and numbers of lineages that have close relatives vs. no close relatives in other archipelagoes. If an archipelago has been colonized by a disproportionately high number of lineages that have diversified, but which have no close relatives in the other archipelagoes, we can assert that lineages that are novel to a given archipelago are strong drivers of total diversity there.

**Comparing diversification of related lineages**—In a sense, related lineages represent a natural experiment where we can test how a given taxon responds evolutionarily to variation in archipelago area. To examine how related lineages diversify within different archipelagoes, we scrutinized the 76 sets of related lineages with a representative lineage in each archipelago. Of these, 37 have a single species in each archipelago, with 30 of these being a nonendemic species shared among the three archipelagoes. At the other end of the spectrum, several sets of related lineages are among the most species-rich in at least one of the three archipelagoes. In most of these, phylogenies indicate that colonists have come from the same source region or have colonized from one of the three archipelagoes to another: Lobelioidae (Campanulaceae; Givnish et al., 2009), *Cyrtandra* (Gesneriaceae; Cronk et al., 2005; Clark et al., 2009), *Melicope* (Rubiaceae; Harbaugh et al., 2008), *Psychotria* (Rubiaceae; Nepokroeff et al., 2003), *Kadua* (Rubiaceae; Kårehed et al., 2008; Motley 2003; Groeninckx et al., 2009), and *Bidens* (Asteraceae; Ganders et al., 2000; V. A. Funk, National Museum of Natural History, Smithsonian Institution, unpublished data). For the remaining lineages, phylogenetic studies with sufficient taxon sampling are not yet available (e.g., *Myrsine* [Primulaceae], *Peperomia* [Piperaceae], and *Coprosma* [Rubiaceae]).

We assessed the degree to which related lineages have similar tendencies to speciate within different archipelagoes. We considered sets of related lineages with multiple species in at least one archipelago to exhibit some capacity for cladogenesis. Therefore, if related lineages in two archipelagoes have only a single species, but the related lineage in the third has multiple species, we included that set. We performed correlation analysis comparing the numbers of species in each archipelago, again log-transforming species number to reduce skewness. Positive correlations would indicate that if a lineage speciates extensively in one archipelago, its related lineages speciate extensively in the other archipelago.

## RESULTS

These archipelagoes have clear SARs (Fig. 2). ISARs for the Marquesas and Societies Islands were both significant ( $P < 0.05$ ), but only the ISAR for Hawaiian Islands that excluded the

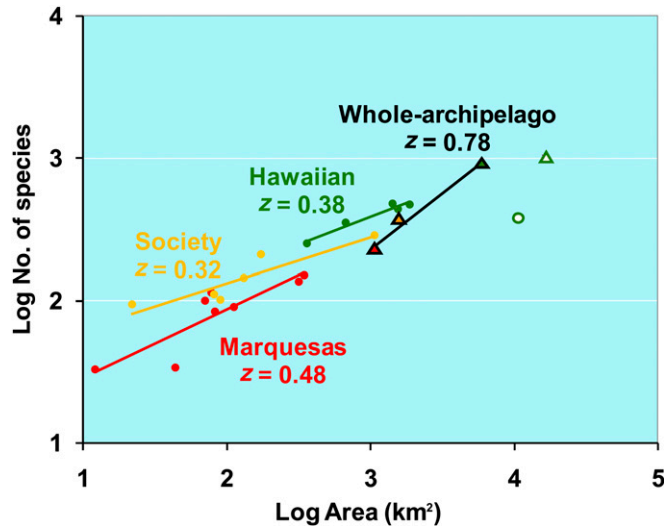


Fig. 2. Species–area relationships. Dots indicate individual islands, with corresponding regression lines for SARs for islands within each archipelago (ISARs). Triangles indicate whole archipelagoes, with black regression line indicating the SAR for whole archipelagoes (ASAR). Islands <500 m a.s.l. were excluded; values for the island of Hawai'i and the archipelago including it are shown as a hollow circle and triangle, respectively, but were not included in the SAR and associated  $z$ -value shown here (see Methods for explanation).

Island of Hawai'i was significant (Table 1). The  $z$ -values of the three significant ISARs range between 0.32 and 0.48, falling roughly within the range of values asserted by Rosenzweig (1995) to be normal for island groups. The ASAR was not significant in either case (although this was expected); however, the fit was better when excluding the Island of Hawai'i. The ASAR exhibits a very high  $z$ -value of 0.78, close to the theoretical value of 1.0 attributed to interprovincial SARs (Rosenzweig 1995).

The number of net colonization events increased with total archipelago area: Marquesas, 156; Societies, 230; Hawai'i, 258. Subtracting these numbers from total numbers of species in each archipelago represents the number of species contributed by net cladogenesis: Marquesas, 73; Societies, 140; Hawai'i, 743. The contribution of net cladogenesis thus increases with area at a rate approximately five times that of net colonization (Fig. 3). When including the island of Hawai'i, which adds considerable area but few endemic species, the net cladogenesis contribution exhibited a  $z$ -value of 0.95 compared with 0.18 for the net colonization contribution; when excluding the Island of Hawai'i regressions exhibited a better fit, and  $z$ -values were somewhat higher at 1.26 and 0.25, respectively.

In all three archipelagoes, distributions of lineage  $S$  were strongly right-skewed, with many species contained in a few diverse lineages and a majority of lineages being monospecific (Fig. 4), consistent with patterns reported elsewhere (Price, 2004; Domínguez-Lozano et al., 2010). The number of anagenetic lineages increased gradually, while the Society Islands had the highest number of nonendemic lineages. The total proportion of monospecific lineages was higher in the Societies (82%) and Marquesas (83%), than in the Hawaiian Islands (66%). A large number of lineages in each archipelago had closely related lineages in at least one other archipelago (Fig. 5). Within each archipelago, there was no significant disproportion

in the numbers of multispecies lineages that were unique to a given archipelago.

The ANOVA indicates that for both small and large cladogenetic lineages, mean lineage size is significantly larger in the Hawaiian Islands, while there were no significant differences in lineage size between the other two archipelagoes (Table 2). Comparing the two analyses, there is a much greater disparity in mean lineage size for large lineages. For example, large lineages in Hawaiian Islands contained on average more than twice the number of species as those in the Marquesas, whereas small lineages only had nominal (but significant) differences. When the sizes of related lineages among archipelagoes were compared, there were significant positive correlations for each pairwise combination (Table 3). Lineages that speciated extensively in one archipelago were likely to have close relatives that do so in the other archipelagoes.

## DISCUSSION

According to Rosenzweig's (1995) provincial theory, areas with large proportions of endemic species are characterized as evolutionary provinces whose species pools are generated primarily by internal diversification, with a SAR among provinces exhibiting very high  $z$ -values. The SARs in Fig. 2 are remarkably consistent with the nested SAR model proposed by Rosenzweig with a high interprovincial  $z$ -value, modest intraprovincial  $z$ -value and higher intercepts for intraprovincial SARs of larger provinces. Islands of a comparable area in different archipelagoes strongly differ in  $S$ . Although our analysis underscores the relationship of archipelago area to diversity, disentangling the influence of habitat availability from area per se proves more elusive (Ricklefs and Lovette, 2001). Island area typically correlates positively with the range of habitats available, as measured by number of climate types, elevation range, or other metrics both within Pacific archipelagoes (Mueller-Dombois and Fosberg, 1998; Price, 2004) and elsewhere (Fernández-Palacios and Andersson, 2000; Whittaker and Fernández-Palacios, 2007). Individual Hawaiian Islands have greater area than all of the islands of the other two archipelagoes with the exception of Tahiti. Not surprisingly, the Hawaiian Islands include a wider range of climatic habitats, especially at higher elevations (although the highest elevation habitats are far less species-rich than at lower elevations that are more comparable to the other archipelagoes (Price, 2004)). Moreover, several of the Hawaiian Islands are composites of two or more volcanoes which support isolated regions of habitat with their own endemic species (Price, 2004), whereas only Tahiti represents such a composite in another archipelago. The Hawaiian Islands may therefore simply promote colonization and diversification by providing a greater range of habitats and isolation opportunities. Nonetheless, where there are comparable islands in different archipelagoes, species richness contrasts sharply. For example, despite having a very similar area, maximum elevation, and suite of habitats, the Hawaiian island of Lāna'i supports nearly twice as many species as the Marquesan island of Nuku Hiva, and in fact more species than the entire Marquesas archipelago combined (Fig. 2). This may reflect a case of cladogenetic processes within a region that influence diversity at more local scales (Rosenzweig and Ziv, 1999). In this case, both allopatric speciation between islands and the additional speciation afforded to some clades as a result of larger island area (Gavrilets and Losos, 2009) generate a larger species pool in the Hawaiian

TABLE 1. Regression statistics for species–area relationship (SARs). For the Hawaiian Islands, island SAR (ISAR) and the whole archipelago SAR (ASAR), values including and excluding the influence of the island of Hawai‘i are given.

Lineage	Type	$R^2$	$c$	$z$
Marquesas	ISAR	0.77*	0.99	0.48
Societies	ISAR	0.83*	1.48	0.32
Hawaii	ISAR	0.24 (ns)	2.26	0.10
Hawaii (excluding Island of Hawai‘i)	ISAR	0.95*	1.44	0.38
Whole archipelagoes	ASAR	0.96 (ns)	0.89	0.50
Whole archipelagoes (excluding Island of Hawai‘i)	ASAR	0.98 (ns)	0.03	0.78

Islands; islands such as Lāna‘i that may be below the threshold for within-island speciation for some taxa may nonetheless receive multiple colonists from neighboring islands that promoted speciation. Therefore local diversity, often correlated with regional diversity (Caley and Schluter, 1997), can be indirectly influenced by the speciation–area effect via postspeciation dispersal from nearby islands.

The young island of Hawai‘i makes up a large proportion of its archipelago’s area, yet is comparatively depauperate in total species and single-island endemics for its area (Price, 2004), suggesting that its biota is primarily comprised of species dispersed from older islands. Givnish et al. (2009) estimated that 1.5 to 2.0 Myr is required for species assembly to saturate an island with *Cyanea*, a species-rich clade of lobelioids, and hence the younger age of Hawai‘i Island renders it as yet unsaturated for this group. Such an island represents a case of dynamic disequilibrium where evolutionary processes cannot keep pace with changes in island configuration (Heaney, 2000). This is also consistent with the speciation pulse hypothesis

proposed by Whittaker et al. (2007, 2008) whereby very young, large islands lack the topographic complexity or requisite time needed to accrue large numbers of endemic species. Because the other archipelagoes lack a comparable very large young island, it is most appropriate to consider SARs that omit the effects of the island of Hawai‘i when comparing archipelagoes. By removing the contribution of this island’s area and endemic species from the archipelago totals, both the Hawaiian Islands’ ISAR and the ASAR exhibit better fits (Fig. 2). Apart from this, geologic history is remarkably consistent among the three island archipelagoes with individual islands ranging between 1 and 6 Myr in age (Clague, 1996; Blais et al., 2002; Brousse et al., 1990), and therefore explanations beyond geologic history must be pursued.

Colonization history does not fully explain why the Hawaiian Islands have so many more species than the other archipelagoes. The total number of colonist lineages is certainly shaped by enhanced colonization thanks to a target-area effect (Lomolino, 1990) and a lower rate of extinction (MacArthur and Wilson, 1967). Over geologic time, islands with greater area may also buffer species from the vicissitudes of climatic change, permitting more lineages to survive to the present. Moreover, the Hawaiian Islands support subalpine and alpine habitats on the islands of Hawai‘i and Maui (Gagné and Cuddihy, 1990) and almost certainly on older islands in the geologic past (Carson and Clague, 1995). This has likely accommodated colonists that would be unlikely to establish in the other archipelagoes, such as *Tetramolopium* (Asteraceae) from the highlands of New Guinea (Lowrey, 1995) and numerous taxa now recognized as having colonized from temperate areas of North America (Baldwin and Wagner, 2010). Nonetheless, the number of species added by net colonization increases only modestly with area, with a slope that might be expected from purely ecological and population processes. The number added by in situ cladogenesis increases at a far higher rate (Fig. 3) and determines much more of the slope of the ASAR among whole floras.

There is also little support for the prospect that the Hawaiian Islands have been disproportionately enhanced by novel colonization events by taxa predisposed to diversify. Several groups have diversified greatly in the Hawaiian Islands without having colonized the other archipelagoes including the Madiinae (silversword alliance in the Asteraceae (Baldwin and Sanderson, 1998) and *Schiedea* (Caryophyllaceae; Nepokroeff et al., 2005). However, lineages such as *Ixora* (Rubiaceae) and *Phyllanthus* (including *Glochidion*; Phyllanthaceae) have apparently undergone moderate radiations in the Marquesas and Society Islands, yet have not colonized the Hawaiian Islands. Essentially, lineages that are unique to a given archipelago appear to be no more prone to diversify than those that have related taxa in multiple archipelagoes (e.g., *Coprosma*, *Cyrtandra*, *Kadua*, *Melicope*, *Peperomia*, *Psychotria*). Instead, solid majorities of the largest lineages in all three archipelagoes have close relatives in at least one of the other two.

Related lineages act more or less like replicates in a natural experiment where most conditions are held relatively constant while archipelago (and island) area is varied. Clearly, there is a wide range of species number among lineages within each given archipelago, with most lineages in each consisting of a single species and a small number of diverse lineages accounting for most diversity added after colonization. Therefore, by examining the behavior of monotypic vs. diverse lineages, the full range of responses to variation in area can be explored. On one end of the spectrum are those 38 sets of lineages that have a single related (in many

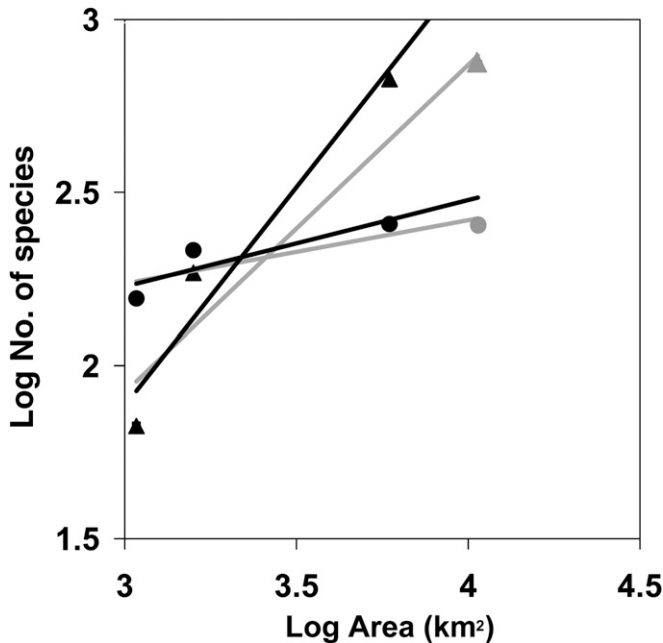


Fig. 3. Colonization vs. cladogenesis. ASARs representing the contribution of colonization (dots) and cladogenesis (triangles) to the species pools of the three archipelagoes. Data points and regression line for the Hawaiian Islands excluding the island of Hawai‘i are shown in black. Those including the island of Hawai‘i are shown in gray.



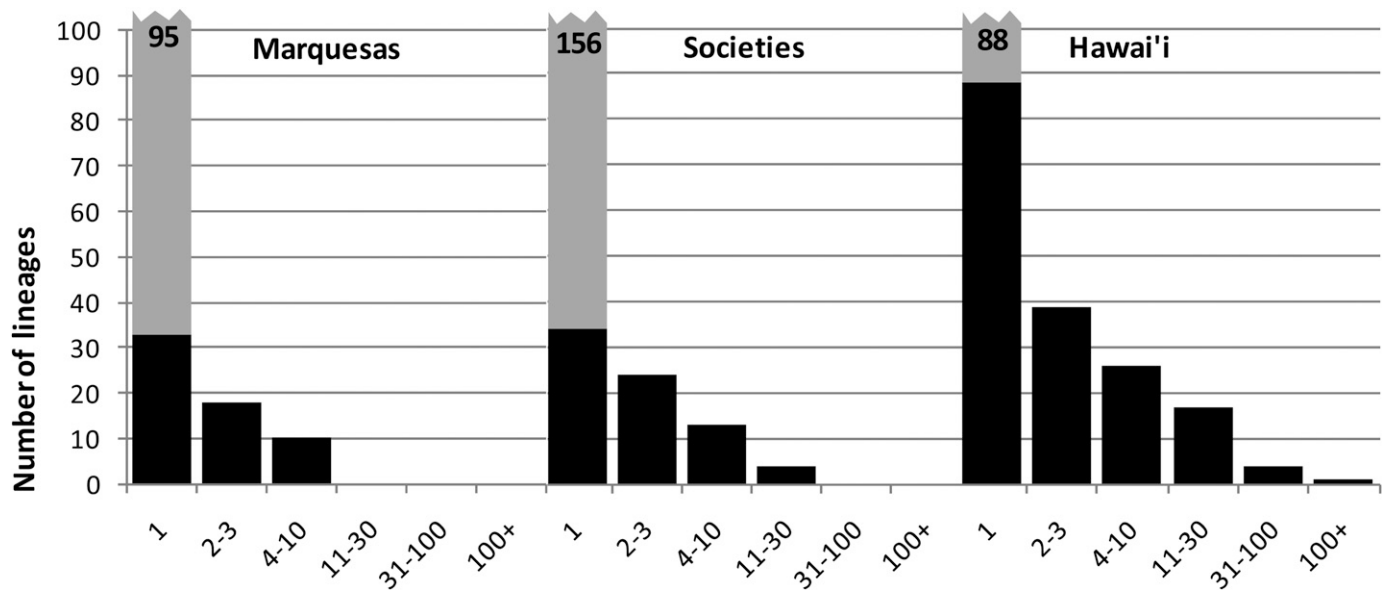


Fig. 4. Distribution of lineage size. Numbers of single-species lineages that have differentiated from ancestral species to form an endemic species (anagenetic lineages) and lineages with multiple endemic species (cladogenetic lineages) are shown in black. Single-species lineages consisting of non-endemic species are shown in gray with the total number indicated near the break at the top. Numbers of endemic lineages are given in logarithmically increasing class sizes of species number.

cases, conspecific) species in each archipelago. For such lineages, larger and larger land areas appear to have no effect on species richness, and therefore they may be below the area threshold necessary for speciation to occur (Gavrilets and Losos, 2009). Effectively, the ASAR for these has a  $z$ -value of 0. Considering that remote islands filter for highly dispersable taxa (Carlquist, 1974), many of these taxa are likely to frequently disperse between islands of a given archipelago, and consequently species in monospecific lineages tend to have large range sizes as measured by the number of islands occupied (Price and Wagner, 2004). Thus, the maintenance of a wide spatial scale of gene flow reduces the likelihood of speciation (Kisel and Barraclough, 2010). It appears from this analysis that most clades which fail to diversify in one archipelago also fail to do so elsewhere.

At the other end of the spectrum are those highly divergent taxa that have far more species in larger land areas. These lineages are more sensitive to area than moderately speciating lineages (which can be seen as intermediate in sensitivity) as evidenced by the large disparity mean lineage size. A closer look at some of the large lineages with close relatives in each of the archipelagoes further underscores the contribution of the largest lineages (Table 4). Moreover, the correlation between lineage size in each archipelago and that of related lineages in other archipelagoes suggests that the degree of speciation may be replicated among related taxa in different archipelagoes. However, true replication of adaptive radiation is rare because often groups radiate differently in separate regions (Losos, 2010). Nonetheless, the comparatively rare tendency to speciate is clearly much stronger in lineages in the Hawaiian Islands. Losos and Schluter (2000) report a similar phenomenon with a dramatic increase in species number with area within a clade of adaptively radiating *Anolis* lizards. The  $z$ -value reported for *Anolis* lizards in the Greater Antilles (0.78; Triantis et al., 2008) is much greater than that for the whole reptile fauna (0.47; based on data from Wright (1981)). While *Anolis* are a diverse lineage representing large portions of the overall faunas

(Losos et al., 2006; Wright, 1981), other taxa with representatives across the region presumably exhibit smaller  $z$ -values that balance against the high  $z$ -value of *Anolis* lizards. This agrees with our finding that those lineages that speciate extensively are highly sensitive to the island or archipelago area. The ASAR for whole floras can be considered essentially an additive function of all lineages together, and therefore highly diverse, area-sensitive lineages likely have a disproportionate contribution to the steep slope of the ASAR.

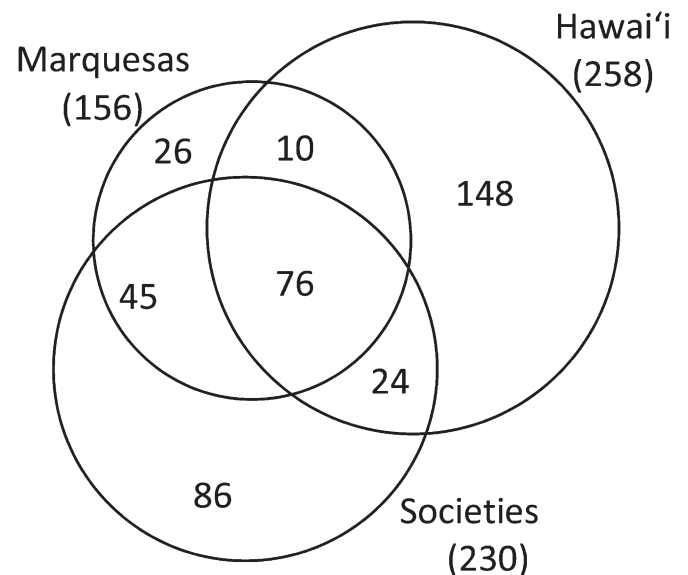


Fig. 5. Comparison of related lineages among archipelagoes. Total numbers of lineages for each archipelago are in parentheses. Numbers of lineages that are unique or related among two or all three archipelagoes are conceptualized by overlapping circles.

TABLE 2. ANOVA of lineage size (*S*) for three archipelagoes. All lineages exhibiting cladogenesis (i.e., those with at least two species) within each archipelago were analyzed. Within each archipelago, lineages were classified as large or small lineages by ranking lineages by size and partitioning them into halves. Analyses were run to make separate comparisons among small and large lineages. Degrees of freedom (df), sum of squares (SS), *F*-ratio (*F*), probabilities (*P*), and means are given for each analysis. Species number (*S*) was log-transformed for comparison of means among archipelagoes. Asterisk indicates groups associated with a significantly greater value of *S* ( $P < 0.05$ ). In both analyses, the Hawaiian Islands had significantly larger means than the other archipelagoes. Means were back-transformed for comparison.

Comparison	df	All			Marquesas			Societies			Hawai'i		
		SS	<i>F</i>	<i>P</i>	<i>N</i>	Log <i>S</i>	<i>S</i>	<i>N</i>	Log <i>S</i>	<i>S</i>	<i>N</i>	Log <i>S</i>	<i>S</i>
Large lineages	2	1.82	9.77	>0.001	14	0.68	4.77	20	0.78	6.00	43	1.04*	10.97
Small lineages	2	0.11	6.96	0.002	14	0.30	2.00	20	0.33	2.13	44	0.39*	2.46

These observations leave us with two related questions: (1) Why area? (2) Why certain clades? Speciation may be promoted by larger islands in several ways. First, they may provide more heterogeneous environments. While island area, elevation, and various measures of complexity tend to covary, analyses have shown the importance of habitat variation in promoting adaptive radiation (Givnish, 2010; Losos and Parent, 2009). On the other hand, Losos and Ricklefs (2009) note that some islands in the Lesser Antilles, which contain higher elevations and diverse habitats, harbor few species of *Anolis* lizards and do not exhibit intra-island speciation. Larger islands, by being topographically more complex, may permit allopatric speciation (Losos, 1998). An examination of sister-species pairs of Hawaiian plants suggests that intra-island speciation is as common as inter-island speciation and that some islands harbor sister species on separate volcanic mountains (Price and Wagner, 2004). Indeed, several of the Hawaiian Islands have topographically distinct volcanic mountains whereas in the other archipelagoes, only Tahiti consists of two distinct volcanic mountains (Fig. 1). Givnish (2010) also points out that with lower extinction rates, species may persist longer on large islands increasing the time available to diverge from ancestors (however, this would promote anagenesis rather than cladogenesis). Other work suggests that larger islands promote larger population sizes from which beneficial mutations might arise (Gavrilets and Vose, 2005).

A central finding in this examination was establishing the context of different kinds of lineages. A majority of lineages in all three archipelagoes did not speciate to form multiple species within an archipelago (Fig. 4). A small number of diverse lineages not only contributed disproportionately to the species pool, but also to differences in total species numbers related to area. Kisel and Barraclough (2010) estimated the *minimum* geographic extent needed for speciation in differ taxa; however, a corollary to this is that there is likely considerable variation in the *actual* geographic extent required for speciation by different lineages in a major taxonomic group occupying the same island or archipelago and that only a small fraction may be

TABLE 3. Correlation matrix of species number (Log *S*) in related lineages for two archipelagoes. Related sets of lineages demonstrating potential for cladogenesis (two species in at least one archipelago) were analyzed to compare the number of species present in each pairwise combination of archipelagoes ( $N = 36$ ). Pearson's correlation coefficients are given; *P*-values were all <0.001.

Archipelago	Societies Log <i>S</i>	Hawai'i Log <i>S</i>
Marquesas Log <i>S</i>	0.798	0.682
Societies Log <i>S</i>		0.623

responsive to the minimum value for that group. The presence of numerous local endemics within large lineages suggests that limited dispersal both promotes isolation leading to allopatric speciation and a limited range size for the resulting species (Givnish et al., 1995; Givnish 1998, 2010; Price and Wagner, 2004). Also, while some taxa such as *Cyrtandra* diversify into species with similar habitat preferences, others including well-known cases like the Madiinae (Baldwin et al., 1991) and lobelioids (Givnish et al., 2009) constitute adaptive radiations with widely disparate habitat, morphology, and ecological interactions. Indeed, even modest radiations may exhibit clearly adaptive differences (Givnish, 2010). For example, in the Marquesas *Bidens henryi* is a robust shrub, whereas the related *Bidens fatuhivaensis* (W. L. Wagner, unpublished new species) is an herbaceous creeper adapted to windswept ridges. Ecological characteristics almost certainly play a role: Givnish (2010) highlights the importance of forest understory taxa with fleshy fruits that are poorly dispersed by sedentary forest birds. Not surprisingly, nearly all of the lineages listed in Table 4 have fleshy fruits, although this is also a common trait even among nonspeciating lineages. On the other hand, Price and Wagner (2004) found that while bird-dispersed groups had larger lineages, taxa that are dispersed internally by birds (endozoochory) or externally by birds (ectozoochory) were equally prone to diversify. This likely stems from the fact that in the Hawaiian Islands several diverse lineages consist of species typically occupying open, dry, or rocky environments such *Schiedea*, *Bidens*, and members of the silversword alliance. In conclusion, Gavrilets and Losos (2009) assert that there may be no single answer as to why some lineages adaptively radiate. Instead, clade-specific combinations of traits underscore the role of ecology in shaping evolution's path.

Some of the concepts outlined here may be tested elsewhere; however, few evolutionary provinces are as simple or self-contained as these island systems. Several criteria would need to be met to dissect SARs in a comparable way: (1) control of spatial and temporal constraints, (2) availability comprehensive species range data, and (3) extensive phylogenetic analyses. This may be possible for oceanic islands and perhaps some mountain ranges, whose spatial boundaries and geologic histories are sharply defined and whose species pools are of modest size and can be summarized by a reasonable number of phylogenetic analyses. Examples include the Antillean reptile fauna with established SAR observations (Wright, 1981; Ricklefs and Lovette, 2001) and at least one well-studied diverse group (Losos et al., 2006); the Philippine mammalian fauna, with extensive phylogenetic work and distributional data available (Jansa et al., 2006; Heaney 1986); and the floras of several archipelagoes within Macaronesia, also with extensive phylogenetic data available (Reyes-Betancort et al., 2008; Domínguez Lozano et al., 2010).



TABLE 4. Species number (*S*) within closely related cladogenetic lineages for three archipelagos.

Lineage	Family	<i>S</i>		
		Marquesas	Societies	Hawaiian
Lobelioidae	Campanulaceae	2	5	125
<i>Cyrtandra</i>	Gesneriaceae	8	16	58
<i>Melicope/Platydesma</i>	Rutaceae	7	2	52
<i>Peperomia</i>	Piperaceae	5	7	22
<i>Kadua</i>	Rubiaceae	4	2	21
<i>Myrsine</i>	Primulaceae	4	11	20
<i>Bidens</i>	Asteraceae	9	9	19
<i>Labordia/Geniostoma</i>	Piperaceae	2	2	16
<i>Coprosma</i>	Rubiaceae	6	5	12
<i>Wikstroemia</i>	Thymeliaceae	2	2	12
<i>Psychotria</i>	Rubiaceae	10	11	11
<i>Pipturus</i>	Urticaceae	3	3	4

We expect that as more lineages are assessed, the relationship of available area (and its close associate, habitat) to the most diverse lineages in particular will help define the quantitative nature of regional-scale diversity patterns. Reconstructing the phylogenetic mechanisms underlying regional species pools in this manner may illuminate how interactions between evolutionary and ecological processes may influence diversity at multiple scales (Rosenzweig, 1995; Ricklefs and Schluter, 1993; Webb et al., 2002).

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