

**Tempo and mode of diversification of the Hawaiian biota, with an examination
of the evolutionary history and biogeography of a species-rich Hawaiian plant
group, *Peperomia* (Piperaceae)**

by

Jun Ying Lim

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Committee in charge:

Professor Charles R Marshall, Chair

Professor Rosemary Gillespie

Professor Paul Fine

Professor David Ackerly

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Abstract

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The diversity of the biota of any place and time is often the product of a long and complex history of ecological and evolutionary assembly through the fundamental processes of immigration, speciation and extinction. This biotic assembly typically occurs amid a backdrop of constant abiotic and biotic change at multiple spatiotemporal scales. Given this potentially complex abiotic and biotic history, investigating the core processes that underlie the assembly of regional biotas, as well as the abiotic, biotic and historical factors that influence them, is a major challenge at the intersection of biogeography, macroevolution and ecology.

Oceanic islands provide ideal opportunities to investigate the processes underlying the assembly of regional biotas. Given their volcanic origins, their landscapes represent initial blank slates that are then populated by successful long-distance dispersal events by various organisms, and the subsequent diversification of some of these colonist lineages. Furthermore, their relatively predictable geologic histories and lifespans (i.e., ontogenies) make the study of how the diversification of lineages are shaped over geologic time-scales especially tractable, compared to the more complex abiotic and biotic histories that often shape continental, mainland biotas. Remote hotspot archipelagoes such as that of Hawaii are especially exciting case studies, as they are composed of islands formed in sequence through the movement of the Pacific tectonic plate over a relatively stationary mantle hotspot, and so that each island captures a record of diversification at different stages. The multiple “snapshots” of diversity provided by the differently-aged islands of the Hawaiian archipelago, as well as their well-defined and quantifiable ontogenies, allow the diversities observed on each of the main islands to be leveraged to understand how diversity on islands change through the lifespan of an island, as if each island were a different point on a time series. In Chapter 1, I investigate whether, and how, the changing geologic backdrop (in this case, island area as each island grows and later subsides) has shaped the diversification (speciation, immigration and extinction) of Hawaiian plant and animal lineages on each of the islands. I used a

geologically informed diversity-dependent model of species richness change that incorporates estimates of how island area has changed through time, while also taking into account island-specific ontogenetic differences among the four current main islands / island complexes of the Hawaiian archipelago, and tested my models against alternative models that do not account for island ontogenetic changes¹. I find that, at the broadest temporal scales, the geologic dynamics of the Hawaiian Islands have had a profound influence on the macroevolutionary history of most of the 14 endemic lineages examined, with all lineages undergoing radiations as islands grow, and most of them now undergoing long-term evolutionary declines as the islands undergo subsidence and erosion with age.

As mentioned above, the isolation and *de novo* formation of the Hawaiian Islands imposes a strong filter, limiting successful colonization of the islands to a subset of mainland plant and animal groups that have the traits necessary for long-distance dispersal. As a result, it has often been assumed that the Hawaiian Islands often represent a biogeographic sink for many lineages, with colonization of the remote islands representing “dead ends” in the history of dispersal of lineages that prove successful. In some cases, this is certainly true, with some lineages evolving characteristics that reduce dispersal ability relatively quickly upon successful colonization. However, molecular phylogenetic data are slowly challenging this narrative, and it is increasingly demonstrated that the Hawaiian archipelago may instead also play a fundamental role as a biogeographic source for other parts of the Pacific and even mainland areas. In Chapter 2, testing this more nuanced view of the biogeographic history of Hawaiian lineages in the context of the greater Pacific, I constructed a molecular phylogeny of one of the most species-rich angiosperm radiations in the Pacific, *Peperomia* (Piperaceae), using full plastome sequences generated via a high-throughput shotgun sequencing approach. The final tree consisted of about half the total number of species described in the Pacific. Incredibly, I found that the Pacific has played host to four separate and distinct colonist lineages that originated from the Neotropics, although whether these colonization events occurred through direct dispersal from South and Central America, or via indirect routes of dispersal through the Afro and Paleotropics remain unclear. Nonetheless, in support of the newer view of the role of the Hawaiian Islands in Pacific biogeography, my molecular phylogeny paints a picture of frequent dispersal within the south Pacific, with two independent radiations of *Peperomia* on Hawaii, and subsequent southwards dispersal of some individuals derived from one of these radiations to the Marquesas Islands. My results emphasize the importance of expanding the biogeographic lens through which many island lineages are typically viewed, and future global-level sampling will shed more light on the role of the islands of the Pacific in generating the diversity of many globally important plant lineages.

Lastly, while my first chapter focuses on the role of landscape dynamism on the tempo of diversification on Hawaii, and my second chapter focuses on the role of the Hawaiian Islands in the biogeographic history of lineages in the greater Pacific, the third chapter of this dis-

¹This work is already published and is included in this dissertation with permission from my sole author, who is also chair of the dissertation committee and approved this dissertation. The citation is as follows: Lim, J.Y. & Marshall, C.R. (2017) The true tempo of evolutionary radiation and decline revealed on the Hawaiian archipelago. *Nature*, **543**, 710 – 713.

sertation instead takes a closer look at whether the climatic niches of lineages may influence the modes of speciation among eight large radiations of endemic plant groups. The central hypothesis is that the climatic niche of lineages may play a role in shaping the inter-island dispersal of species, and hence the geographic isolation of populations on different islands. For instance, a wet forest species on one island may be expected to more easily colonize wet forests on other islands (i.e., climatic niche conservatism). If climatic niche conservatism were a dominant force in shaping the mode of diversification, one may expect cladogenetic events in allopatry to be associated with lower rates of climatic niche evolution relative to cladogenetic events in sympatry (here defined as sister lineages co-occurring on at least one island). To test this idea, I reconstructed the phylogenetic relationships within eight species-rich plant radiations on Hawaii, and inferred the geographic context of all cladogenetic events in each plant group using probabilistic biogeographic models. I then looked at whether cladogenetic events in sympatry (i.e., sister lineages that overlap in biogeographic range) versus cladogenetic events in allopatry (diverged sister lineages that occur on different islands) were associated with higher or lower rates of climatic niche evolution. I found, in a combined analysis of all groups examined, that rates of climatic niche evolution do not appear to be explained by differences in speciation mode. However, two of the plant groups examined (*Schiedea* and *Kadua*) show significant but opposing relationships between speciation mode, with lineages of *Kadua* showing lower rates of niche evolution in allopatry and lineages of *Schiedea* diverging in allopatry associated with higher rates of niche evolution. Overall, my results suggest that lineage-specific differences likely have a strong influence on rates of climatic niche evolution and their interaction with dispersal and speciation.

Overall, oceanic islands are, and will likely remain, powerful microcosms by which strategies for understanding how mainland biotas are developed. The three chapters of this dissertation highlight the need for a multi-faceted approach in studying the ecological and evolutionary assembly of regional biotas: from its response to geologic changes over long-time scales (Chapter 1), the larger biogeographic context from which biotas are assembled (Chapter 2), to the often context-specific role of climatic niche evolution in shaping the dispersal and speciation of lineages (Chapter 3).

To my parents, Lim Cheng Ann and Liew Gim Huay,
for supporting my intellectual pursuits since I was little,

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And to my wife, Melissa,
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Contents

Contents	ii
List of Figures	iii
List of Tables	iv
1 Time-varying diversification rates in Hawaiian endemic clades driven by island ontogeny	1
2 <i>Peperomia</i> of the Pacific (Piperaceae)	24
3 The role of climatic niche evolution in driving speciation in the Hawaiian flora	39
Bibliography	51

List of Figures

1.1	Generalized growth and decay of the Hawaiian islands	3
1.2	Species numbers and inferred diversity trajectories of Hawaiian clades for the major islands of the Hawaiian archipelago	4
1.3	Species accumulation rates inferred for the 14 clades analyzed under the island ontogeny model	6
1.4	Representative inferred diversity trajectories and carrying capacities on the oldest island, Kauai, under the island ontogeny model	7
1.5	Schematic description of the island ontogeny model	16
1.6	Sensitivity of the model comparison results in uncertainties in the ontogenies of the islands	17
1.7	Sensitivity of island ontogeny model to uncertainties in area estimates of older islands	18
2.1	Exemplar endemic <i>Peperomia</i> of Hawaii showing the morphological diversity and growth habit of the group	26
2.2	Best maximum likelihood (ML) phylogenetic tree showing evolutionary relationships among Pacific taxa	30
3.1	Bayesian maximum a posteriori trees for the eight Hawaiian plant lineages with mapped (minimum, mean and maximum) moisture categories.	45
3.2	Inferred biogeographic histories of Hawaiian plant lineages under the best-fit DEC+J model	47

List of Tables

1.1	Species richness values for each of the 14 clades for each of the four major islands	9
1.2	Estimated time of growth, time of decay, current area, estimated area at the last glacial maximum, and estimated maximum area for the major Hawaiian islands	11
1.3	Parameter estimates using mean dates for island habitable area and island maximum area	19
1.4	Parameter estimates using oldest dates for island habitable area and youngest dates for island maximum area	20
1.5	Parameter estimates using oldest dates for island habitable area and oldest dates for island maximum area	21
1.6	Parameter estimates using youngest dates for island habitable area and youngest dates for island maximum area	22
1.7	Parameter estimates using youngest dates for island habitable area and oldest dates for island maximum area	23
3.1	Empirical data sets for Hawaiian plant lineages analyzed	42
3.2	Number of allopatric and sympatric cladogenetic events for each plant lineage under both strict and relaxed definitions inferred under best-fit DEC and DEC+J models	44
3.3	Effect size (and standard errors) of the effect of speciation mode on rate of niche evolution	46

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Chapter 1

Time-varying diversification rates in Hawaiian endemic clades driven by island ontogeny

Summary

Establishing the relationship between rates of change in species richness and biotic and abiotic environmental change is a major goal of evolutionary biology. While exquisite fossil and geologic records provide insight in rare cases (Ezard *et al.*, 2011), most groups lack high quality fossil records. Consequently, biologists typically rely on molecular phylogenies to study the diversity dynamics of clades, usually by correlating changes in diversification rate with environmental or trait shifts (Baldwin & Sanderson, 1998; Rabosky, 2014; Reyes *et al.*, 2014; Valente *et al.*, 2015; Onstein *et al.*, 2016). However, inferences drawn from molecular phylogenies can be limited due to the challenge of accounting for extinct species, making it difficult (Liow *et al.*, 2010; Quental & Marshall, 2011; Morlon *et al.*, 2011) to accurately determine the underlying diversity dynamics that produce them. Here, using a geologically informed model of the relationship between changing island area and species richness for the Hawaiian archipelago, we are able to infer the rates of species richness change for 14 endemic groups over their entire evolutionary histories without the need for fossil data, or molecular phylogenies. We find that these endemic clades underwent evolutionary radiations characterized by initially increasing rates of species accumulation, followed by slow downs. In fact, for most groups on most islands their time of evolutionary expansion has long past, and they are now undergoing previously unrecognized long-term evolutionary decline. Our results show how landscape dynamism can drive evolutionary dynamics over broad time scales (Jetz & Fine, 2012), including driving species loss that is not readily detected using molecular phylogenies, or without a rich fossil record (Quental & Marshall, 2013). We anticipate that examination of other clades where the relationship between environmental change and species richness change can be quantified will reveal that many other living groups

have also experienced similarly complex evolutionary trajectories, including long-term and ongoing evolutionary decline.

Introduction

Islands provide an extraordinary opportunity for unraveling the nature of diversity dynamics (MacArthur & Wilson, 1963, 1967; Warren *et al.*, 2015; Rominger *et al.*, 2015). This is in part because the fundamental processes of speciation, extinction and immigration are directly influenced by their geophysical attributes such as area, and because it is possible to examine the response of the biota to the dramatic changes in these attributes that occur over island lifespans (Whittaker *et al.*, 2008; Fattorini, 2009; Geist *et al.*, 2014; Borregaard *et al.*, 2015). In particular, remote tectonic hotspot archipelagoes such as Hawaii offer a special opportunity for quantifying the relationship between species richness change and major environmental change. First, because they are composed of islands that formed in sequence, they capture a record of evolutionary radiations at different stages of their unfolding (Whittaker *et al.*, 2008; Borregaard *et al.*, 2015), akin to a fossil record. And second, each island has a well-defined ontogeny, from its initial emergence, subaerial growth, and then slow decline as it tectonically subsides and erodes (Whittaker *et al.*, 2008; Borregaard *et al.*, 2015)(Figure 1.1). Hence, while each individual island only provides a single snapshot of species richness, we can leverage the observed diversities on differently aged islands to shed light on how species richness responds to changes in island environment.

Here, we develop a geologically informed diversity-dependent model of species richness change (Figure 1.5) that incorporates how island area has changed through time, and how this impacted species richness and species accumulation rates (the speciation and immigration rates minus the extinction rate). We tested it with 14 endemic clades of the Hawaiian archipelago, including the iconic Hawaiian honeycreepers and silverswords. The model breaks each island's ontogeny into two phases: island growth as it accumulates subaerial lava flows, and island decline as the island loses area through subsidence and erosion. Quantification of the temporal trajectories and rates of species richness change was achieved by solving modified versions of the standard equation for logistic growth, one each for island growth and decay. The modifications allowed the clade-specific carrying capacities and intrinsic species accumulation rates to vary with time (see Methods). The inferred temporal trajectories of maximum carrying capacity were derived from the temporal trajectories of island area change (Figure 1.1), using well-established species-area relationships (see Methods), where the durations of growth and decay were determined using geologic data (Lipman & Calvert, 2013; Clague & Sherrod, 2014), with maximum areas derived from bathymetric data (Table 1.2, see Methods).

To compute the trajectories of species richness and species accumulation rates, we estimated the maximum intrinsic species accumulation rate ($r_{0,max}$) and maximum carrying capacity (K_{max}) per unit area for each clade (see Methods). These estimates were those that best predicted the observed species richness (Table 1.1) by the modified equations for

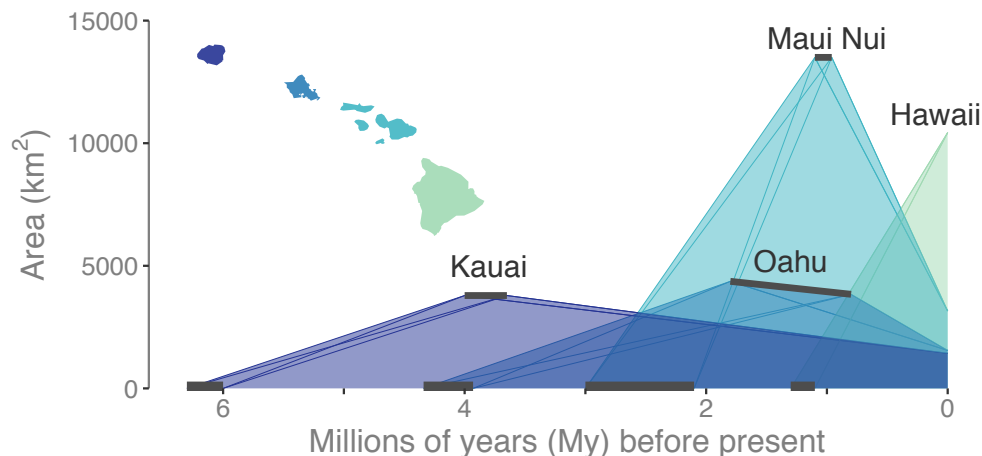


Figure 1.1: Generalized growth and decay of the Hawaiian islands used in the island ontogeny model. Given that the islands of Maui, Molokai, Kahoolawe, and Lanai were connected for most of their history, we treat them as a single entity, Maui Nui. Black bars on the x axis, and at maximum area, indicate ranges of uncertainty in the times of first habitability and maximum area, respectively (Table 1.2, see Methods), and in the case of Oahu, uncertainty in the maximum size as well (see Methods). Time is measured from when each island first became habitable. Myr, million years.

logistic growth for each of the four major islands, after controlling for the differences in each islands size and ontogeny (Figure 1.1, see Methods).

We tested the ability of our island ontogeny model (Ontogeny K) to predict the current observed species richness on each island against two other models in an Akaike Information Criterion framework. These models were logistic growth with fixed island-specific carrying capacities (Island K), and logistic growth with the same fixed carrying capacity for all islands (Single K) (see Methods).

Results and Discussion

The inferred diversity trajectories and AIC weights, the relative support for the alternative hypotheses, are shown in Figure 1.2. On average, the island ontogeny model outperformed the alternative models; the mean AIC weights for the Ontogeny K , Island K , and Single K models were 0.58, 0.23, and 0.19 respectively, with median values of 0.67 (with an interquartile range of 0.26–0.86), 0.18 (0.09–0.36), and 0.08 (0.03–0.31). The Ontogeny K model was the best-supported model for nine of the 14 clades, while another three clades have substantial support ($\Delta\text{AIC} < 2$) even though the model was not the best supported for these clades (see Methods, Table 1.3). These results were generally robust to uncertainties in the durations of island growth and decay, or in the estimated maximum areas of the older islands (see Methods, Figures 1.6 and 1.7, Tables 1.3–1.7). The results were also insensitive

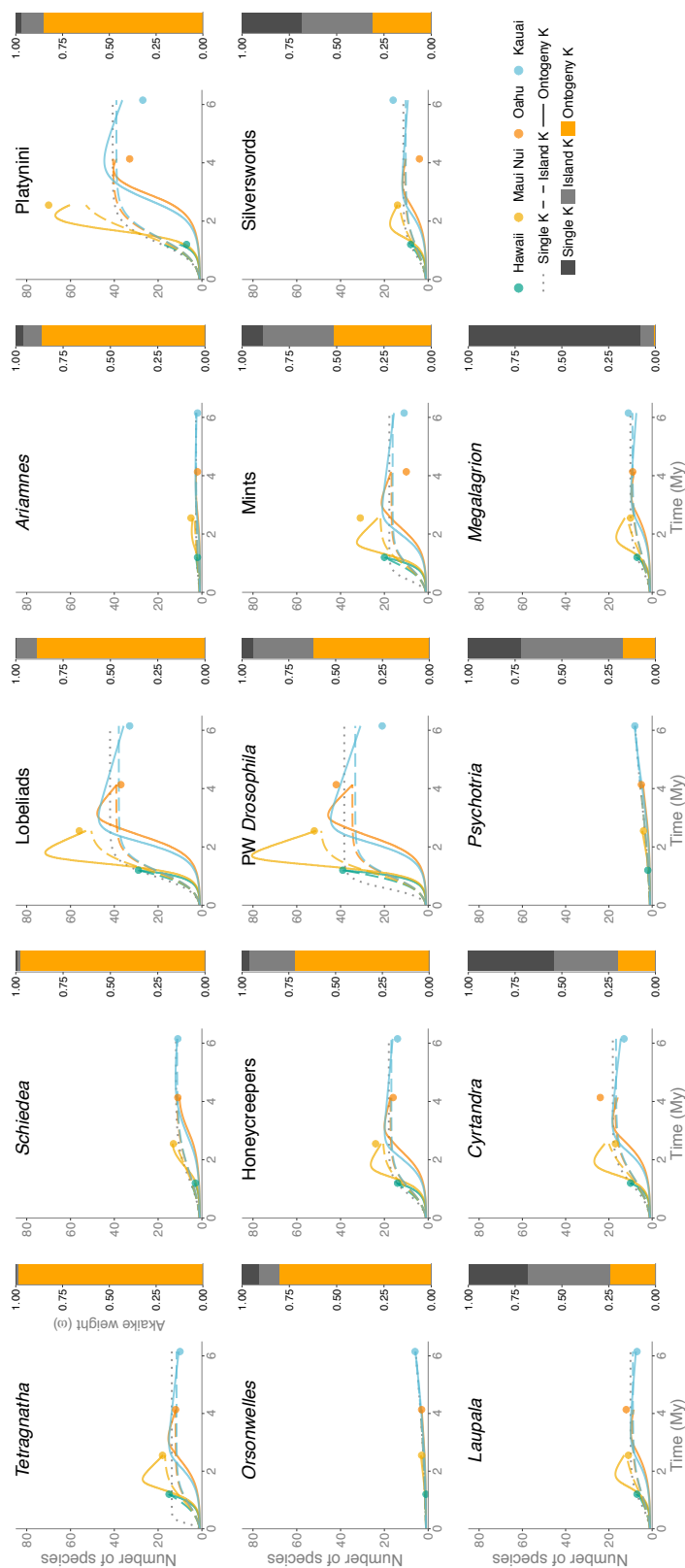


Figure 1.2: Species numbers and inferred diversity trajectories of Hawaiian clades for the major islands of the Hawaiian archipelago. The observed species richness values (points) for each clade on each major island are shown (Table 1.1), with the best fit diversity trajectories under the three models of species accumulation: the island ontogeny model (Ontogeny K), the island-specific fixed carrying capacity model (Island K), and a model where each island shares the same fixed carrying capacity (Single K). AIC weights for the models are given to the right of each panel.

to substitution of the current area of the islands with the considerably larger areas 20,000 years ago at the last glacial maximum (Table 1.2), when sea level was some 120 meters lower (Weigelt *et al.*, 2016). This indicates that the recent glacial-interglacial sea-level oscillations played only a minor role in the long-term evolutionary dynamics of the archipelago (see Methods, Figure 1.6, Tables 1.3–1.7).

The strong performance of the island ontogeny model is not unexpected given the humped diversity patterns across the archipelago seen today for many clades (Figure 1.3), and is consistent with the predictions of the general dynamic model of oceanic island biogeography (Whittaker *et al.*, 2008; Borregaard *et al.*, 2016; Chen *et al.*, 2011) including the observation that intermediate age islands often, paradoxically, have more diversity than younger and older islands (Whittaker *et al.*, 2008; Fattorini, 2009; Geist *et al.*, 2014; Borregaard *et al.*, 2016). The reason is that very young islands, even large ones like the Big Island of Hawaii, have not yet had time for species to accumulate, whereas intermediate age islands, in our case Maui Nui, are old enough to have accumulated many species and are still relatively large, while the older islands have typically shrunk sufficiently to have reduced diversity compared with intermediate age islands. However, we note that diversity patterns need not be humped under the island ontogeny model, for example, see *Orsonwelles* (Figure 1.2).

In the two clades where the island ontogeny model did not receive substantial support (where $\Delta\text{AIC} > 2$), the humped diversity pattern is not seen (Figure 1.2). The reasons why the island ontogeny model does not fit well for these groups, or fit better for the other clades, are currently unknown, but presumably these clades responded to island ontogeny idiosyncratically, beyond the island-specific ontogenetic differences already taken into account. Some factors might include unique landscape complexity, local climates, ecosystems, or geologic histories that decouple relevant habitat area from overall island area (Borges & Hortal, 2009). Stochastic factors, including priority effects, may also have played a role in establishing different diversity dynamics for the same clade on different islands. Finally, it is possible that human-driven extinction, especially undocumented extinction in pre-European times, or incomplete or non-uniform taxonomy, might have added noise that cloaks the true signal.

With the maximum intrinsic species accumulation rates ($r_{0,max}$) and maximum carrying capacities (K_{max}) derived from the island ontogeny model (Table 1.3), we were able to infer the history of species accumulation rates for each clade (see Methods equations 7, 8; Figure 1.3). The trajectories all show a growth phase with hyper-exponential species accumulation rates (the species accumulation rates increase with time) on all islands, the result of early-phase exponential growth typical of logistic growth, accentuated by the expanding geographic area. For most groups on most islands this was followed by a decreasing rate of species accumulation. In fact, for most clades the species accumulation rates become negative on the three older islands, a phenomenon not anticipated by visual inspection of their molecular phylogenies. This includes 11 clades on the islands of Maui Nui and Oahu, and 12 of the 14 clades on Kauai. The estimated species accumulation rates are as low as -0.76 species/species million years. Thus, the island ontogeny model, to the extent that it captures the true evolutionary dynamics, provides a complement to the fossil record as a way of identifying

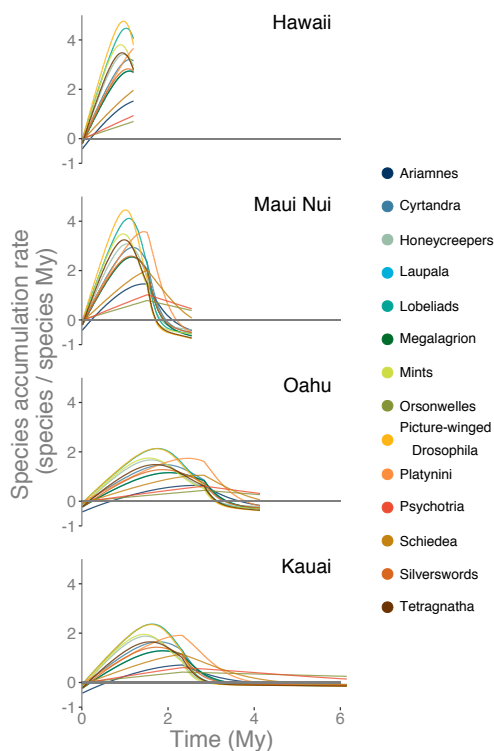


Figure 1.3: Species accumulation rates inferred for the 14 clades analyzed under the island ontogeny model. All trajectories exhibit hyper-exponential initial rates, followed by slow-downs, which become negative for most clades on the three older islands. Time is measured from when each island first became habitable (Table 1.2). The negative rates at the earliest stages of island growth reflect the fact that islands are initially too small to support even a single species.

negative accumulation rates on evolutionary timescales.

On the Big Island of Hawaii all clades still have positive species accumulation rates, and thus none have yet reached their maximum species numbers on that island, consistent with previous data that show that Big Island is under-saturated in species richness (Gillespie & Baldwin, 2010; Price, 2004; Price & Wagner, 2011). For nine clades their species accumulation rates are now decreasing, indicating that each has accumulated sufficient species for crowding to begin to reduce the rate of generation of new species despite the growth of the island. Conversely, five clades have accumulated species sufficiently slowly, or have such high carrying capacities, that the increasing area since the inception of the Big Island has led to steadily increased rates of species accumulation with time. In this context, our approach probably provides better estimates of the maximum rates of evolutionary radiation than do rates estimated from molecular phylogenies; most clades are not currently at their peak rate of diversification and so rates of diversification estimated from phylogenies will be underestimates (Figure 1.3).

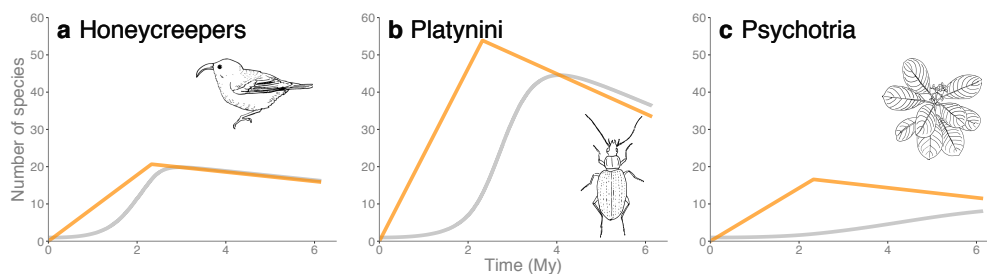


Figure 1.4: Representative inferred diversity trajectories (grey) and carrying capacities (orange) on the oldest island, Kauai, under the island ontogeny model. (a) A clade where the species richness closely follows the falling carrying capacity as Kauai decays, after initial hyper-exponential growth. (b), A clade where the diversity trajectory does not follow the carrying capacity as closely. (c) A clade where the geological processes of island growth and decay are much faster than the clade’s rate of species accumulation, resulting in still-increasing species richness on Kauai.

Furthermore, our model shows that species richness trajectories need not closely track the time-varying carrying capacity. During the growth phase there is often a considerable lag between the carrying capacity and their realized species richness (Figure 1.4), whereas during the decay phase diversity trajectories may either closely follow the declining carrying capacity (e.g., the honeycreepers, Figure 1.4a), or extinction debt can steadily accumulate in a growing diversity overshoot (e.g., Platyninid beetles, Figure 1.4b), a phenomenon also seen in Cenozoic mammal clades (Quental & Marshall, 2013). Less common are clades where the realized diversity has yet to reach their carrying capacity even on the oldest island Kauai, which thus still have positive species accumulation rates despite the advanced age of the island (e.g., the plant genus *Psychotria*, Figure 1.4c). In general, species richness was often not particularly close to the estimated equilibrium diversity, complementing observations that the avifaunas of other archipelagos exhibit a mixture of equilibrial and non-equilibrium dynamics (Valente *et al.*, 2015; Ricklefs & Bermingham, 2004).

Overall, the Hawaiian clades in evolutionary decline are those with rates of species accumulation that are fast compared with the pace of geologic change. Conversely, clades that are still diversifying even on the older islands are those with rates of species accumulation that are slow compared with the pace of geologic change. These observations indicate that both the nature of the environmental change and the intrinsic biological characteristics of the clade are important in determining the nature of the clades diversity dynamics (Borges & Hortal, 2009).

Given the pervasiveness of long-term geological and climatic change, for example, the complex patterns of environmental change over the last 65 million years (Zachos *et al.*, 2001), our results open up the possibility that many species groups may have similarly unrecognized complexity in their diversification histories. In particular, the loss of area and annual productivity in temperate and tropical moist forest biomes (Jetz & Fine, 2012) and

the contraction of the marine tropics in the eastern Pacific (Hall Jr, 2002) over the last 10–15 million years suggests that many groups are in long-term evolutionary decline, a possibility not easily deduced from molecular phylogenies, or seen in the absence of a good fossil record.

Methods

Schematic representation of the island ontogeny model

I have diagrammed the essential elements of the model in Figure 1.5 . Each step is described below.

Hawaiian species richness data

We chose Hawaiian endemic clades that met two criteria: (1) they are monophyletic and hence derive from a single colonization event of the archipelago; and (2) the most recent common ancestor of each group was inferred to have colonized the archipelago when Kauai was the only major island present, or before the formation of Kauai. Species diversities for each clade on each of the islands or island complex were compiled from the literature (Table 1.1).

Island ontogenies: estimating the durations of growth and decay

The duration of island growth (t_g) is the length of time from when the island first became habitable to the time it reached maximum size, while the duration of decay (t_d) is the length of time from when the island reached maximum size to the present. Estimating the durations of island growth and decay is made difficult by the fact that the lavas that were emplaced when each island was first habitable are now buried deep beneath the current surface of the island, and by the fact that the cessation of growth (and thus the beginning of decay) is not marked by a sharp change in the chemistry of the erupted lavas (Lipman & Calvert, 2013; Clague & Sherrod, 2014), which typically continue to erupt well after each volcano reached maximum size. We circumvented these difficulties by bracketing the duration of growth (and thus the duration of island decay).

As a conservative lower bound on the time of first habitability, we used an estimate of the inception of island growth on the seafloor. Specifically, we used the estimates of Clague & Sherrod (2014) based on the distance of the oldest volcano of each island from the current position of the hot spot divided by the long-term rate of Pacific plate movement over that hot spot. For Kauai and Oahu we used a rate of 10 cm per year (Clague & Sherrod, 2014). Ni’ihau does not appear to have ever been subaerially connected to Kauai (Flinders *et al.*, 2010), so we excluded it from our analysis. For Maui Nui we used an extrapolation of Lipman & Calvert’s (2013) ‘Kea Trend’ of 8.6 cm per year for the time of birth of its first high-altitude volcano, West Molokai (see their figure 15B). Neither Penguin Bank, nor the

Table 1.1: Species richness values for each of the 14 clades for each of the four major islands

Taxon	Hawaii	Maui Nui	Oahu	Kauai	Species count references	Monophyly and arrival before Oahu emergence references
Animals						
Honeycreepers	14	24	16	14	Pratt 2005	Fleischer <i>et al.</i> 1998; Lerner <i>et al.</i> 2011
PW <i>Drosophila</i>	39	52	42	21	Magnacca & Price 2015	Magnacca & Price 2015
<i>Tetragnatha</i>	15	18	12	10	Nishida 2002	Gillespie <i>et al.</i> 1997
<i>Orsonwelles</i>	1	3	3	6	Nishida 2002; Hormiga <i>et al.</i> 2003,	Hormiga <i>et al.</i> 2003
<i>Ariamnes</i>	2	5	2	2	Nishida 2002; Gillespie & Rivera 2007	Gillespie <i>et al.</i> 2018
<i>Laupala</i>	7	11	12	7	Nishida 2002; Otte 2000; Shaw 2000	Shaw 1996
Platynini	7	70	33	27	Nishida 2002; Liebherr & Zimmerman 2000; Liebherr & Short 2006; Liebherr 2001, 2006, 2003	Cryan <i>et al.</i> 2001
<i>Megalagrion</i>	7	10	9	11	Nishida 2002; Jordan <i>et al.</i> 2003	Jordan <i>et al.</i> 2003
Plants						
Lobeliads	29	56	37	33	Wagner <i>et al.</i> 1999, 2005, 2012	Givnish <i>et al.</i> 2009
<i>Cyrtandra</i>	10	17	24	13	Wagner <i>et al.</i> 1999, 2005, 2012	Cronk <i>et al.</i> 2005; Clark <i>et al.</i> 2009; Johnson <i>et al.</i> 2017
Silverswords	8	14	4	16	Wagner <i>et al.</i> 1999, 2005, 2012	Baldwin & Sanderson 1998
<i>Psychotria</i>	2	4	5	8	Wagner <i>et al.</i> 1999, 2005, 2012	Nepokroeff <i>et al.</i> 2003b
<i>Schiedea</i>	3	13	11	11	Wagner <i>et al.</i> 1999, 2005, 2012	Soltis <i>et al.</i> 1996; Willyard <i>et al.</i> 2011
Mints	20	31	10	11	Wagner <i>et al.</i> 1999, 2005, 2012	Lindqvist & Albert 2002

transient subaerial connection between Oahu and Molokai appear to have ever been high enough to generate orographic rainfall, so they were also excluded from the analysis. For the Big Island of Hawaii, the oldest volcano Mahukona was apparently never high enough to create its own rainfall (with a maximum height of only 351 m; Carson & Clague 1995) and had resubmerged before Kohala became habitable, so we used the estimate of (Lipman & Calvert, 2013) of 1.3 million years for the inception of Kohala as the lower bound on the time of first habitability of the Big Island.

As an upper bound on the time of first habitability area, we used the age of the oldest exposed lava on each of the island, provided by Clague and Sherrod 2014, under the assumption that the island was already habitable before the emplacement of those lavas.

Turning to the time of cessation of growth (and the beginning of decay), as a lower bound we used the age of youngest dated tholeiitic lava as provided by Clague and Sherrod (2014; their figure 14), traditionally associated with the end of growth of the volcanic shield. This corresponds to faster growth, and longer decay times. Growth substantial enough to outpace tectonic subsidence can occur during the eruption of more alkali lavas typically attributed to late shield growth (Clague & Sherrod, 2014; Lipman & Calvert, 2013), so we used the

youngest lavas of late stage shield growth (Clague & Sherrod 2014; their figure 14) as an upper bound on the time of maximum area (corresponding to longer growth, and the shortest possible duration of island decay).

The minimum, maximum, and average values of t_g and t_d are given in Table 1.2. For the analyses presented in Figure 1.2 we used the mean estimates of the times of first habitability and maximum growth.

Island ontogenies: estimating maximum areas

Given that Hawaii is about as large as it has ever been (Moore & Clague, 1992), we used its current area (10,434 km², see Table 1.2) as its maximum size. For the other islands the maximum area was estimated by exploiting the long-recognized fact that the angle of repose of lavas erupted under water is considerably steeper than for subaerially erupted lavas (Mark & Moore, 1987; Carson & Clague, 1995). Thus, the greatest subaerial area can be determined by locating this change in slope in bathymetric data (which, owing to tectonic subsidence, is typically 800–1,000 m below sea level for the older islands).

For Maui Nui, Price and Elliott-Fisk 2004 used this approach estimate its maximum size at 14,000 km², given the current sea level, and 14,600 km² if the sea level was \sim 120 m lower, as it was during the last glacial-driven low stand. Given the time of maximum area, approximately 0.96–1.1 million years ago, precedes the onset of the major Pleistocene glacial periods, we used their interglacial sea-level estimate. However, Price and Elliot-Fisk’s (2004) estimate includes the 500 km² Penguin Bank, which only had a maximum height of \sim 500 m (Price & Elliott-Fisk, 2004) about 2.2 million years ago, and thus was probably too low to support any of the groups analysed in this study. Further, it was almost certainly submerged by 1.1 million years ago, the time that Maui Nui was at its maximum size. Thus, we excluded the area of Penguin Bank from our estimate of the maximum area of Maui Nui, and assumed it had a maximum area of 13,500 km².

For Oahu and Kauai, in the absence of literature estimates of their maximum areas, we calculated the maximum area of each of their major volcanoes, and then for Oahu summed the values for two major volcanoes taking into account the fact that the older volcano (Wai’anae) had already lost area via subsidence by the time that the younger volcano (Ko’olau) reached its maximum size. The subsidence rate was approximated by taking the difference between the estimated maximum and current area, divided by the estimated time of decay. To estimate the maximum area (A_{max}) of each volcano we multiplied its current area (A_{curr}) by $(h_{max}/h_{now})^2$, where h_{max} is the estimated maximum height (Carson & Clague, 1995), and h_{now} is the current height. The maximum heights were taken from the literature (Carson & Clague, 1995; Moore & Clague, 1992) and equal the present height of each volcano, plus the distance below sea level of the change in the angle of repose described above. For Oahu, given that it consists of two major volcanoes, Wai’anae and Ko’olau, we simply apportioned the current area of the island in proportion to maximum areas on the basis of their estimated heights.

Table 1.2: Estimated time of growth (t_{growth}), time of decay (t_{decay}), current area (A_{curr}), estimated area at the last glacial maximum (A_{LGM} ; data from Weigelt *et al.* 2016), and estimated maximum area (A_{max}) for the major Hawaiian islands.

Island / island complex	A_{curr}	A_{LGM}	A_{max}	$t_{first\ habitable}$			t_{maxA}			t_{growth}				t_{decay}					
				max	mean	min	max	mean	min	YS	YL	OS	OL	mean	YS	YL	OS	OL	mean
Hawaii	10,434	11,151	10,434	1.3	1.2	1.1	0	0	0	1.1	1.1	1.3	1.3	1.2	0	0	0	0	0
Maui Nui	3,155	5,913	13,500	3	2.55	2.1	1.1	1.03	0.96	1	1.14	1.9	2.04	1.52	1.1	0.96	1.1	0.96	1.03
Oahu	1,548	2,400	4,121	4.34	4.135	3.93	1.8	1.3	0.8	2.13	3.13	2.54	3.54	2.835	1.8	0.8	1.8	0.8	1.3
Kauai	1,431	1,955	3,787	6.3	6.15	6	4	3.825	3.65	2	2.35	2.3	2.65	2.325	4	3.65	4	3.65	3.825

Translating geographical areas into carrying capacities

To translate our island area trajectories (Figure 1.1) into carrying capacity trajectories, we used the Arrhenius power law relationship (Triantis *et al.*, 2012) between species richness (S) and geographical area (A), where S is proportional to A^z . Of the numerous proposed numerical relationships proposed to capture the relationship between S and A , this provides the best fit to island species richness across a wide range of data (Triantis *et al.*, 2012). We used z values of species-area relationships reported in the literature. We note that if species diversities on one or more islands are not close to equilibrium, then the species-area relationship may not yield accurate values of z . Consequently, for the vascular plants groups we analysed (lobeliads, mints, silverswords, *Viola*, *Psychotria*, *Schiedea*), we used Price and Wagner’s (2011) estimate of the speciesarea relationship ($z = 0.38$) for the native Hawaiian flora which excludes the Big Island of Hawaii, given that the Big Island has a disproportionately low diversity for its large area. For the arthropod clades (*Laupala*, *Orsonwelles*, *Tetragnatha*, Platynini, *Ariamnes*, picture-winged *Drosophila*, *Megalagrion*), we used a z value of 0.49 for the archipelago, also excluding the Big Island (Peck *et al.*, 1999). Finally, we used a z value of 0.271 for the Hawaiian archipelago drepanids (honeycreepers) which remains unchanged with the inclusion of the Big Island (Juvik & Austring, 1979).

Relationship between time of maximum area and time of maximum carrying capacity

As a volcano shrinks in area, erosional process may continue to create biologically meaningful topological complexity, and thus maximum carrying capacity may post-date the time of maximum area (Whittaker *et al.*, 2008; Borregaard *et al.*, 2016). However, most of the Hawaiian islands are made of multiple volcanoes, so that by the time each island complex had ceased its subaerial growth there was already considerable topological complexity due to both the presence and erosion of the older volcanoes. Furthermore, rates of initial subsidence are high so that area is initially lost quite quickly. For example, Price and Elliott-Fisk (2004) estimate that in the first 200,000 years after Maui-Nui ceased growing, it lost 23–30% of its area owing to subsidence. Thus, while topological complexity increases with time, it appears that total area drops sufficiently fast to more than offset this factor – hence using the time of maximum area as a proxy for the time of maximum carrying capacity seems reasonable.

Furthermore, our upper bracket on the time of maximum growth almost certainly post-dates the time of maximum area and thus may serve as good proxy for maximum carrying capacity that includes the trade-off between maximum area and increased topographic complexity.

Island ontogeny model

The island ontogeny model uses the standard formulation for logistic growth, except that the intrinsic species accumulation rate (immigration, plus in situ speciation, minus extinction) and carrying capacity first grow linearly with time as the island grows, and then decay linearly with time as the island tectonically subsides and erodes. Use of the simplifying assumption of rates of linear growth and decay led to analytical solutions to the differential equations for species change with time, while nonlinear rates could not be solved analytically; nor do we have the data available to adequately quantify any nonlinearities that might have occurred in growth and decay of the islands (except perhaps for the Big Island of Hawaii, Lipman & Calvert 2013). Thus, for the growth phase, which lasts for time t_g , the rate of change in the species richness (S_g) is given by:

$$\frac{dS_g}{dt} = r_{0,max} \left(\frac{t}{t_g} \right) S_g \left(1 - \frac{S_g}{K_{max}(\frac{t}{t_g})} \right) \quad (1)$$

where $r_{0,max}$ is the maximum intrinsic species accumulation rate, and K_{max} is the maximum carrying capacity, which are both realized when the island is at maximum size at the end of the growth phase (when $t = t_g$). Equation (1) has the boundary condition of a species richness of 1 at the inception of island growth, namely $S_g = 1$ when $t = 0$.

The decay phase of the island lasts for time t_d , after which the island has lost a proportion, p , of its maximum carrying capacity. The rate of change in the species richness is given by:

$$\frac{dS_d}{dt} = r_{0,max} \left[1 - p \left(\frac{t}{t_d} \right) \right] S_d \left(1 - \frac{S_d}{K_{max} \left[1 - p \left(\frac{t}{t_d} \right) \right]} \right) \quad (2)$$

The proportion of the maximum carrying capacity each island has lost since its maximum size, p , is given by

$$p = 1 - (A_{current}/A_{max})^z \quad (3)$$

Equation (2) has the boundary condition of a species richness of $S_g(t_g)$ at the inception of island decay, namely $S_d(t = 0) = S_g(t_g)$. Equations (1) and (2) were solved using Mathematica (Wolfram Research, Inc, 2015).

To account for island-specific ontogenetic differences, we scaled the actual maximum carrying capacity (K_{max}) and maximum intrinsic species accumulation rate ($r_{0,max}$) to each islands size. We did this by normalizing island differences to the island with the largest maximum area, Maui Nui. To this end, island-specific modifications were made to equations (1) and (2) by substituting K_{max} and $r_{0,max}$ with

$$K_{max,i} = h_i \cdot K_{max,MauaNui} \quad (4)$$

$$r_{0,max,i} = h_i \cdot r_{0,max,MauaNui} \quad (5)$$

where the scaling factor for island i is given by

$$h_i = (A_{max,i}/A_{max,MauaNui})^z \quad (6)$$

Estimating the clade-specific maximum carrying capacity (K_{max}) and intrinsic diversification rates ($r_{0,max}$)

By leveraging the chronosequence of the Hawaiian archipelago, we were able to estimate the values of these parameters using the observed species richness across the four island/island groups of the archipelago (Table 1.1). Each island, owing to differences in its ontogenetic stage, effectively provides a different temporal snapshot of the diversification history for each clade. Thus, we estimated the values for $r_{0,max}$ and K_{max} by finding their values that provided the best fit to the island-specific species richness values using nonlinear least-squares regression, with the R package `minpack.lm` (Elzhov *et al.*, 2015). To initialize the nonlinear regression algorithm, we specified starting values for $r_{0,max}$ and K_{max} using the average diversification rate ($\log(\text{diversity}/\text{island age})$) and the mean observed diversity across the islands respectively. The analytical solutions for both the differential equations describing the island growth and decay phases contained imaginary and ordinary error functions, which we calculated using functions in the `pracma` R package (Borchers, 2015). However, because the accurate calculation of the values of the imaginary error function required greater floating-point precision than the default settings in R, we also used the `Rmpfr` package (Maechler, 2015) where necessary. The best-fit values of K_{max} and $r_{0,max}$ for each clade are given in Table 1.3.

Computing instantaneous rates of species accumulation

The instantaneous rate of species accumulation during the growth stage, $r_g(t)$, and rate of species loss during the decline stage, $r_d(t)$, were calculated using

$$r_g(t) = r_{0,max}(t/t_g - S_g(t)/K_{max}) \quad (7)$$

$$r_d(t) = r_{0,max}(1 - pt/t_d - S_d(t)/K_{max}) \quad (8)$$

which use island-specific scaling factors for K_{max} and $r_{0,max}$ (equations 4–6), and the time varying values of species richness as an island grows (S_g) and decays (S_d), provided by the solutions to equations (1) and (2).

Model comparison

We evaluated the performance of our island ontogeny model (Ontogeny K) using an information-theoretic approach (Burnham & Anderson, 2002) against two other models, logistic growth with a single fixed universal carrying capacity (Single K), and logistic growth with island-specific fixed carrying capacities (Island K). The models were compared by first fitting each model to the island-specific species richness data (Table 1.1) using nonlinear least-squares regression, implemented using the R package `minpack.lm` (Elzhov *et al.*, 2015). We then compared the performance of the models using Akaike weights, which represents a measure of the relative likelihood of each model given the data. Given that all the models have the same number of parameters (that is, two) and the same number of data points (that is, four), there was no need to use AICc, the correction for small sample sizes, given that the AIC and AICc weights and AIC and AICc differences are identical (Burnham & Anderson, 2002). We also computed the differences in the AIC values (ΔAIC), where $\Delta\text{AIC} < 2$ indicates substantial support for a model, even if it is not the best model (Burnham & Anderson, 2002)(the best model always has a ΔAIC of zero).

For the Single K model, we assumed that each island had the same clade-specific time-invariant carrying capacity (K) and intrinsic species accumulation rate (r_0). For the Island K model, we assumed the carrying capacity (K) and intrinsic species accumulation rate (r_0) for each island was proportional to its current area, normalized to the area of the biggest island, raised to the clade-specific species-area power law coefficient (z).

Sensitivity analyses

The island ontogeny model depends on island-specific parameter values for island growth and decay. However, there is significant uncertainty in the durations of growth and decay (Figure 1.1; Table 1.2). To determine how sensitive model selection is to these uncertainties, we re-ran all the analyses with the four combinations of the oldest and youngest estimates of the time of first habitability, and the longest and shortest durations of island growth for all islands (which correspond to the shortest and longest duration of island decay, respectively). In addition, because short-term climatic oscillations may have an impact on island biotas through their effect on isolation and area, we also ran all of these analyses with the last glacial maximum island areas (Table 1.2, data from Weigelt *et al.* 2016). For 11 of the 14 clades, the various combinations of growth and decay durations had very little effect on the Akaike weights (Figure 1.6). For three of the groups, the plant genus *Psychotria*, the spider genus *Orsonwelles*, and the plant clade *Schiedea*, the analyses run with the older island estimates with the shorter subsequent island growth find much less support than with the average durations, but found stronger support with the youngest island age estimates. Replacing the current areas with the last glacial maximum areas had almost no effect, except for *Tetragantha*, where the use of last glacial maximum areas led to slightly poorer fits (Figure 1.6). This suggests that short-term climatic cycles have had very little effect on the observed diversities of Hawaiian clades relative to the evolutionary dynamics driven by the longer-term

geological changes experienced by the Hawaiian Islands.

Finally, we assessed model selection sensitivity to uncertainties in the estimated maximum areas (A_{max}) of the two older islands. To estimate these maximum areas, we used the ratio of the maximum height to the current height times the current area (see above), assuming that the islands lost area only because of subsidence. However, the islands also lost area owing to mega-landslips (Clague & Sherrod, 2014), so using the current area to estimate the loss of area due to subsidence probably underestimates A_{max} . Thus, we re-ran the model fitting after increasing A_{max} for the two older islands by an arbitrary 60%. However, it is also likely that the islands lost height owing to erosion in addition to subsidence, which, all else being equal, leads to an overestimate of A_{max} . Thus, we also re-ran the model fitting after decreasing the maximum size of the two older islands by an arbitrary 40%. For both analyses, there were no systematic changes in the AIC weights and most of the changes were small, except for *Orsonwelles*, *Schiedea*, and *Psychotria* (Figure 1.7) which had either no, or only slightly, humped species richness distributions, and which also showed sensitivity to use of last glacial maximum areas.

Code availability

Analysis scripts are available at <https://github.com/junyinglim/hawaiiDivDynamics>. All the data used in our analyses are given in the Supplementary Tables, or in the appropriate section of the Methods.

Supplementary Figures

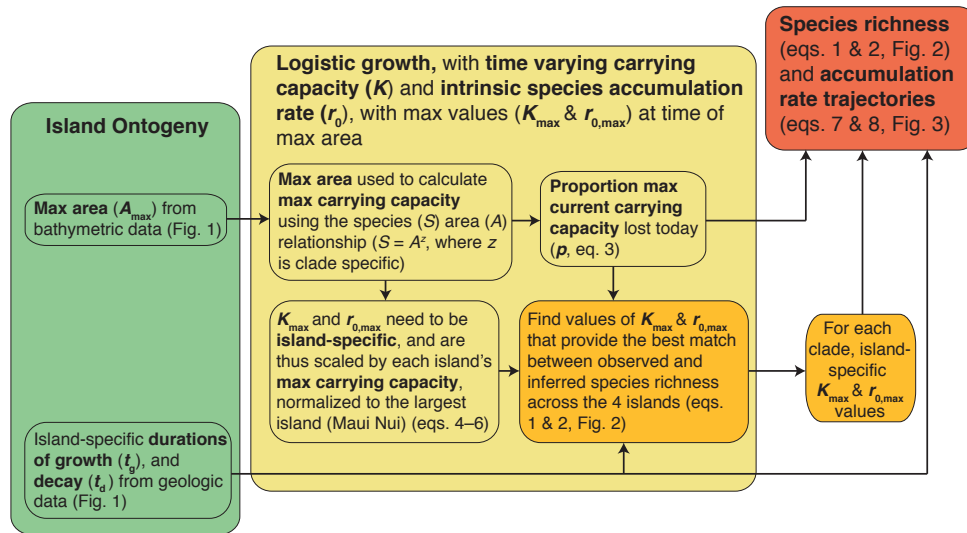


Figure 1.5: Schematic description of the island ontogeny model

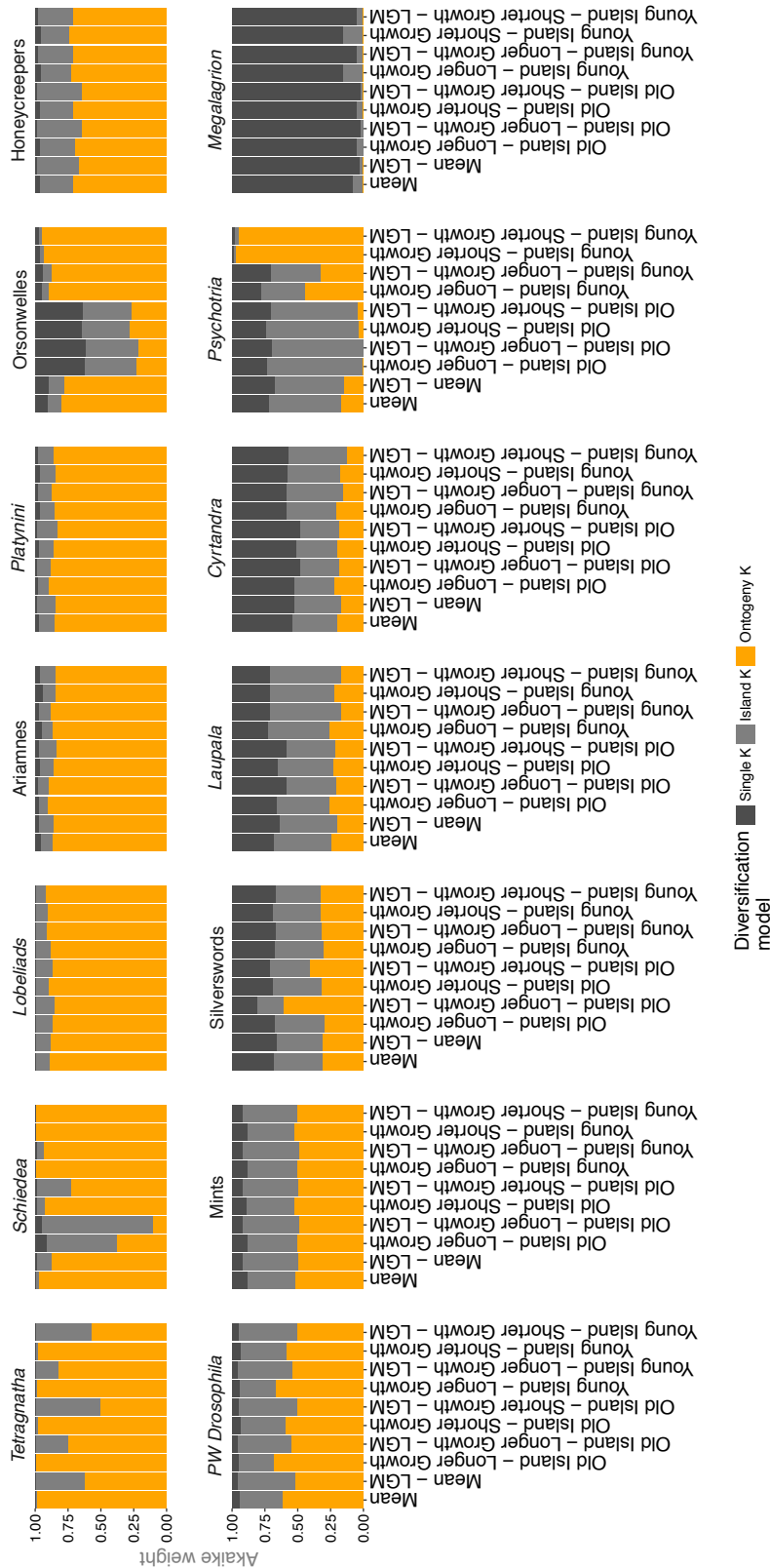


Figure 1.6: Sensitivity of the model comparison results in uncertainties in the ontogenies of the islands. See Figure 1.1 and Table 1.2. For the columns labelled ‘Mean’, the mean values of the duration of growth (t_{growth}), and decay (t_{decay}) were used; ‘Old Island’ means oldest estimate of time of first habitability was used; ‘Young Island’ means youngest estimate of time of first habitability was used; ‘Longer Growth’ means oldest estimate of time of maximum area was used; ‘Shorter Growth’ means oldest estimate of time of maximum area was used. The corresponding values of $r_{0,max}$ and K_{max} can be found in Tables 1.3–1.7.

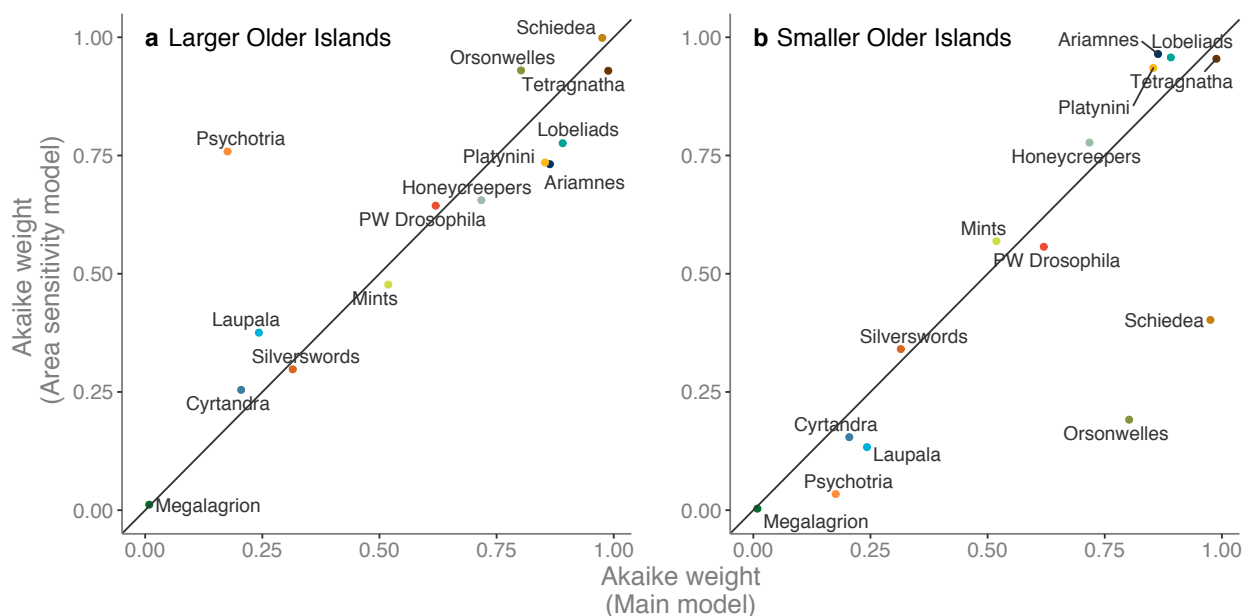


Figure 1.7: Sensitivity of island ontogeny model to uncertainties in area estimates of older islands. (a) AIC weights for the island ontogeny model (x axis) plotted against the weights when the maximum area of the two older islands (Kauai and Oahu) were increased by 60% (y axis). (b) AIC weights for the island ontogeny model (x axis) plotted against the weights when the maximum areas of the two older islands were decreased by 40% (y axis). If there were no changes in the AIC weight for a clade, its data point would lie on the diagonal line.

Supplementary tables

Table 1.3: Parameter estimates using mean dates for island habitable area and island maximum area.

Taxon	Model	$r_{0,max}$		K_{max}		AIC	w
		Est.	S.E.	Est.	S.E.		
<i>Ariamnes</i>	Single K	2.1	5.97	2.68	1.1	19.31	0.05
	Island K	1.1	0.75	6.79	2.48	17.84	0.11
	Ontogeny K	2.54	1.77	6.44	1.42	13.8	0.84
<i>Cyrtandra</i>	Single K	2.52	1.04	18.19	3.35	28.27	0.49
	Island K	2.03	0.71	34.8	7.96	29.22	0.3
	Ontogeny K	5.31	2.14	32.22	7.15	29.96	0.21
Honeycreepers	Single K	3.47	1.6	17.96	3.1	27.95	0.05
	Island K	2.79	0.43	28.48	3.27	24.68	0.25
	Ontogeny K	6.49	0.9	28.92	2.44	22.63	0.7
<i>Laupala</i>	Single K	2.59	1.15	10.01	1.59	22.44	0.35
	Island K	1.86	0.46	22.34	3.83	22.37	0.36
	Ontogeny K	5.02	1.46	20.24	3.27	22.87	0.28
Lobeliads	Single K	3.81	1.22	41.93	7.17	34.69	0.01
	Island K	3.2	0.28	79.61	6.81	29.23	0.12
	Ontogeny K	7.37	0.45	80.23	4.07	25.32	0.87
<i>Megalagrion</i>	Single K	2.53	0.41	10.05	0.6	14.59	0.85
	Island K	1.74	0.27	22.77	2.42	18.28	0.14
	Ontogeny K	5.06	1.54	19.81	3.38	23.16	0.01
Mints	Single K	6.7	121.48	17.74	6.91	34.44	0.12
	Island K	3.25	1	33.88	9.82	32.24	0.36
	Ontogeny K	7.92	2.77	35.05	8.69	31.54	0.52
<i>Orsonwelles</i>	Single K	0.37	0.16	13.05	20.03	12.38	0.06
	Island K	0.37	0.14	31.9	43.27	12.11	0.07
	Ontogeny K	0.76	0.13	266.75	1850.82	6.91	0.88
Platynini	Single K	2.9	2.11	40.73	15.19	40.46	0.04
	Island K	2.59	0.98	97.84	25.82	37.94	0.15
	Ontogeny K	4.48	2.4	96.55	19.69	34.52	0.81
<i>Psychotria</i>	Single K	0.6	0.1	9.52	1.82	10.83	0.23
	Island K	0.59	0.07	19.48	2.73	8.83	0.63
	Ontogeny K	1.12	0.16	25.12	7.84	11.94	0.13
PW <i>Drosophila</i>	Single K	6.27	20.26	38.32	9.16	36.69	0.09
	Island K	3.57	0.48	83.76	14.43	34.21	0.31
	Ontogeny K	8.63	1.17	84.91	11.85	32.87	0.6
<i>Schiedea</i>	Single K	1.75	0.59	11.84	1.67	21.66	0.01
	Island K	1.52	0.25	23.6	2.7	19.37	0.02
	Ontogeny K	2.59	0.2	23.79	1.46	11.96	0.97
Silerswords	Single K	2.74	2.5	11.32	3.82	29.49	0.29
	Island K	2.1	0.99	21.69	7.07	28.9	0.39
	Ontogeny K	5.28	3.01	20.7	6.48	29.27	0.32
<i>Tetragnatha</i>	Single K	13.86	395074.02	13.75	2.47	26.22	0
	Island K	2.84	0.22	29.2	2.33	19.52	0.05
	Ontogeny K	7.38	0.36	28.98	1.05	13.79	0.94

Table 1.4: Parameter estimates using oldest dates for island habitable area and youngest dates for island maximum area. This assumes an older island with a long growth phase.

Taxon	Model	$r_{0,max}$		K_{max}		AIC	w
		Est.	S.E.	Est.	S.E.		
<i>Ariamnes</i>	Single K	1.75	3.85	2.88	1.08	19.19	0.04
	Island K	1.04	0.68	6.75	2.29	17.48	0.09
	Ontogeny K	2.19	1.39	6.52	1.51	12.99	0.87
<i>Cyrtandra</i>	Single K	2.33	0.97	18.11	3.3	28.29	0.5
	Island K	1.91	0.72	34.04	7.7	29.47	0.28
	Ontogeny K	5.01	1.95	31.68	6.93	29.84	0.23
Honeycreepers	Single K	3.17	1.42	17.98	3.08	27.93	0.05
	Island K	2.55	0.38	28.48	3.16	24.5	0.26
	Ontogeny K	6.01	0.83	28.58	2.39	22.56	0.69
<i>Laupala</i>	Single K	2.37	1.04	10.01	1.57	22.41	0.36
	Island K	1.73	0.44	21.98	3.72	22.52	0.34
	Ontogeny K	4.85	1.35	19.78	3.16	22.77	0.3
Lobeliads	Single K	3.49	1.1	41.98	7.13	34.67	0.01
	Island K	2.94	0.26	79.47	6.55	29	0.13
	Ontogeny K	6.83	0.42	78.85	3.96	25.24	0.86
<i>Megalagrion</i>	Single K	2.34	0.38	10.03	0.59	14.57	0.9
	Island K	1.65	0.3	22.11	2.55	19.26	0.09
	Ontogeny K	4.78	1.48	19.36	3.4	23.35	0.01
Mints	Single K	10.36	24805.95	17.86	6.91	34.43	0.12
	Island K	2.98	0.91	34.01	9.73	32.21	0.37
	Ontogeny K	7.38	2.67	34.44	8.59	31.62	0.5
<i>Orsonwelles</i>	Single K	0.3	0.13	31.21	145.05	11.27	0.31
	Island K	0.31	0.11	59.51	177.8	11.19	0.33
	Ontogeny K	0.74	0.19	300	3729.31	10.99	0.36
Platynini	Single K	2.4	1.92	42.9	14.94	40.24	0.03
	Island K	2.17	0.97	98.94	25.7	37.56	0.12
	Ontogeny K	4.09	1.48	95.91	16.8	33.59	0.85
<i>Psychotria</i>	Single K	0.53	0.06	10.6	1.87	7.88	0.18
	Island K	0.52	0.04	22.09	2.59	4.92	0.81
	Ontogeny K	0.97	0.25	34.93	33.01	15.72	0
PW <i>Drosophila</i>	Single K	5.56	14.13	38.33	9.16	36.69	0.08
	Island K	3.29	0.44	83.7	14.33	34.2	0.27
	Ontogeny K	8.01	1.04	83.33	10.9	32.38	0.66
<i>Schiedea</i>	Single K	1.59	0.54	11.76	1.52	20.95	0.09
	Island K	1.33	0.2	23.67	2.31	17.77	0.47
	Ontogeny K	2.53	0.48	22.91	3.05	17.89	0.44
SILVERSWORDS	Single K	2.49	2.23	11.33	3.78	29.48	0.3
	Island K	1.93	0.92	21.6	6.82	28.87	0.4
	Ontogeny K	4.2	2.98	20.49	6.61	29.44	0.3
<i>Tetragantha</i>	Single K	11.81	101599.75	13.75	2.47	26.22	0
	Island K	2.62	0.2	29.15	2.26	19.36	0.04
	Ontogeny K	6.89	0.31	28.38	0.92	12.93	0.96

Table 1.5: Parameter estimates using oldest dates for island habitable area and oldest dates for island maximum area. This assumes an older island with a short growth phase.

Taxon	Model	$r_{0,max}$		K_{max}		AIC	w
		Est.	S.E.	Est.	S.E.		
<i>Ariamnes</i>	Single K	1.75	3.85	2.88	1.08	19.19	0.05
	Island K	1.04	0.68	6.75	2.29	17.48	0.12
	Ontogeny K	2.25	1.64	6.38	1.37	13.61	0.83
<i>Cyrtandra</i>	Single K	2.33	0.97	18.11	3.3	28.29	0.51
	Island K	1.91	0.72	34.04	7.7	29.47	0.28
	Ontogeny K	4.92	2.01	32.17	7.28	30.12	0.2
Honeycreepers	Single K	3.17	1.42	17.98	3.08	27.93	0.05
	Island K	2.55	0.38	28.48	3.16	24.5	0.26
	Ontogeny K	5.98	0.82	28.97	2.41	22.53	0.69
<i>Laupala</i>	Single K	2.37	1.04	10.01	1.57	22.41	0.38
	Island K	1.73	0.44	21.98	3.72	22.52	0.36
	Ontogeny K	4.61	1.38	20.21	3.36	23.12	0.26
Lobeliads	Single K	3.49	1.1	41.98	7.13	34.67	0.01
	Island K	2.94	0.26	79.47	6.55	29	0.12
	Ontogeny K	6.8	0.4	80.39	3.98	25.12	0.87
<i>Megalagrion</i>	Single K	2.34	0.38	10.03	0.59	14.57	0.9
	Island K	1.65	0.3	22.11	2.55	19.26	0.09
	Ontogeny K	4.71	1.43	19.79	3.4	23.24	0.01
Mints	Single K	10.36	24805.95	17.86	6.91	34.43	0.12
	Island K	2.98	0.91	34.01	9.73	32.21	0.36
	Ontogeny K	7.28	2.5	35.18	8.62	31.45	0.52
<i>Orsonwelles</i>	Single K	0.3	0.13	31.21	145.05	11.27	0.27
	Island K	0.31	0.11	59.51	177.8	11.19	0.28
	Ontogeny K	0.72	0.17	300	3474.4	10.21	0.45
Platynini	Single K	2.4	1.92	42.9	14.94	40.24	0.04
	Island K	2.17	0.97	98.94	25.7	37.56	0.14
	Ontogeny K	4.14	2.3	95.3	15.71	34.08	0.82
<i>Psychotria</i>	Single K	0.53	0.06	10.6	1.87	7.88	0.18
	Island K	0.52	0.04	22.09	2.59	4.92	0.79
	Ontogeny K	0.91	0.14	39.52	27.82	11.73	0.03
PW <i>Drosophila</i>	Single K	5.56	14.13	38.33	9.16	36.69	0.09
	Island K	3.29	0.44	83.7	14.33	34.2	0.33
	Ontogeny K	7.96	1.1	85.01	12.13	33.04	0.58
<i>Schiedea</i>	Single K	1.59	0.54	11.76	1.52	20.95	0.01
	Island K	1.33	0.2	23.67	2.31	17.77	0.07
	Ontogeny K	2.25	0.2	23.83	1.7	12.53	0.92
SILVERSWORDS	Single K	2.49	2.23	11.33	3.78	29.48	0.28
	Island K	1.93	0.92	21.6	6.82	28.87	0.39
	Ontogeny K	4.89	2.73	20.76	6.41	29.19	0.33
<i>Tetragantha</i>	Single K	11.81	101599.75	13.75	2.47	26.22	0
	Island K	2.62	0.2	29.15	2.26	19.36	0.06
	Ontogeny K	6.81	0.34	29.04	1.08	13.96	0.94

Table 1.6: Parameter estimates using youngest dates for island habitable area and youngest dates for island maximum area. This assumes younger islands with a long growth phase.

Taxon	Model	$r_{0,max}$		K_{max}		AIC	w
		Est.	S.E.	Est.	S.E.		
<i>Ariamnes</i>	Single K	2.54	7.12	2.85	1.1	19.29	0.06
	Island K	1.31	0.87	6.63	2.53	18.19	0.11
	Ontogeny K	2.83	1.91	6.53	1.59	14.08	0.83
<i>Cyrtandra</i>	Single K	2.73	1.09	18.34	3.46	28.24	0.45
	Island K	2.16	0.63	36.48	8.17	28.81	0.34
	Ontogeny K	5.79	2.27	32.3	6.93	29.68	0.22
Honeycreepers	Single K	3.79	1.78	17.95	3.15	28	0.05
	Island K	3.08	0.5	28.5	3.52	25.07	0.23
	Ontogeny K	7.1	1.01	28.81	2.5	22.82	0.71
<i>Laupala</i>	Single K	2.86	1.29	10.02	1.64	22.51	0.32
	Island K	2.05	0.46	22.83	3.97	22.22	0.36
	Ontogeny K	5.53	1.53	20.27	3.13	22.48	0.32
Lobeliads	Single K	4.14	1.34	41.94	7.3	34.76	0.01
	Island K	3.52	0.33	79.89	7.47	29.78	0.12
	Ontogeny K	8.05	0.52	79.84	4.3	25.79	0.87
<i>Megalagrion</i>	Single K	2.77	0.46	10.08	0.62	14.67	0.71
	Island K	1.91	0.22	23.48	2.05	16.55	0.28
	Ontogeny K	5.48	1.67	19.84	3.36	23.03	0.01
Mints	Single K	11.64	15350.82	17.72	6.91	34.43	0.13
	Island K	3.57	1.12	33.85	10.03	32.3	0.37
	Ontogeny K	8.7	3.15	34.79	8.81	31.69	0.5
<i>Orsonwelles</i>	Single K	0.37	0.2	13.04	24.7	13.41	0.05
	Island K	0.38	0.18	29.7	46.17	13.2	0.05
	Ontogeny K	0.91	0.16	47.58	50.3	7.51	0.9
Platynini	Single K	3.15	2.26	41.48	16.12	40.63	0.05
	Island K	3.01	1.04	97.17	28.63	38.62	0.13
	Ontogeny K	5.44	2.57	96.13	18.36	35.01	0.82
<i>Psychotria</i>	Single K	0.68	0.15	8.77	1.8	13.31	0.21
	Island K	0.68	0.12	17.71	2.86	11.98	0.4
	Ontogeny K	1.39	0.18	20.17	3.57	12.08	0.39
PW <i>Drosophila</i>	Single K	8.94	217.54	38.32	9.14	36.67	0.08
	Island K	3.9	0.53	83.97	14.72	34.26	0.27
	Ontogeny K	9.42	1.24	84.58	11.35	32.56	0.64
<i>Schiedea</i>	Single K	1.99	0.68	11.86	1.89	22.62	0
	Island K	1.73	0.32	23.89	3.33	21.18	0.01
	Ontogeny K	3.04	0.23	23.91	1.42	12.02	0.98
Silverswords	Single K	3.09	2.93	11.29	3.89	29.52	0.3
	Island K	2.36	1.06	21.84	7.38	28.96	0.39
	Ontogeny K	5.7	3.38	20.61	6.62	29.4	0.31
<i>Tetragnatha</i>	Single K	13.28	57188.44	13.68	2.48	26.23	0
	Island K	3.1	0.26	29.3	2.49	19.87	0.05
	Ontogeny K	8.07	0.4	28.83	1.06	13.83	0.95

Table 1.7: Parameter estimates using youngest dates for island habitable area and oldest dates for island maximum area. This assumes younger islands with a short growth phase.

Taxon	Model	$r_{0,max}$		K_{max}		AIC	w
		Est.	S.E.	Est.	S.E.		
<i>Ariamnes</i>	Single K	2.54	7.12	2.85	1.1	19.29	0.07
	Island K	1.31	0.87	6.63	2.53	18.19	0.12
	Ontogeny K	3.15	2.06	6.42	1.25	14.29	0.82
<i>Cyrtandra</i>	Single K	2.73	1.09	18.34	3.46	28.24	0.46
	Island K	2.16	0.63	36.48	8.17	28.81	0.35
	Ontogeny K	5.37	2.47	32.76	7.39	30.05	0.19
Honeycreepers	Single K	3.79	1.78	17.95	3.15	28	0.05
	Island K	3.08	0.5	28.5	3.52	25.07	0.23
	Ontogeny K	7.05	0.99	29.18	2.52	22.78	0.72
<i>Laupala</i>	Single K	2.86	1.29	10.02	1.64	22.51	0.34
	Island K	2.05	0.46	22.83	3.97	22.22	0.39
	Ontogeny K	5.35	1.59	20.68	3.39	22.96	0.27
Lobeliads	Single K	4.14	1.34	41.94	7.3	34.76	0.01
	Island K	3.52	0.33	79.89	7.47	29.78	0.11
	Ontogeny K	8.02	0.51	81.3	4.32	25.67	0.88
<i>Megalagrion</i>	Single K	2.77	0.46	10.08	0.62	14.67	0.71
	Island K	1.91	0.22	23.48	2.05	16.55	0.28
	Ontogeny K	5.43	1.61	20.27	3.38	22.95	0.01
Mints	Single K	11.64	15350.93	17.72	6.91	34.43	0.12
	Island K	3.57	1.12	33.85	10.03	32.3	0.36
	Ontogeny K	8.58	2.96	35.48	8.84	31.54	0.52
<i>Orsonwelles</i>	Single K	0.37	0.2	13.04	24.7	13.41	0.03
	Island K	0.38	0.18	29.7	46.17	13.2	0.03
	Ontogeny K	0.81	0.13	85.25	172.31	6.46	0.94
Platynini	Single K	3.15	2.26	41.48	16.12	40.63	0.05
	Island K	3.01	1.04	97.17	28.63	38.62	0.13
	Ontogeny K	5.46	2.6	97.19	16.66	35.02	0.82
<i>Psychotria</i>	Single K	0.68	0.15	8.77	1.8	13.31	0.01
	Island K	0.68	0.12	17.71	2.86	11.98	0.02
	Ontogeny K	1.24	0.07	21.67	1.95	4.6	0.96
PW <i>Drosophila</i>	Single K	8.94	217.54	38.32	9.14	36.67	0.1
	Island K	3.9	0.53	83.97	14.72	34.26	0.33
	Ontogeny K	9.37	1.3	86.15	12.53	33.16	0.57
<i>Schiedea</i>	Single K	1.99	0.68	11.86	1.89	22.62	0
	Island K	1.73	0.32	23.89	3.33	21.18	0
	Ontogeny K	2.91	0.11	23.64	0.62	6.24	1
Silverswords	Single K	3.09	2.93	11.29	3.89	29.52	0.28
	Island K	2.36	1.06	21.84	7.38	28.96	0.38
	Ontogeny K	5.77	3.18	21.07	6.51	29.16	0.34
<i>Tetragantha</i>	Single K	13.28	57190.42	13.68	2.48	26.23	0
	Island K	3.1	0.26	29.3	2.49	19.87	0.07
	Ontogeny K	7.98	0.43	29.48	1.2	14.66	0.93

Chapter 2

Peperomia (Piperaceae) of the Pacific: a complex pattern of long-distance dispersal, and multiple radiations on the Hawaiian Islands

Introduction

Covering about 50% of the Earth's surface, the Pacific Ocean plays host to some 25,000 islands (Koppers, 2009). Many island chains, such as the Hawaiian Islands and the archipelagos of French Polynesia, and are among the most isolated landmasses on Earth. Their origins, through hot spot volcanism (Neall & Trewick, 2008), mean that their present biotas are necessarily assembled from dispersal, and subsequent diversification of colonists to those islands. The strong dispersal barriers imposed by this geographic setting have also given rise to both taxonomically disharmonious and highly endemic floras derived from a limited subset of plant groups that possess characteristics, at least originally, that have enabled them to overcome barriers to establishment through long-distance dispersal (Carlquist, 1974; Gillespie *et al.*, 2012). Given the geologically dynamic and complex geographic setting of islands in the Pacific, the biogeographic and evolutionary history of plant lineages of the Pacific have been of great interest, particularly the interplay between dispersal and in-situ diversification in generating the diversity that we see today (Fosberg, 1948; Carlquist, 1980; Wagner *et al.*, 1999; Keeley & Funk, 2011).

The Hawaiian Islands in particular, owing to their extreme geographic isolation (up to 3,800 km from the closest continent), plays host to one of the most unique floras in the Pacific and the world, with over 90% of their angiosperm diversity endemic to the islands (Wagner *et al.*, 1999). Reflecting this geographic isolation, the biogeographic sources of the Hawaiian flora are incredibly diverse, ranging from the South Pacific, Asia, and North America to the Arctic (Keeley & Funk, 2011). Many of the most species-rich plant groups

on the islands, such as the iconic silverswords (Baldwin *et al.*, 1991; Baldwin & Sanderson, 1998), *Melicope* (Appelhans *et al.*, 2018), lobeliads (Givnish *et al.*, 2009; Knox & Li, 2017), and mints (Lindqvist & Albert, 2002), have been found to represent evolutionary radiations derived from single colonization events. However, the biogeographic history of many Hawaiian plant groups can be more complex. Some genera on Hawaii are derived from multiple colonization events. For example, the two native species of *Rubus* appear to represent two repeat colonization events from North America (Howarth *et al.*, 1997), and the eight species of Hawaiian *Scaveola* may be derived from up to three separate dispersal events (Howarth *et al.*, 2003). Other Hawaiian lineages have more complex patterns of dispersal, with other islands in the Pacific serving as stepping-stones, or even serving as biogeographic sources for other parts of the Pacific. The Hawaiian sandalwoods, for example, are derived from a long-distance colonization event from Australia, but there has been dispersal from Hawaii to the Bonin Islands in the West Pacific, and the populations in Hawaii have also served as a source to other islands in the eastern Polynesia (Harbaugh & Baldwin, 2007).

Peperomia Ruiz & Pavon (Piperaceae) is among the most diverse, widespread, and naturally-occurring genera in the Pacific. The non-woody genus, with over 1,600 species, is one of the largest angiosperm genera in the world (Frodin, 2004). Pantropical and most diverse in the Neotropics (Samain *et al.*, 2009), the genus is also successful in the Pacific (ca. 100 species, Florence 1997; Smith 1981; Wagner *et al.* 1999; Sykes 2016), having colonized almost all major islands, where they form a notable terrestrial and epiphytic component of mesic and wet forests (Florence, 1997; Wagner *et al.*, 1999). However, despite their broad geographic distribution and diversification across the Pacific, their biogeographic history, evolutionary relationships and pattern of diversification in the Pacific has been unclear.

Given the geographic scale of the greater Pacific, the *Peperomia* of the Hawaiian archipelago (Figure 2.1) represent an ideal focal point for understanding the biogeography of the group for several reasons. Firstly, the largest concentration of *Peperomia* diversity on any island system in the Pacific is on the Hawaiian archipelago, where the genus is represented by 25 native species (23 of which are endemic to the archipelago, Wagner *et al.* 1999, 2005), or nearly a quarter of the species diversity of the genus in the Pacific. Secondly, the two non-endemic indigenous taxa to the Hawaiian archipelago, *Peperomia blanda* var. *floribunda* (Miq.) H. Hüber (syn: *P. leptostachya* (Hook. & Arn.) Düll) and *P. tetraphylla* (G. Forst) Hook. & Arn., have a broad global geographic range that encompasses the south and west Pacific (e.g., French Polynesia, Micronesia, Australasia), and may represent putative sister taxa to hypothetical colonists across the Pacific. Lastly, the flora of Hawaii has undergone a recent taxonomic revision (Wagner *et al.*, 1999, 2005), and is among the best studied and collected in the Pacific. Many of the taxa on other islands (Smith, 1981) have not had repeat collections since the type collections, making the evaluation of alternative taxonomic hypotheses challenging.

Wagner *et al.* (1999) hypothesized, based on morphological affinities among the native taxa of *Peperomia*, that the species of the Hawaiian archipelago were the result of as many as four separate colonization events. The only attempt to develop a molecular phylogenetic hypothesis of evolutionary relationships among Hawaiian and some Polynesian taxa appears

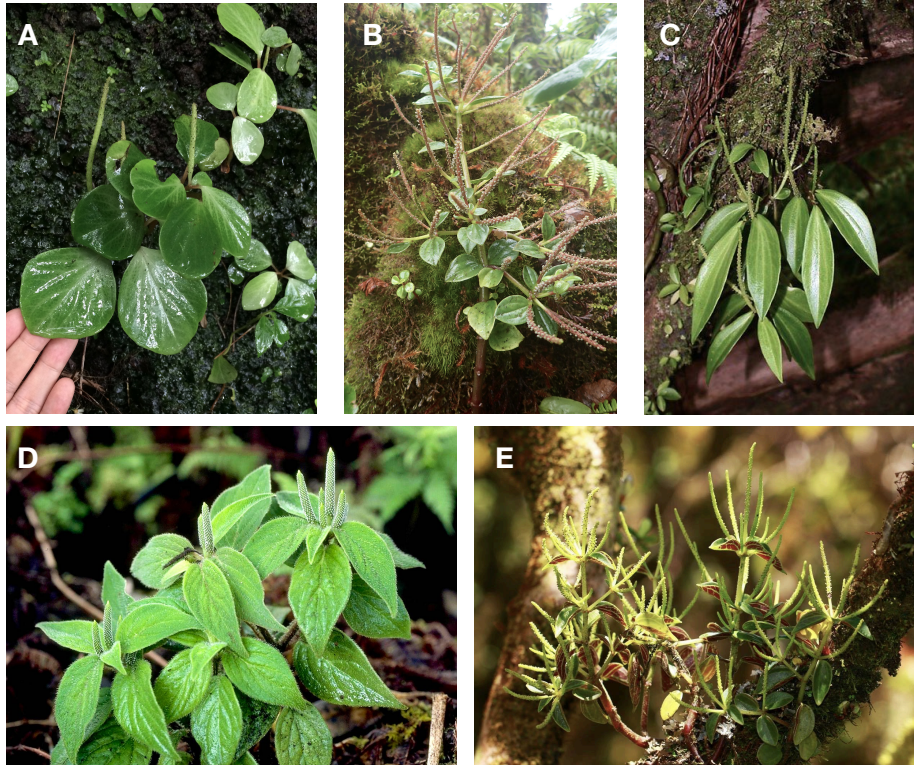


Figure 2.1: Exemplar endemic *Peperomia* of Hawaii showing the morphological diversity and growth habit of the group. (A) *P. latifolia*, Koolau range, Oahu; (B) *P. globulanthera*, East Maui; (C) *P. oahuensis*, Upper Lumaha'i Valley, Kaua'i; (D) *P. hirtipetiola*, Olinda pipeine, East Maui; (E) *P. cookiana*, Mt. Kaala, Oahu. Photo credits: A: Jun Ying Lim, B: Hank Oppenheimer, C and D: Warren Wagner, E: Francis Joy

to support the polyphyly of Hawaiian *Peperomia* and hence the derivation of the Hawaiian taxa from multiple colonization events, but relationships among endemic species of *Peperomia* remains inconclusive due to limited taxonomic sampling and poor phylogenetic support (Bradley, 2002).

Given their high dispersal ability (Valdebenito *et al.*, 1992; Frenzke *et al.*, 2016) and broad distribution across the Pacific, a greater understanding of their evolutionary history and biogeography will help inform our understanding of Pacific biogeography broadly, as well as the spatial and temporal context of diversification of the group worldwide. Here, I elucidate the evolutionary history of *Peperomia* of Hawaii and the greater Pacific using a whole-genome shotgun sequencing approach ("genome skimming"; Straub *et al.* 2012),

a rapid and cost-effective method to generate full chloroplast genomes (Malé *et al.*, 2014; Ripma *et al.*, 2014; Twyford & Ness, 2016). To better determine the potential biogeographic sources of taxa in the Pacific, I include of a number of mainland taxa from Africa and Asia, with a focus on taxa in South and Central America. To examine the timing and patterns of diversification of Pacific *Peperomia*, I also calibrate our tree using secondarily calibrations from the literature.

Materials and Methods

Taxon sampling

My taxonomic sampling spanned the Pacific and the Pacific Rim, including Micronesia, Southeast Polynesia (the Society, Marquesas and Austral islands), Fiji, Samoa, Australia, New Caledonia, New Zealand and Japan, with particular emphasis on Hawaiian taxa. For Hawaiian species that occur across multiple islands, I collected multiple accessions across its geographic range where possible. In total, 50 accessions of the 24 native Hawaiian taxa (out of the total 25) were included. Tissue from a herbarium specimen of the presumably extinct Hawaiian endemic taxon, *P. degeneri*, was collected, but DNA extraction was unsuccessful.

To better sample from potential source areas of the Pacific *Peperomia*, I used the subgeneric classification of Frenzke *et al.* (2015), the most recent and comprehensive revision of the genus to inform our sampling. Like most of the taxa native to the Pacific, almost all of the Hawaiian taxa have been recently assigned to the subgenus *Micropiper* (Miq.) Miq. (Frenzke *et al.*, 2015). As such, I included 9 taxa representing the subgenus *Micropiper* from Africa, Asia (China and Japan), South America and Central America, with special focus on the widespread *P. blanda* and taxa from various other subgenera.

The final *Peperomia* taxon sampling consisted of 117 accessions representing at least 58 species, 103 of which are Pacific taxa. In addition to this, I included two *Piper* and one *Macropiper* species as outgroup taxa to *Peperomia*.

Voucher specimens (see Appendix) are housed in the Bishop Museum (BISH), National Herbarium at the Smithsonian (US), National Tropical Botanical Garden (PTBG), University of California Herbarium (UC) and the South Pacific Regional Herbarium (SPRH).

Library preparation and sequencing

120 samples representing at least 58 taxa of *Peperomia* were sequenced. To get a rough estimate of plastome coverage, I used the published genome size of a closely-related species, *Peperomia blanda* ($n = 11$; 1.55 pg), from the Kew Gardens C-values database (Bennett & Leitch, 2012) and an available complete chloroplast genome of *Piper* (Lee *et al.* 2015). However, because the ploidy of most of the taxa endemic to Hawaii appear to be double that of mainland species ($n = 22$; Notoatmodjo 1967), I assumed the genome sizes to be

double that of the reported 1.55 pg for *Peperomia blanda* as a conservative estimate when determining our multiplex strategy.

Genomic DNA from each sample was extracted from 10 - 20 mg of silica-dried leaf tissue using Qiagen DNAeasy plant mini kits (Qiagen, U.S.A.) following manufacturer protocols. Between 300 - 500 ng of DNA for each sample was then sonicated for 18 - 20 one-minute cycles using a Bioruptor (Diagenode, Denville, NJ). Each sonication cycle consisted of a 30 second burst, followed by a 30 second pause. The number of sonication cycles was originally optimized to maximize the number of fragments within a 400 - 600 base pair range, but where the fragment size distribution of sonicated samples was still too large as verified on a 1.2X agarose gel, additional cycles were performed. The resulting DNA was then prepared for sequencing following Meyer & Kircher Meyer & Kircher (2010) with a few notable exceptions: 1) post-sonicated genomic DNA fragments were first purified using Sera-Mag magnetic beads (GE Healthcare Life Sciences, MA, U.S.A.) at a fairly low ratio (0.7:1.0 to reaction volume), 2) fragments were ligated to adapters with 7 bp "barcodes", and 3) post-PCR enriched libraries were purified using a 1:1 ratio to reaction volume to ensure the complete removal of any low molecular weight fragments, primer dimer and/or unincorporated adapters. Resulting libraries were then quantified using a Qubit fluorometer v3 (Thermo Fisher Scientific, MA, U.S.A.) and pooled at equimolar ratios. Dual-indexed libraries were sequenced on a single lane of Illumina HiSeq v4000 using a 150 base pair paired-end sequencing strategy at the QB3 sequencing facility at the University of California, Berkeley.

Plastome sequence assembly

Sequencing reads were trimmed using Trimmomatic v0.36 (Bolger *et al.*, 2014) using a 10-base sliding window and a base quality clipping minimum threshold of 20. To generate plastomes sequences for each taxon, I performed reference-guided assembly using a Burrows-Wheeler transformation-based aligner (Li & Durbin, 2009) under default parameters and a published annotated chloroplast genome of *Piper kadsura* (Lee *et al.* 2015; Genbank accession KT223569) as a reference. Mapped reads were sorted and indexed, and the read depth for each sample determined, using samtools v1.8 (Li *et al.*, 2009). Consensus sequences were then called using bcftools v0.1.15 (Danecek *et al.*, 2011). Custom pipeline scripts are available online (<https://github.com/junyinglim/peperomiaPhylo>).

Phylogenetic analysis

A total of 78 plastome protein-coding genes were concatenated and aligned using MAFFT v7.215 (Katoh & Toh, 2008). One gene, *ycf1*, was excluded due to a high percentage of ambiguities in assembled sequences. I additionally included the reference sequence for *Piper kadsura* in our final alignment.

Maximum likelihood tree searches were implemented using RAxML-HPC v8.2.11. (Stamatakis, 2006), using a GTR substitution model with gamma-distributed among site rate

variation. To avoid overfitting, only an unpartitioned analysis was performed. Phylogenetic support for nodes was evaluated with 1,000 rapid bootstrap replicates (Stamatakis *et al.*, 2008).

Divergence time estimation

In the absence of any fossil record of *Peperomia* and a fairly limited fossil record of its sister genus *Piper*, previous studies of *Peperomia* (Smith *et al.*, 2008; Symmank *et al.*, 2011; Naumann *et al.*, 2011) have relied on external calibrations of fossils from closely related families within Piperales, namely either that of Sauraceae (Smith & Stockey, 2007) and / or *Lactoris* (Aristolochiaceae)(Zavada & Benson, 1987). Smith *et al.* (2008), using the 91.2 Mya age of *Lactoris* fossils to fix the divergence time of *Piper* and *Peperomia* within Piperaceae, recovered a Cretaceous crown age of *Peperomia* (88.9 Mya). Symmank *et al.* (2011) using a molecular phylogenetic dataset of exemplar taxa across Piperales (Wanke *et al.*, 2007) and both non-parametric rate smoothing penalized-likelihood and relaxed clock analyses recovered a Paleogene stem age for *Peperomia* (~57 Mya). For this paper, I use a recently described *Piper* fossil from the late-Cretaceous (66 - 68 Mya) as a minimum age calibration for the divergence time between *Peperomia* and *Piper* (Martínez *et al.*, 2015). Taxonomic placement of the afore-mentioned leaf fossil was based on a comprehensive comparative analysis of leaf characters among genera within Piperales, including *Peperomia*. In addition, I set a maximum age on the divergence between the two genera to 90.7 Mya, representing the upper 95% highest posterior density estimate of the split between Piperaceae and its sister family, Sauraceae, in a recent extensively calibrated time tree of angiosperms (Magallón *et al.*, 2015).

I used the semi-parametric rate-smoothing approach of Sanderson 1997, implemented in the program TreePL (Smith & O'Meara, 2012). The optimal rate smoothing parameter value was evaluated by cross validation of five values separated by one order of magnitude, between 0.1 - 1000.

Results

Plastome assembly

Among the 120 samples sequenced, assembled plastomes had a read depth (measured as the average number of reads that mapped to any position of the reference) that ranged between 7 - 327 x, with an average depth of 60 x. The final plastome alignment had a total length of 63,265 bp, with about 9.4% of sites parsimony informative.

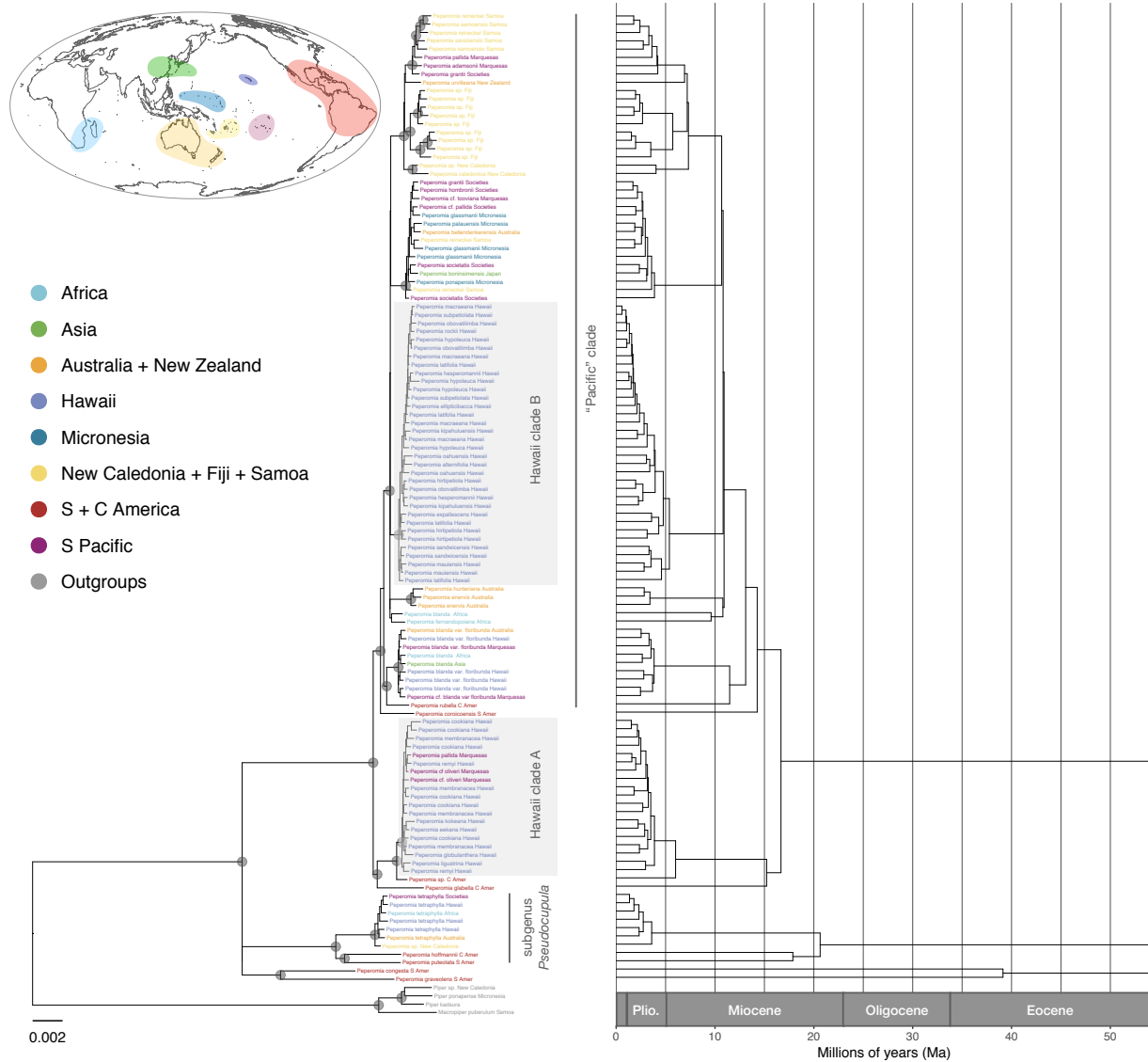


Figure 2.2: Best maximum likelihood (ML) tree from RAXML analysis (left), and the corresponding chronogram (right) inferred using non-parametric rate-smoothing implemented in TreePL. Split between *Peperomia* and *Piper* (90.7 Mya) not shown. Nodes > 80 bootstrap support are indicated with grey circles. Taxa are coloured by their respective geographic regions. The two Hawaiian endemic clades are highlighted in grey boxes.

Maximum likelihood phylogenetic analysis

The ML analysis strongly supports a sister relationship between a clade containing *Peperomia* taxa from the subgenus *Micropiper* and a clade containing *Peperomia* species of the

subgenus *Fenestratae* (*P. congesta*), species of the subgenus *Pseudocupula*, and *P. graveolens*. Within the latter clade, the best ML tree suggest a sister relationship (albeit poorly supported) between two well-supported groups: 1) *P. graveolens* and *P. congesta*, and 2) *P. tetraphylla* and two other species, *P. hoffmannii* and *P. graveolens* (collectively of subgenus *Pseudocupula*). *P. tetraphylla*, a widespread species across the Pacific and mainland areas formed a monophyletic group, and thus represents a separate lineage to colonize the Pacific.

The Pacific taxa were recovered in two large clades (Figure 2.2), both of which sister to different South or Central American taxa. The first clade (sister to a Central American taxon) consists of some endemic Hawaiian and Marquesan taxa (“Hawaii clade A”). The second clade, sister to the South American species *P. coriocoensis*, consists of taxa from the greater Pacific, including some from mainland areas in Asia and Africa. Within this larger group, most accessions of the widespread taxon, *P. blanda* var. *floribunda*, form a strongly supported monophyletic group that was recovered as sister to a Caribbean species, *P. rubella*.

While species-level relationships within this second larger “Pacific” clade are less well supported, there is substantial support for some clades that appear to be biogeographically structured: the remaining endemic Hawaiian taxa (“Hawaii clade B”) and Fijian taxa respectively form well-supported groups. However, placement of taxa from Samoa, South Polynesia, Australia and New Zealand are not well defined in the tree and their relationship to other taxa do not have strong bootstrap support.

Species-level relationships within the two endemic Hawaiian clades (Hawaii clade A and Hawaii clade B) are not fully resolved. However, the two clades appear to be taxonomically coherent, with each clade containing assemblages of different endemic species.

Divergence time estimation

Rate-smoothed absolute time calibration using TreePL estimate a mid-Cretaceous split between *Peperomia* and *Piper* at approximately 90.7 million years ago (Mya), just below the maximum age constraint imposed. The crown divergence time of *Peperomia* was in the early Eocene, (ca. 54.2 Mya). In general, the age of clades in the Pacific were fairly young, with most of the lineages sampled originating in the Pliocene. Crown divergence times for the two endemic Hawaiian clades, Hawaii clade A and Hawaii clade B are approximately 3.9 Mya and 5.4 Mya respectively. However, the split between “Pacific” clades and mainland taxa are considerably older. Hawaii clade A shared a common ancestor with a Central American taxon approximately 6.0 Mya, whereas the second “Pacific” clade containing the rest of the Pacific taxa diverged from the lineage leading to *P. coriocoensis* approximately 14.3 Mya. *P. blanda* shared a common ancestor with sister taxon, *P. rubella*, approximately 11.8 Mya.

Discussion

Implications for Pacific biogeography

While interspecific relationships in the Pacific are not well-resolved, there is strong support for a Neotropical origin for taxa in the Pacific *Peperomia*. *P. tetraphylla* was recovered as sister to Neotropical taxa from the *Peperomia* subgenus *Pseudocupula* (*P. hoffmannii* and *P. puteolata*), corroborating other studies of phylogenetic relationships among subgenera in *Peperomia* (Wanke *et al.*, 2006; Frenzke *et al.*, 2015). Among the *Peperomia* subgenus *Micropiper*, both the greater “Pacific” clade and the “Hawaii clade A” were well-supported as sister groups to mainland South and Central American *Micropiper* species. Furthermore, nested within the larger “Pacific” clade, most of the accessions of *P. blanda* form a clade that was placed as a sister group to a Caribbean species, which suggests that *P. blanda* may even represent a separate colonization event. As such, the taxa of the Pacific appear represent at least three (to possibly four) colonization events out of the Neotropics, the first giving rise to Hawaii clade A, the second giving rise to the larger Pacific clade, with perhaps a separate colonization by *P. blanda*, and the last representing a separate colonization by a different subgenus entirely, *P. tetraphylla*, which is now widespread globally.

The Neotropics have acted as a substantial biogeographic source of global tropical species diversity (Antonelli *et al.*, 2015). This appears to be consistent with diversity of the genus being highest in the Neotropics but fairly depauperate in the Old World and Afrotropics. However, the directionality of dispersal out of the Neotropics remains unclear. A parsimonious hypothesis would be a westward colonization of the islands in the Pacific from tropical America, as opposed to a eastwards stepping stone pattern of dispersal through the Afrotropics, but I did not have sufficient sampling of African and South East Asian taxa to robustly test this hypothesis. A previous study of *Peperomia* biogeography also suggested a Neotropical origin, but could not rule out secondary dispersal from Africa due to limited sampling (Smith *et al.*, 2008). Furthermore, it is also possible that the taxa in the Pacific may be derived from both westward, as well as eastward dispersals from the Neotropics, that is, indirectly through Africa and the Paleotropics. Further sampling will likely elucidate a more coherent biogeographic history of the group at the global scale.

While there is some biogeographic structure in the phylogeny (e.g., Fiji, Hawaiian Islands), the lack of clear biogeographic structure among taxa from the rest of the Pacific suggest a highly complex history of dispersal. Endemic Marquesan taxa appear to be polyphyletic and represent multiple colonizations from other parts of the Pacific. Some endemic Marquesan taxa are derived from a colonization event from Hawaii, but other endemic Marquesan taxa have been placed in well-supported clades containing taxa from Samoa, the Societies, and Micronesia. This pattern of multiple colonizations is unlike most other endemic plant groups in the Marquesas (Hembry, 2018), with the exception of *Melicope* (Rutaceae) which may have colonized the Marquesas islands from Hawaii twice (Appelhans *et al.*, 2014). A similar pattern of multiple origins for the endemic *Peperomia* of the Society Islands is consistent with early phylogenetic work on the group in the Pacific (Bradley, 2002).

Overall, the observed pattern of long-distance dispersal and the assembly of Pacific island groups from dispersal of colonists from multiple biogeographic sources is perhaps unsurprising given the long-distance dispersal capabilities of the genus (Valdebenito *et al.*, 1992; Symmank *et al.*, 2011; Frenzke *et al.*, 2016). Dispersal of the fruits of *Peperomia* may be aided by the movement of migratory birds, as has been argued to be for many Hawaiian plant lineages such as the silverswords (Carlquist, 1980; Baldwin *et al.*, 1991) and mints (Lindqvist & Albert, 2002). However, the multiple origins of the endemic taxa on many of the archipelagoes included in our study suggest that long-distance dispersal may be especially frequent in the group. Other bird-dispersed groups such as *Coprosma* (Rubiaceae) (Cantley *et al.*, 2014, 2016) and *Melicope* (Rutaceae) (Harbaugh *et al.*, 2009; Appelhans *et al.*, 2014, 2018) have an equally complex pattern of dispersal in the Pacific, and some endozoochorous lineages like the *Coprosma* have undergone evolutionary changes in fruit colouration that may increase their appeal to birds (Cantley *et al.*, 2016). *Peperomia* species in the Pacific, on the other hand, produce fruits that are small and release sticky exudates, or in some taxa, possess hooked appendages (Frenzke *et al.*, 2015, 2016). These fruit characteristics, coupled with the epiphytic habit of many Pacific taxa, make them especially well adapted for epizoochorous long-distance dispersal by birds or volant mammals (Frenzke *et al.*, 2016).

Nonetheless, while a pattern of dispersal from multiple sources has played an important role in shaping patterns of diversity in the Pacific, our results also show that some island systems have played host to small *in situ* radiations. Taxa sampled in Fiji appear to be derived from a single ancestor (Figure 2.2), whereas the two major radiations of endemic Hawaiian taxa are derived from separate colonization events. The Fijian and Hawaiian Islands represent two large diversity hotspots in the Pacific, with 19 and 23 endemic species respectively, and the relatively large size of the islands in those archipelagoes (the largest islands of each archipelago, Viti Levu and the Big Island of Hawai'i are over 10,000 km² in size) may provide a wide range of habitats for ecological speciation (Hortal *et al.*, 2009) and opportunities for geographic isolation within individual islands.

Relationships among Hawaiian taxa

My results strongly support four separate colonization events to Hawaii: 1) *P. tetraphylla*, 2) *P. blanda* var. *floribunda*, 3) a colonist that gave rise to Hawaii clade A, and 4) a colonist that gave rise to Hawaii clade B. The four colonization events of *Peperomia* to the Hawaiian Islands represents the largest number of colonizations of any flowering plant genus to the archipelago (Howarth *et al.*, 2003; Keeley & Funk, 2011). The only other genera on the archipelago whose species are known to be derived from more than one colonization event that have been confirmed by molecular analyses include *Scaevola* (Howarth *et al.*, 2003), *Rubus* (Alice & Campbell, 1999; Howarth *et al.*, 1997), *Euphorbia* (Yang *et al.*, 2018), *Coprosma* (Cantley *et al.*, 2014, 2016), *Lysimachia* (Oh *et al.*, 2013; Yan *et al.*, 2018) and the sandalwoods, *Santalum* (Harbaugh & Baldwin, 2007).

Nonetheless, the *Peperomia* on Hawaii stands out among other genera derived from multiple colonization events in that two of the events have undergone significant diversification.

Hawaii clade A consists of seven endemic species whereas Hawaii clade B consists the remaining fifteen endemic species. The position of the presumably extinct, *P. degeneri* is not clear, but has been suggested to be closely allied to *P. latifolia* in clade B (Wagner *et al.*, 1999). Some variation notwithstanding, species in clade A are morphologically less robust and tend to have longer and thinner spikes, whereas species in clade B tend to be more robust with shorter, thicker spikes. This is somewhat surprising for the genus in general; there are many homoplasious characters and a lack of clear synapomorphies, even at the infrageneric level (Samain *et al.*, 2009). Nonetheless, morphological and ecological adaptations that may explain differences in diversity between the two clades are not apparent, although the older crown age for Hawaii clade B may suggest a longer time for species accumulation.

Hawaiian endemic *Peperomia* have been argued to represent a spectacular case of polyploidization with subsequent dysploidy, (Carr, 1998) with reported gametic chromosome numbers (n) of 22 among most endemic taxa (Skottsberg, 1955; Notoatmodjo, 1967), in contrast to the base number $n = 11$ for *P. blanda* (Bennett & Leitch, 2012) and other mainland taxa (Samuel & Morawetz, 1989; Jose *et al.*, 1994). However, our results suggest that the two endemic clades on Hawaii may be derived from two separate ancestors. Unfortunately, karyotype studies for other Pacific taxa are not known and so cannot be compared but patterns of further chromosomal evolution from the putatively ancestral $n = 22$ state appears to be partly support the two recovered Hawaiian endemic clades in our phylogenetic analysis. Gametic chromosome numbers for four of the seven endemic species (*P. membranacea*, *P. cookiana*, *P. kokeana*, *P. globulanthera*) in clade A have been reported to be $n = 44$, suggesting an additional polyploidization after colonization of the archipelago (Notoatmodjo, 1967). Patterns of chromosome numbers in Hawaii clade B appear less clear cut, with high levels of infraspecific variation in chromosome number in several taxa (Notoatmodjo, 1967).

Timing of diversification in the Pacific

Estimates of divergence times within the group suggest diversification of extant species in the Pacific to be fairly recent, with most speciation events occurring within the early-mid Pliocene (Figure 2.2). This pattern of diversification in the Miocene-Pliocene appears to be an increasingly consistent theme among other species-rich Pacific-wide plant radiations (e.g., *Coprosma* Cantley *et al.* 2016, *Melicope* Appelhans *et al.* 2018; *Cyrtandra*, Johnson *et al.* 2017), and seems to coincide with the oldest geologic ages of the current high islands in the Societies, Hawaii and Samoa (Neall & Trewick, 2008). One interpretation for the diversification for these groups is that their dispersal and diversification may have been promoted by the formation of the current islands.

The crown ages of both Hawaiian endemic clades are estimated to be a little younger than the oldest island of Kauai, and thus consistent with *in situ* diversification on the archipelago. The crown age of Hawaii clade B (5.4 Mya) is consistent with a Kauai colonization of the clade. The crown age of Hawaii clade A is substantially younger (3.9 Mya), but given the age of the split between Hawaii clade A and a Central American taxon dated to around 6.0 Mya, this does not preclude a Kauai colonization of the clade as well.

The estimated 10.8 Mya stem age of Hawaii clade B, however, predates the age of the oldest sub-aerial lavas sampled on the oldest high island of Kauai, at 6.3 Mya (Clague & Sherrod, 2014; Lim & Marshall, 2017). The old stem age may be partly due to the limited sampling of mainland taxa which may give rise to younger stem ages, but may also reflect changes in island availability and configuration over the past 5 - 10 Mya. Most Hawaiian lineages have crown ages that are younger than Kauai (Price & Clague, 2002; Keeley & Funk, 2011), but the current high islands are the product of a mantle plume which has also produced a more-or-less continuous chain of islands (many of which now submerged as sea mounts) throughout the Cenozoic. However, the islands that directly predated Kauai (between 8 - 5 Mya) rarely exceeded 1,000 metres in elevation and were relatively small, and so may have greatly restricted colonization of high-elevation lineages, as well as the diversification of resident lineages (Price & Clague, 2002). The pre-Kauai stem age of one of the Hawaiian *Peperomia* endemic clades may thus reflect a long history of diversification, pruned by extinction during a bottleneck in island sizes produced by the hotspots, followed by a second pulse of diversification as the current high islands were formed. This scenario is not unlikely given the high dispersal capacities and the ecological diversity within the group, and pre-Kauai colonizations have also been suggested for other plant groups such as the lobeliads (Givnish *et al.* 2009) or *Hillebrandia* (Clement *et al.*, 2004).

Ultimately, given the transience of islands over geologic time scales (Lim & Marshall, 2017), the timing of diversification of *Peperomia* in the Pacific likely reflects a history of opportunistic dispersal that is highly dependent upon the relative isolation, size and spatial configuration of source pools at any given time within the Pacific.

Appendix

Voucher information for all samples used in this study. Voucher data is in the following format: taxon name, study/extraction ID, geographic locality, collector and number, herbarium abbreviation (in parantheses), and any additional notes.

Macropiper puberulum Benth., PEZ-164, Samoa (Savaii), *D.Lorence 10610* (PTBG); ***Peperomia adamsonia*** Yunck., PEZ-298, Marquesas Islands (Hiva Oa), *K.R.Wood 17686* (PTBG); ***Peperomia alternifolia*** Yunck., JYL-42, Hawaiian Islands (Maui), *J.Lim 42* (UC); ***Peperomia bellendkerensis*** Domin, PEZ-297, Australia, *E.M.Joyce 3* (CNS); ***Peperomia blanda*** (Jacq.) Kunth, PEZ-265, China (Guangxi), *Li J.-M. 6262* (PE), PEZ-248, Madagascar, *Bernard 1497* (MO), PEZ-249, Madagascar, *Rakotonirina 1133* (MO); ***Peperomia blanda var. floribunda*** (Miq.) H.Hüber, JYL-38, Hawaiian Islands (Maui), *J.Lim 38* (UC), JYL-51, Hawaiian Islands (Kauai), *J.Lim 51* (UC), PEZ-192, Hawaiian Islands (Kauai), *K.R.Wood 14893* (PTBG), PEZ-215, Marquesas Islands (Ua Poa), *D.Lorence 9111* (PTBG), PEZ-223, Hawaiian Islands (Oahu), *Togikawa s.n.*, cultivated at UC Botanical Garden, garden no. 2018.0532, PEZ-292, Australia, *R.Jensen 1985* (BRI, CNS); ***Peperomia cf. blanda var. floribunda*** (Miq.) H.Hüber, PEZ-290, Marque-

sas Islands (Nuku Hiva), *J.-Y. Meyer* 3316 (PAP); *Peperomia boninsimensis* Makino, PEZ-302, Japan (Bonin Islands), voucher of cultivated specimen at Koishikawa Botanical Gardens (TI) *Peperomia caledonica* C. DC., PEZ-250, New Caldeonia, *McPherson* 18208 (MO); *Peperomia congesta* Kunth, PEZ-172, Colombia, *P.C. Hutchinson & J.K. Wright* 6593 (UC), voucher of cultivated specimen at UC Botanical Garden, garden no. 64.0869; *Peperomia cookiana* C. DC., JYL-33, Hawaiian Islands (Maui), *J.Lim* 33 (UC), JYL-45, Hawaiian Islands (Maui), *J.Lim* 45 (UC), JYL-49, Hawaiian Islands (Maui), *J.Lim* 49 (UC), JYL-71, Hawaiian Islands (Oahu), *J.Lim* 71 (UC, BISH), PEZ-190, Hawaiian Islands (Kauai), *K.R. Wood* 15989 (PTBG), PEZ-191, Hawaiian Islands (Kauai), *K.R. Wood* 15597 (PTBG); *Peperomia coroicoensis* Yunck., PEZ-251, Bolivia, *Araujo* 2129 (MO); *Peperomia eekana* C. DC., PEZ-198, Hawaiian Islands (Maui), *K.R. Wood* 15059 (PTBG); *Peperomia ellipticibacca* C. DC., JYL-61, Hawaiian Islands (Oahu), *J.Lim* 61 (UC, BISH); *Peperomia enervis* F. Muell., PEZ-295, Australia, *E.M. Joyce* 5 (CNS), PEZ-296, Australia, *E.M. Joyce* 6 (CNS); *Peperomia expallescens* C. DC., PEZ-202, Hawaiian Islands (Maui), *K.R. Wood* 11493 (PTBG); *Peperomia fernandopoiana* C. DC., PEZ-253, Madagascar, *Razoazanany* 97 (MO); *Peperomia glabella* (Sw.) A. Dietr., PEZ-254, Nicaragua, *Stevens* 34572 (MO); *Peperomia glassmanii* Yunck., PEZ-096, PEZ-200, Micronesia (Pohnpei), *K.R. Wood* 13516 (PTBG), PEZ-210, Micronesia (Pohnpei), *S. Perlman* 21454 (PTBG) *Peperomia globulanthera* C. DC., PEZ-184, Hawaiian Islands (Maui), *H. Oppenheimer* H101610 (US); *Peperomia grantii* Yunck., PEZ-106, Society Islands (Tahiti), *J.-F. Butaud* 2975 (PAP), PEZ-285, Society Islands (Tahiti), *J.-Y. Meyer* 3311 (PAP); *Peperomia graveolens* Rauh & Barthlott, PEZ-179, Ecuador, original collector not known, no voucher made due to lack of flowering material, sample from cultivated specimen at UC Botanical Garden, garden no. 83.1092; *Peperomia hesperomannii* Wawra, JYL-56, Hawaiian Islands (Kauai), *J.Lim* 56 (UC), PEZ-222, Hawaiian Islands (Kauai), *K.R. Wood* 17406 (PTBG); *Peperomia hirtipetiola* C. DC., PEZ-189, Hawaiian Islands (Maui), *K.R. Wood* 13486 (PTBG), PEZ-205, Hawaiian Islands (Maui), *K.R. Wood* 15929 (PTBG), PEZ-221, Hawaiian Islands (Maui), *K.R. Wood* 16702 (PTBG); *Peperomia hoffmannii* C. DC., PEZ-183, Costa Rica, original collector not known, voucher of cultivated specimen at UC Botanical Garden in UC, garden no. 52.1319; *Peperomia hombronii* C. DC., PEZ-108, Society Islands (Tahiti), *J.-F. Butaud* 2977 (PAP) *Peperomia hunteriana* P.I.Forst, PEZ-293, Australia, *C. Costion* 2263 (CNS); *Peperomia hypoleuca* Miq., PEZ-098, PEZ-136, PEZ-201, Hawaiian Islands (Hawaii), *K.R. Wood* 12425 (PTBG), PEZ-148, Hawaiian Islands (Hawaii), *W.L. Wagner* 5975 (US); *Peperomia kiphuluensis* H.St. John & Lamoureux, PEZ-185, Hawaiian Islands (Maui), *H. Oppenheimer* H101606 (US), PEZ-194, Hawaiian Islands (Maui), *K.R. Wood* 15607 (PTBG); *Peperomia kokeana* Yunck., PEZ-197, Hawaiian Islands (Kauai), *K.R. Wood* 15158 (PTBG); *Peperomia latifolia* Miq., JYL-41, Hawaiian Islands (Maui), *J.Lim* 41 (UC), JYL-44, Hawaiian Islands (Maui), *J.Lim* 44 (UC), PEZ-214, Hawaiian Islands (Kauai), *K.R. Wood* 17442 (PTBG), PEZ-219, Hawaiian Islands (Kauai), *K.R. Wood* 17396 (PTBG); *Peperomia ligustrina* Hillebr., PEZ-224, Hawaiian Islands (Maui), *H. Oppenheimer* H51703 (US); *Peperomia macraeana* C. DC., JYL-50, Hawaiian Islands (Maui), *J.Lim* 50 (UC), JYL-59, Hawaiian Islands (Oahu), *J.Lim*

59 (UC), JYL-68, Hawaiian Islands (Oahu), *J.Lim 68* (UC, BISH), JYL-70, Hawaiian Islands (Oahu), *J.Lim 70* (UC, BISH); ***Peperomia mauiensis*** Wawra., JYL-37, Hawaiian Islands (Maui), *J.Lim 37* (UC), JYL-39, Hawaiian Islands (Maui), *J.Lim 39* (UC); ***Peperomia membranacea*** Hook. & Arn., JYL-31, Hawaiian Islands (Maui), *J.Lim 31* (UC), JYL-67, Hawaiian Islands (Maui), *J.Lim 67* (UC), JYL-73, Hawaiian Islands (Oahu), no voucher due to lack of flowering material, cultivated at UC Botanical Garden, garden no. 2018.0559, PEZ-193, Hawaiian Islands (Kauai), *K.R. Wood 15391* (PTBG), PEZ-211, Hawaiian Islands (Kauai), *K.R. Wood 17457* (PTBG); ***Peperomia oahuensis*** C. DC., JYL-53, Hawaiian Islands (Kauai), *J.Lim 53* (UC), PEZ-196, Hawaiian Islands (Kauai), *K.R. Wood 15757* (PTBG); ***Peperomia obovatilimba*** C. DC., JYL-3, Hawaiian Islands (Hawaii), *J.Lim 3* (UC), PEZ-186, Hawaiian Islands (Maui), *H.Oppenheimer H101604* (US), PEZ-187, Hawaiian Islands (Maui), *H.Oppenheimer H101609* (US); ***Peperomia cf. oliveri*** J.Florence & W.L.Wagner, PEZ-287, Marquesas Islands (Nuku Hiva), *J.-Y.Meyer 3313* (PAP), PEZ-289, Marquesas Islands (Nuku Hiva), *J.-Y.Meyer 3315* (PAP); ***Peperomia palauensis*** C. DC., PEZ-102, Micronesia (Palau, Mecherchar), *S.Perlman 20851* (PTBG); ***Peperomia pallida*** A.Dietr., PEZ-212, Marquesas Islands (Ua Huka), *K.R. Wood 10499* (PTBG), PEZ-218, Marquesas Islands (Ua Poa), *K.R. Wood 10457* (PTBG); ***Peperomia cf. pallida*** A.Dietr., PEZ-291, Society Islands (Tahiti), *J.-Y.Meyer 3317* (PAP); ***Peperomia ponapensis*** C. DC., Micronesia (Kosrae), *K.R. Wood 14780* (PTBG); ***Peperomia puteolata*** Trel., PEZ-174, Peru, *Bennett 0462A* (UC), sample from specimen cultivated at UC Botanical Garden, garden no. 65.0663; ***Peperomia reineckei*** C. DC., PEZ-163, Samoa (Savaii), *D.Lorence 10596* (PTBG), PEZ-165, Samoa (Savaii), *D.Lorence 10618* (PTBG), PEZ-169, Samoa (Savaii), *K.R. Wood 16951* (PTBG), PEZ-170, Samoa (Upolu), *K.R. Wood 16900* (PTBG); ***Peperomia remyi*** C. DC., JYL-40, Hawaiian Islands (Maui), *J.Lim 40* (UC), PEZ-206, Hawaiian Islands (Kauai), *K.R. Wood 16535* (PTBG); ***Peperomia rockii*** C. DC., PEZ-203, Hawaiian Islands (Molokai), *K.R. Wood 10607* (PTBG); ***Peperomia cf. rubella*** Hook., PEZ-304, from cultivated specimen on Maui, *H.Oppenheimer H101701* (US); ***Peperomia samoensis*** Warb., PEZ-162, Samoa (Savaii), *D.Lorence 10614* (PTBG), PEZ-168, Samoa (Upolu), *K.R. Wood 16922* (PTBG); ***Peperomia sandwicensis*** Miq., JYL-55, Hawaiian Islands (Kauai), *J.Lim 55* (UC), PEZ-208, Hawaiian Islands (Kauai), *K.R. Wood 17428* (PTBG); ***Peperomia savaiiensis*** Whistler, PEZ-166, Samoa (Savaii), *D.Lorence 10619* (PTBG); ***Peperomia skottsbergii*** C. DC. ex Skotts., PEZ-239, Juan Fernandez Islands, *JBN 1043* (JBN), original collector not known, voucher made of cultivated specimen; ***Peperomia societatis*** J.W.Moore, PEZ-105, Society Islands (Moorea), *J.-F.Butaud 2973* (PAP), PEZ-107, Society Islands (Tahiti), *J.-F.Butaud 2951* (PAP); ***Peperomia subpetiolata*** Yunck., PEZ-226, Hawaiian Islands (Maui), *H.Oppenheimer H41611* (US), PEZ-228, Hawaiian Islands (Maui), *H.Oppenheimer H41613* (US); ***Peperomia tetraphylla*** (G.Forst.) Hook. & Arn., JYL-36, Hawaiian Islands (Maui), *J.Lim 36* (UC), JYL-74, Hawaiian Islands (Oahu), *J.Lim 74* (UC), PEZ-213, Hawaiian Islands (Kauai), *K.R. Wood 17434* (PTBG), PEZ-267, South Africa, *J.S.Burrows 8924* (MO), PEZ-284, Society Islands (Tahiti), *J.-Y. Meyer 3310* (PAP), PEZ-294, Australia, *R.Jensen 2020* (CNS); ***Peperomia cf. tooviiana*** J.Florence, Marquesas Islands (Nuku Hiva), *J.-Y.Meyer 3314*

(PAP); *Peperomia urvilleana* A.Rich., PEZ-177, New Zealand (North Island), *Sauceda s.n.* (UC), horticultural voucher of specimen cultivated at UC Botanical Garden, garden no. 92.0332; *Peperomia sp.*, PEZ-180, Mexico, *Bartholomew 926*, no voucher due to lack of flowering material in propagated plants, cultivated at UC Botanical Garden, garden no. 81.0942; *Peperomia sp.*, PEZ-246, New Caledonia, *Lowry 5617* (MO); *Peperomia sp.*, PEZ-269, New Caledonia, *J.Munzinger 6537* (MO); *Peperomia sp.*, PEZ-272, Fiji (Taveuni), *S.Pene 003* (USP); *Peperomia sp.*, PEZ-273, Fiji (Taveuni), *S.Pene 020* (USP); *Peperomia sp.*, PEZ-275, Fiji (Taveuni), *S.Pene 047* (USP); *Peperomia sp.*, PEZ-276, Fiji (Taveuni), *S.Pene 055* (USP); *Peperomia sp.*, PEZ-278, Fiji (Taveuni), *S.Pene 061* (USP); *Peperomia sp.*, PEZ-280, Fiji (Taveuni), *S.Pene 081* (USP); *Peperomia sp.*, PEZ-281, Fiji (Taveuni), *S.Pene 082* (USP); *Peperomia sp.*, PEZ-282, Fiji (Taveuni), *S.Pene 085* (USP); *Peperomia sp.*, PEZ-283, Fiji (Taveuni), *S.Pene 087* (USP); *Piper ponapense* C. DC., PEZ-204, Micronesia (Pohnpei), *K.R.Wood 13509* (PTBG); *Piper sp.*, PEZ-247, New Caledonia, *McPherson 19040* (MO).

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Chapter 3

The role of climatic niche evolution in driving speciation in the Hawaiian flora

Introduction

The factors driving the interplay between climatic niche evolution and speciation remain a big question in evolutionary biology and ecology (Wiens, 2004; Wiens & Graham, 2005; Ackerly *et al.*, 2006; Kozak & Wiens, 2006; Pyron *et al.*, 2014; Jezkova & Wiens, 2018). Niche conservatism, the tendency for lineages to retain ancestral ecological characteristics through time, has been argued to be an important mechanism by which ecology may drive speciation (Pyron *et al.*, 2014). Specifically, because the probability of colonization of novel habitats by individuals of a species may be dependent upon the degree to which individuals are already pre-adapted to the climatic conditions of the receiving area, it has been hypothesized that climatic niche or habitat preferences may have a strong influence in constraining patterns of dispersal and subsequent reproductive isolation and speciation. As a consequence, lineages undergoing divergence in allopatry may be expected to be more similar in climatic niche. On the other hand, it has been argued that local climatic adaptation and subsequent selective pressure against immigrants (Rundle & Nosil, 2005; Nosil, 2012) can be a major driver of genetic divergence within populations in climatically heterogeneous environments (e.g., "isolation by environment"; Sexton *et al.* 2014; Papadopoulos *et al.* 2014; Wang *et al.* 2013) and give rise to ecological speciation in sympatry. In this scenario, one may expect lineages originating in sympatry to be more dissimilar in climatic niches.

Both climatic niche conservatism and divergence in speciation likely operate simultaneously, but their relative importance in driving the contrasting modes of speciation remains unclear (Pyron *et al.*, 2014; Pitteloud *et al.*, 2017; Jezkova & Wiens, 2018). Nonetheless, the relative degree to which climatic niche conservatism and divergence in shaping the evolutionary and biogeographic history of regional biotas will necessarily depend upon the spatial

scale, the propensity of different lineages for climatic niche differentiation, and the relative accessibility of different habitats (Donoghue & Edwards, 2014).

Oceanic islands such as the Hawaiian Islands are ideal model systems to examine the role of niche evolution in shaping the diversification of the flora across the archipelago (Price & Wagner, 2004). The Hawaiian Islands play host to one of the most unique floras in the world, with over 90% of its angiosperm flora found nowhere else. Due to its physical isolation (approx. 3,800 km from the closest continent), the Hawaiian flora has been assembled entirely from long-distance dispersal and subsequent diversification of colonist lineages (Fosberg, 1948; Wagner *et al.*, 1999; Baldwin & Wagner, 2010). This allows us to evaluate the role of niche evolution in speciation modes, in a consistent spatial temporal framework (Warren *et al.*, 2015). Furthermore, owing to their large range in size, elevation, geologic age, as well as the influence of island topography on local-scale climate, the Hawaiian islands possess an incredible range of habitats, from lowland dry forests, wet forests, to alpine deserts (Ziegler, 2002). This habitat diversity has been long argued to be a catalyst for the diversification of the flora (Carlquist, 1980), and is a major correlate of diversity across many island systems (Hortal *et al.*, 2009). In fact, many lineages on Hawaii appear to have ecologically diversified across multiple climatic zones (Wagner & Funk, 1995).

Nevertheless, while habitat shifts are often argued to be important in the diversification of Hawaiian lineages owing to the observed ecological diversity within multiple lineages, most studies have either not examined this within a phylogenetically explicit framework, or have only focused on single lineages (Wagner & Funk 1995; Givnish *et al.* 2009; Havran *et al.* 2009; Hobbs & Baldwin 2013). However, some regional-scale studies have shed some insight Price & Wagner 2004; Garcia-Verdugo *et al.* 2014; Steinbauer *et al.* 2016a. Price & Wagner (2004) in the most recent and comprehensive biogeographic study of the entire Hawaiian flora found that the vast majority of allopatric sister species pairs shared the same climatic zone / habitat, whereas sympatric species were about equally likely to occur in the same habitat or different habitats. Lineage-specific differences that may explain patterns of niche evolution among sympatric and allopatric lineages, however, remain unclear. To better understand the role of niche evolution / habitat shifts in speciation, we collate a large phylogenetic dataset of eight of the most species-rich radiations on the Hawaiian archipelago, and use probabilistic biogeographic models to infer modes of speciation throughout their diversification history. If niche conservatism is a dominant force driving speciation among Hawaiian plant lineages, one should expect lineages that diverged in allopatry to exhibit low niche evolution relative to lineages that diverged in sympatry.

Materials and Methods

Hawaiian plant lineages

I identified eight Hawaiian plant lineages that were derived from single colonization events to the Hawaiian archipelago, and represent evolutionary radiations of at least five species (Table

3.1). However, it is also worth noting that several of the most speciose Hawaiian lineages were not included due to the lack of molecular data (e.g., *Myrsine*, *Lipochaeta/Melanthera*) or, where molecular data was available, a lack of sampling within the lineage (e.g., the Hawaiian mints Lindqvist & Albert 2002; lobeliads Givnish *et al.* 2009).

DNA sequences for each species from all lineages were downloaded from the NCBI Genbank database using the program, ‘sumac’ (Freyman, 2015), which uses hierarchical clustering algorithms to identify orthologous sequences and MAFFT (Kato & Toh, 2008) to generate multiple sequence alignments of identified clusters. To ensure the robustness of this pipeline, ‘sumac’ searches were performed using an iterative process by both running it unconstrained and using guide sequences obtained from recently published studies of the respective Hawaiian lineages (see Table 3.1 for references).

Phylogenetic inference and time calibration

For each lineage, we performed a partitioned Bayesian phylogenetic analysis under a GTR substitution model and among-site rate variation modelled using a discretized gamma distribution (Yang, 1994) with four rate categories. I specified a birth-death tree prior (Rannala & Yang, 1996), with a log-normal prior distribution on diversification rates (i.e., birth minus death) with a mean equaling to $\log(\log(S)/t)$, where S is the number of species in the clade and t the crown age of the clade. This corresponds to the expected rate for a constant-rate diversification process to produce the observed number of species (S) given the time for diversification (t). Relative death rate was assumed to be a uniform distribution between 0 and 1.

Prior distributions on the root age (t) for each lineage were obtained from the literature where possible. For silverswords, the root age was assumed to be normally distributed about 3.5 million years ago (Mya), with a standard deviation of 1.5, following the posterior distribution of crown ages obtained through a joint biogeographic and phylogenetic study by Landis *et al.* (2018). For *Pritchardia*, we used a normal distribution with mean (Bacon *et al.*, 2012a). For all other lineages, we used a normal distribution with mean of 6.0 ± 0.5 and a maximum age of 6.3 Mya to reflect the most recent and oldest estimate of the origin of Kauai respectively, the oldest of the current high islands (Lim & Marshall, 2017).

Monte Carlo Markov Chain (MCMC) analyses were performed in *RevBayes* (Höhna *et al.*, 2016) and run for 100,000 iterations, with the first 20,000 iterations as burn-in and a move tuning interval every 200 iterations during the burn-in phase. Convergence was evaluated by ensuring each parameter had an effective sample size over 200. Trees and other parameters were sampled every 100 iterations, and the maximum *a posteriori* tree for each lineage calculated for further analyses.

Determining the geographic context of speciation events

Geographic context for each cladogenetic (i.e., speciation) event was determined by inferring ancestral ranges using probabilistic biogeographic models, namely the dispersal, extirpation

Table 3.1: Empirical data sets for Hawaiian plant lineages analyzed

Lineage	Number of species / Species coverage	Phylogenetic markers	Total length (bp)	alignment	References
Silverswords	30 / 26	<i>ITS</i>	735		Baldwin 1992; Baldwin & Robichaux 1995; Friar <i>et al.</i> 2008
<i>Psychotria</i>	11 / 11	<i>ITS, ETS</i>	1,469		Nepokroeff <i>et al.</i> 2003a; Barrabé <i>et al.</i> 2014
<i>Melicope</i> + <i>Platydesma</i>	51 / 40	<i>NIA</i> intron, <i>psbA-trnH</i> spacer, <i>At103</i> , <i>ITS, ETS, MS, trnL-trnF</i> spacer	3,133		Harbaugh <i>et al.</i> 2009; Appelhans <i>et al.</i> 2014
<i>Cyrtandra</i>	57 / 37	<i>ITS, ETS, TC1P, psbA-trnH, trnL</i>	3,604		Clark <i>et al.</i> 2008, 2009; Johnson <i>et al.</i> 2017
<i>Pritchardia</i>	21 / 20	<i>CISP4, RPB2, matK, ndhF</i> gene, <i>trnD-trnT</i> spacers, <i>MS</i>	6,873		Bacon <i>et al.</i> 2012b
<i>Schiedea</i>	31 / 30	<i>GS, petL-psbE</i> spacer, <i>PepC, trnK-matK, trnQ-rps16</i> spacer, <i>petN-psbM, rps16, NIA</i> intron, <i>psbM-trnD, trnT-trnE-trnY, ETS, ITS</i>	11,642		Kapralov & Filatov 2006; Wallace <i>et al.</i> 2009; Willyard <i>et al.</i> 2011; Wallace <i>et al.</i> 2011
<i>Viola</i>	7 / 7	<i>ITS</i>	486		Havran <i>et al.</i> 2009
<i>Kadua</i>	21 / 15	<i>ITS, trnL-trnF</i> spacer, <i>rps16</i> intron	3,002		Church 2003; Kårehed <i>et al.</i> 2008; Groeninckx <i>et al.</i> 2009

and cladogenetic model (DEC)(Ree *et al.*, 2005; Ree & Smith, 2008; Matzke, 2014). DEC models consider changes in geographic range within lineages (anagenetic changes), as well as changes in geographic ranges associated with speciation events (cladogenetic changes) within a maximum likelihood framework. I fit both DEC and DEC+J (an extension of the DEC model that allows for jump speciation cladogenetic events; Matzke 2014) models to maximum *a posteriori* time-calibrated trees and the observed geographic range for each species across the current high islands of the Hawaiian archipelago (Wagner *et al.*, 1999, 2005, 2012): Hawai'i, Maui, Oahu and Kaua'i. Species that occur on the islands of Kaho'olawe, Lana'i and Moloka'i are considered to occur on Maui, as the afore-mentioned islands were once connected to Maui as part of a much larger island for most of its geologic history (Price & Elliott-Fisk, 2004). Only species that are found on the current high islands were included in our biogeographic analysis.

To account for changes in island availability through time, we fit 'epochal' DEC and DEC+J models (Ree & Smith, 2008) which allow for different dispersal probabilities among islands to vary among preset time windows. The oldest geologic age of the subaerial lavas (Clague & Sherrod, 2014) for each island to constrain the earliest possible time of colonization for each island (Lim & Marshall, 2017) and were used to delimit 'epochs'. DEC and DEC+J models were implemented using the R package, *BioGeoBears* (Matzke, 2014).

The geographic state for each daughter lineage after cladogenesis with the highest marginal likelihood was used to classify each node on each phylogeny as being either an "allopatric" or "sympatric" cladogenetic event. Here, we define "sympatric" speciation as a cladogenetic event where resulting sister lineages overlap in their geographic distribution, in contrast to allopatric events which result in sister lineages that do not overlap in their range. I also applied a less stringent definition of allopatry where we included peripatric speciation, a scenario in which one daughter lineage diverges within just one island of a much larger ancestral range (i.e., subset-sympatry *sensu* Matzke 2014).

Estimating rates of niche evolution

One of the largest factors driving broad scale differences in vegetation and taxonomic composition on the Hawaiian islands is precipitation (Gagné & Cuddihy, 1999). Early work characterizing the moisture regime of plant communities on Hawaii, divide the vegetation into three broad categories: wet (> 2500 mm precipitation), mesic (1200 - 2500 mm) and dry (< 1200 mm precipitation) (Gagné & Cuddihy, 1999). However, Gagné & Cuddihy (1999) do not consider other factors (e.g., substrate) in driving water balance in communities. Here, as a proxy for one climatic niche dimension, we use the seven moisture categories of Price *et al.* (2012), which uses an integrated measure of moisture availability that takes into account both precipitation and potential evapotranspiration. Species were scored based on their presence in any of the seven moisture zone categories, including the wettest (maximum) and driest (minimum) zones where they are thought to occur naturally (Figure 3.1). The mean moisture score for each species was taken to be the midpoint between their minimum and maximum moisture scores.

To quantify differences in rates of niche evolution between modes of speciation, we calculated phylogenetic independent contrasts (Felsenstein, 1985) for minimum, mean and maximum moisture categories for each lineage. Three coastal species were removed from our analysis as coastal habitats represent distinct habitats and could not be easily assigned to any moisture category following Price (2004).

I used linear mixed effect models to test whether rates of niche evolution (absolute values of phylogenetic independent contrasts) were different between “allopatric” and “sympatric” speciation modes. To account for lineage-specific differences in rates of niche evolution, we specified lineage as a random effect on the intercept. Linear mixed-effect models were implemented using the R package, *lme4* v1.1-17. To more closely evaluate lineage-level relationships between speciation mode and rates of niche evolution, I also fitted linear models to each lineage separately.

Results

Geographic context of speciation among Hawaiian lineages

In general, sympatry was the predominant speciation mode inferred under both the DEC and DEC+J models implemented in BioGeoBears (Matzke, 2014). Under the strict definition of allopatry, the DEC model inferred a total of 24 allopatric and 146 sympatric cladogenetic events. A greater number of allopatric events was inferred using a DEC+J, relative to the DEC model (52 allopatric and 118 sympatry events)(Table 3.2; Figure 3.2).

However, there was substantial variation in speciation modes among the Hawaiian lineages examined. For example, most speciation within silverswords was consistent with a sympatric mode, whereas most speciation within *Viola* and *Kadua* appear to be associated with allopatric events (Table 3.2; Figure 3.2).

Table 3.2: Number of allopatric and sympatric cladogenetic events for each plant lineage under both strict and relaxed definitions inferred under best-fit DEC and DEC+J models. Under the strict definition, only vicariant and jump speciation events are considered as allopatric events. The relaxed definition includes peripatric speciation (“subset-sympatric”) as allopatric events.

Model	DEC				DEC+J			
	Strict		Relaxed		Strict		Relaxed	
	Sympatric	Allopatric	Sympatric	Allopatric	Sympatric	Allopatric	Sympatric	Allopatric
<i>Cyrtandra</i>	32	4	31	5	22	14	22	14
<i>Kadua</i>	11	1	7	5	5	7	3	9
<i>Melicope + Platydesma</i>	32	7	29	10	30	9	27	12
<i>Pritchardia</i>	13	4	10	7	12	5	12	5
<i>Psychotria</i>	9	1	6	4	7	3	7	3
<i>Schiedea</i>	21	4	18	7	17	8	17	8
Silverswords	24	1	23	2	24	1	23	2
<i>Viola</i>	4	2	4	2	1	5	1	5
Total	146	24	128	42	118	52	112	58

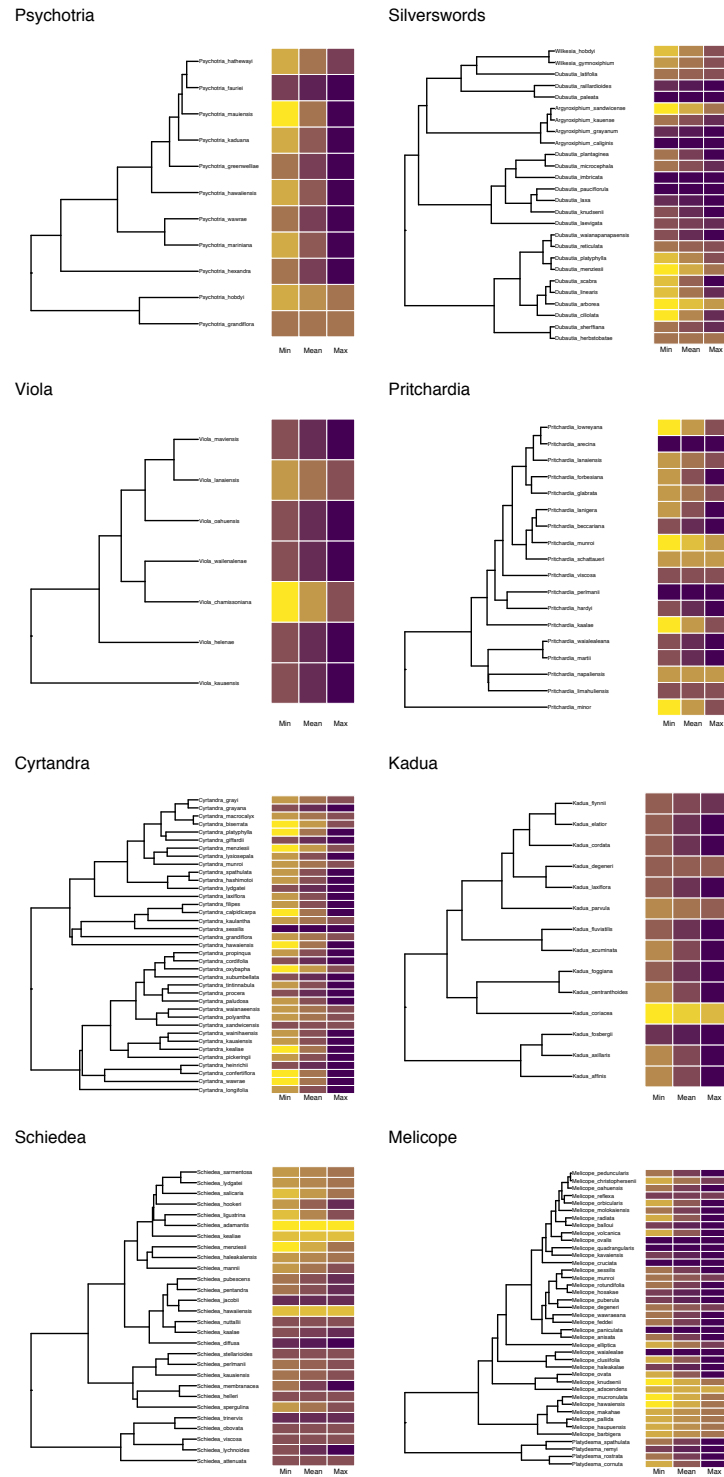


Figure 3.1: Bayesian maximum a posteriori trees for the eight Hawaiian plant lineages with mapped (minimum, mean and maximum) moisture categories.

Rates of niche evolution and mode of speciation

Sister lineages that originated from allopatric speciation events were neither associated with greater nor lower rates of niche evolution compared to sister lineages derived from sympatric cladogenetic events in our full model (Table 3.3). The effect of geographic mode of niche evolution was statistically insignificant under different biogeographic models (Table 3.3) or a relaxed definition of allopatry (results not shown). However, effect sizes tend to be negative when biogeographic events were estimated using a DEC+J model.

When lineages were analyzed separately, there is substantial variation in the effect size and the direction of effect among lineages. Mode of speciation does not appear to explain patterns of niche divergence in general, but there are some notable exceptions. In particular, under a relaxed definition and biogeographic events estimated using the DEC model, allopatric lineages of *Kadua* are associated with lower rates of niche divergence in maximum moisture preference ($p = 0.03$), whereas allopatric lineages of *Schiedea* are associated with higher rates of niche divergence in maximum moisture preference ($p = 0.04$).

Table 3.3: Effect size (and standard errors) of the effect of speciation mode on rate of niche evolution under linear mixed effect models, under a strict definition of allopatry

Variable	DEC				DEC+J			
	Effect size	df	t	p-value	Effect sizes	df	t	p-value
Mean moisture	0.119 ± 0.247	164.5	0.483	0.63	-0.061 ± 0.193	168	-0.3162	0.75
Min moisture	0.226 ± 0.303	165	0.746	0.46	-0.090 ± 0.237	167.7	-0.3812	0.70
Max moisture	0.126 ± 0.247	164.5	0.512	0.61	-0.033 ± 0.193	168	-0.1708	0.86

Discussion

Niche evolution and mode of speciation

Climatic niche conservatism has been hypothesized to explain biogeographic and macroecological patterns at various spatial scales, from patterns of species diversity at global scales (Wiens & Donoghue, 2004), continental-scale biogeographic disjunctions driven by paleoclimatic trends (Mairal *et al.*, 2017), patterns of intercontinental dispersal (Crisp *et al.*, 2009), and the assembly of endemic montane biotas at regional spatial scales (Merckx *et al.*, 2015; Steinbauer *et al.*, 2016b).

In general, we find that rates of niche evolution are not strongly correlated with speciation mode among Hawaiian plant lineages analyzed. Furthermore, across multiple studies, evidence for a general relationship between niche evolution and the geographic context of speciation has been equivocal. For example, Pitteloud *et al.* (2017) found that sister species of *Pyrgus* butterflies that diverged in sympatry were associated with higher rates of climatic niche evolution compared to lineages in allopatry. This suggests a role of niche conservatism

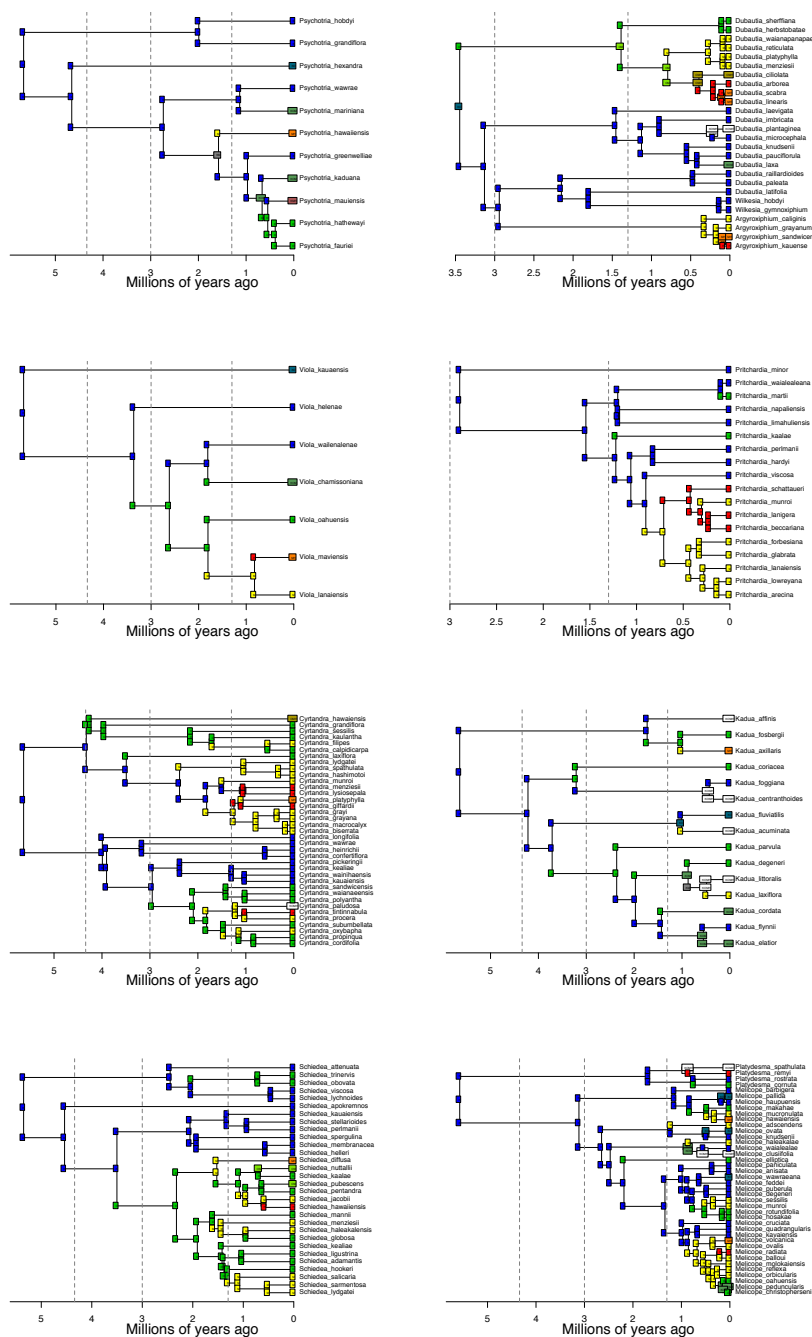


Figure 3.2: Inferred biogeographic histories of Hawaiian plant lineages under the best-fit DEC+J model. Labels on internal nodes represent geographic states with the largest marginal likelihoods, whereas the labels on branches arising from each internal node represent the most likely geographic state of descendant sister lineages immediately after each cladogenetic event. Vertical dotted lines represent the emergence times of the islands of Oahu (4.34 Mya), Maui (3 Mya) and Hawai'i (1.3 Mya) that were used to constrain biogeographic models.

in driving allopatric speciation (Wiens, 2004; Pyron *et al.*, 2014), where populations tracking their preferred climate may get isolated by dispersal to habitats to which individuals are pre-adapted, and are subsequently isolated by intervening non-climatically suitable habitat. On the other hand, local climatic adaptation within a population's range may generate the genetic divergence necessary for ecological speciation in sympatry (Nosil, 2012), giving rise to higher observed rates of climatic niche evolution between sympatric lineages. In contrast, Jezkova & Wiens (2018), in an analysis of 49 allopatric sister species pairs of squamate reptiles, showed that the majority of allopatric sister pairs were associated with higher degrees of climatic niche divergence than expected, contrary to the expectation that niche conservatism may be driving speciation. They argue that while niche conservatism may sometimes drive allopatry in and of itself, climatic divergence may also promote speciation in lineages that were first allopatrically isolated by non-climatic factors.

My results also contrast with previous findings of speciation modes in the Hawaiian flora. Price & Wagner (2004) analyzed 52 sister species pairs and found that the majority of species pairs were sympatric, in line with our results, but also found that the vast majority of allopatric species pairs occurred in the same habitat, whereas sympatric species pairs were only slightly more likely to co-occur in the same habitats. My analysis, however, differs from Price & Wagner (2004) and many others studying the role of niche divergence in speciation (Kozak & Wiens, 2006; Jezkova & Wiens, 2018) in a number of important ways. Firstly, the observed sympatry or allopatry among species pairs may have occurred through secondary range expansion or contraction after divergence and so may not always reflect modes of speciation. However, our biogeographic modelling approach accounts for the possibility of post-speciational changes in biogeographic range. This is because the DEC-type models model dispersal as continuous-time Markov Chain process and thus explicitly accounts for changes in geographic range along branches (see Figure 3.2 for some inferred examples), allowing us to evaluate the most likely geographic states at the base of each branch immediately after each speciation event. Secondly, the phylogenetic independent contrast approach (Felsenstein, 1985) allowed us to control for differences in magnitude of niche shift due to the time of divergence between lineages, with the caveat that niche evolution is assumed to be approximated by a Brownian motion model. Thirdly, we consider all cladogenetic events in the history of target lineages instead of sister species pairs.

Nonetheless, we find large differences in the role of niche evolution and speciation mode among the plant lineages examined. A stark example is the fact that *Kadua* and *Schiedea* showed significant but opposing relationships between geographic mode and patterns of niche divergence. Allopatric lineages of *Kadua* appear to be associated with lower rates of niche divergence compared to lineages originating in sympatry, but allopatric lineages of *Schiedea* appear to be associated with higher rates of niche divergence.

Species of *Schiedea* on Hawaii occupy dry to mesic habitats, whereas *Kadua* tends to occur across mesic-wet habitats, suggesting that the importance of niche evolution in speciation may be context-specific, depending on differences in the niche lability of lineages that specialize in low drylands compared to wetter montane areas, the relative connectivity of the these habitats, and differences in dispersal ability between lineages. Low-elevation dry

habitats are geographically more extensive and form a large continuous band around each of the islands, whereas wetter montane habitats are more geographically isolated to the tops of volcanic shields. My results thus suggest that montane taxa like *Kadua* may be more likely to be isolated allopatrically due to niche conservatism, whereas taxa from drier lowlands (e.g., *Schiedea*) may be more likely to diverge climatically to occupy upland habitats. This pattern is similar to some continental montane systems, where high-elevation assemblages are reported to be pre-dominantly derived from immigration of pre-adapted montane species (Merckx *et al.*, 2015), but there are exceptions where montane taxa are derived from lowland ancestors (Pérez-Escobar *et al.*, 2017). Nonetheless, in the case of the examined radiations on the Hawaiian islands, the relative isolation of biogeographic sources (i.e., other islands) are comparatively much smaller, and so immigration of pre-adapted lineages from wetter high elevation habitats across different islands may play a dominant role in the diversification of high elevation lineages.

Overall, the lack of a general association of niche evolution with speciation mode observed among Hawaiian plant lineages seems to suggest that climatic niche evolution plays a minor role in the geographic context of speciation within Hawaiian lineages. This does not necessarily preclude a role of climatic niche evolution in speciation per se; species belonging to some of the plant lineages examined (e.g., silverswords) exhibit a wide range of ecological preferences and so suggest climatic niche evolution must play at least some role in the diversification of such groups. Instead, my findings suggest that the way in which climatic niche preferences may drive speciation is highly context-dependent and does not manifest in a general way. For example, climatic niche conservatism may facilitate allopatric divergence between populations on different islands, but may equally play a role in allopatric divergence within islands. In addition, while climatic niche divergence may promote speciation within islands, niche divergence may also be common in founder populations established through inter-island dispersal. A lack of a general relationship between niche evolution and speciation mode may thus partly be a consequence of the conflation of multiple spatial scales in this study. Furthermore, other ecological selective pressures may play more important roles in speciation in most plant lineages. Some examples include changes in pollination or fruit dispersal syndrome (Givnish *et al.*, 2009), or adaptation to different edaphic substrates (Savolainen *et al.*, 2006; Hipperson *et al.*, 2016).

Future directions

One source of uncertainty in estimated rates of climatic niche divergence between lineages comes from potential changes in the relative availability and geographic extent of different habitats on the Hawaiian islands throughout their geologic history. Over geologically longer periods, the growth and subsequent decay of islands has had a profound impact of the overall diversification of clades on Hawaii, presumably through the effect of changes in area on the relative size and carrying capacities of habitats (Whittaker *et al.*, 2008; Borregaard *et al.*, 2015; Lim & Marshall, 2017). Over shorter time scales, the islands of Hawaii have similarly undergone oscillations between cool-dry and warm-wet conditions during the

glacial-interglacial cycles over the past 300,000 years, and have also become warmer and wetter over the same period (Sheldon, 2006). This suggests that wetter upland habitats may have undergone repeated cycles of expansion and contraction, and simultaneously, increased and reduced connectivity respectively.

As such, the effect of island ontogeny and climatic forcing on habitat size, and hence the role of niche evolution on speciation, is likely to be complex, especially given a background of global climatic change throughout the Miocene / Pliocene (Zachos *et al.*, 2001). While our model for dispersal and cladogenesis is informed by the geologic dynamics of islands, we do not explicitly apply a context-specific model for niche evolution. A time-varying framework that incorporates the relative accessibility of habitats from paleoclimatic proxies and geodynamic models may give us greater insight into how landscape-level changes may jointly influence speciation and niche evolution.

Lastly, species richness is not only higher in wet habitats compared to lowland dry habitats, but that more species in wet habitats are restricted to the habitat (38%), compared to dry habitat (25%) (Price & Wagner, 2004). Understanding the relative degree to which differences in diversity and endemism between wet and dry habitat may be driven by relatively higher diversification rates within wet habitats or high numbers of immigrant lineages from drier lowland ancestors (Merckx *et al.*, 2015) will give us greater insights into the evolutionary assembly of the Hawaiian flora.

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