

2 RH: Retracing the Hawaiian silversword radiation

3           **Retracing the Hawaiian silversword radiation despite**  
4           **phylogenetic, biogeographic, and paleogeographic**  
5           **uncertainty**

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13           **Abstract**

14     The Hawaiian silversword alliance (Asteraceae) is an iconic adaptive radiation. However, like  
15     many island plant lineages, no fossils have been assigned to the clade. As a result, the clade's  
16     age and diversification rate are not known precisely, making it difficult to test biogeographic  
17     hypotheses about the radiation. In lieu of fossils, paleogeographically structured biogeographic  
18     processes may inform species divergence times; for example, an island must first exist for a clade  
19     to radiate upon it. We date the silversword clade and test biogeographic hypotheses about its ra-  
20     diation across the Hawaiian Archipelago by modeling interactions between species relationships,  
21     molecular evolution, biogeographic scenarios, divergence times, and island origination times us-  
22     ing the Bayesian phylogenetic framework, RevBayes. The ancestor of living silverswords most  
23     likely colonized the modern Hawaiian Islands once from the mainland approximately 5.1 Ma,  
24     with the most recent common ancestor of extant silversword lineages first appearing approxi-  
25     mately 3.5 Ma. Applying an event-based test of the progression rule of island biogeography, we  
26     found strong evidence that the dispersal process prefers old-to-young directionality, but strong  
27     evidence for diversification continuing unabated into later phases of island ontogeny, particularly  
28     for Kaua'i. This work serves as a general example for how diversification studies benefit from  
29     incorporating biogeographic and paleogeographic components.

30     Keywords: Hawaiian silverswords, divergence time estimation, phylogenetic biogeography, island  
31     paleogeography, progression rule

32           **1 Introduction**

33     From Darwin's finches in the Galápagos to the Greater Antillean anoles to the Hawaiian silver-  
34     swords, adaptive radiations in island systems provide biologists with rare and precious glimpses  
35     into how macroevolutionary processes behave (e.g. Blonder et al. 2016; Kamath and Losos 2017;  
36     Lamichhaney et al. 2016). Adaptive radiations in island systems are particularly valuable to re-  
37     searchers as natural experiments, where island communities serve as replicates for studying the  
38     repeatability of evolutionary outcomes through ecological adaptation (Baldwin and Robichaux  
39     1995; Gillespie 2004; Losos 1992; Losos et al. 1998b; Mahler et al. 2013; Grant et al. 2004). One  
40     feature characterizing adaptive radiation is the proliferation of ecological adaptations among

41 closely related lineages as they encounter new regions of niche space, where the radiating clade  
42 is often enriched for disparity and diversity relative to background rates of evolution (Givnish  
43 2015; Schlüter 2000; Simpson 1944; Osborn 1902). Since interspecific competition, access to new  
44 resources, and other spatiotemporal factors drive radiations, timing matters when discussing  
45 adaptive radiations.

46 Yet another common feature of many insular adaptive radiations is that they appear to  
47 result from few—or even one—long-distance dispersal event(s) from a mainland source area  
48 into an island system (Poe et al. 2017; Sato et al. 2001; Silvertown et al. 2005; Baldwin et al.  
49 1991). Under such circumstances, several confluent factors complicate efforts to date when  
50 radiating lineages diverged. Terrestrial species generally suited to dispersing over vast bodies  
51 of water—including plants, arthropods, small lizards, birds, and bats—have relatively sparse  
52 representation in the fossil record (Allison and Bottjer 2011). Once the ancestral lineage of an  
53 incipient radiation has established itself in its new setting, fossils must be recovered from the  
54 island itself in order to time-calibrate the internal divergence events of the radiating clade. Fossil  
55 recovery rates for terrestrial organisms within islands is low, notwithstanding significant finds  
56 from special sites such as lava tubes, bogs, sand dunes, and limestone caves, and sinkholes (e.g.  
57 Burney et al. 2001; Hotchkiss and Juvik 1999; Olson and James 1982). When fossils are available,  
58 assigning them to key divergence events within a radiation is not necessarily easy, in part due to  
59 convergences of traits under island syndromes (Carlquist 1974; Gillespie et al. 1997; Losos et al.  
60 1998a), the loss of anatomical features that readily fossilize (Sansom et al. 2010), and the often  
61 exceptionally short internode distances between the first divergences of a radiation (Gavrilets  
62 and Losos 2009). This set of circumstances is tantalizing to biologists: many of the features  
63 that make adaptive radiations in island systems appealing for study simultaneously undermine  
64 efforts to determine the ages—and, thus, estimate the evolutionary rates—of radiating clades.  
65 Ultimately, less precision when dating an adaptive radiation results in a weaker understanding  
66 of the timing and sequence of key events that constitute the radiation itself.

67 The silversword alliance (Asteraceae) represents one such adaptive radiation (e.g. Judd et al.  
68 2016). Members of the silversword alliance form an endemic Hawaiian clade of 33 species nested  
69 within a larger clade corresponding to subtribe Madiinae, the tarweeds (Baldwin and Wessa  
70 2000). Excluding the silversword alliance, nearly all remaining tarweeds are adapted to the  
71 Mediterranean-like climate of the California Floristic Province of western North America (Bald-  
72 win 2003; Raven and Axelrod 1978). The biogeographic disjunction and phylogenetic relation-  
73 ship between the silversword alliance and continental tarweeds implies at least one long-distance  
74 dispersal event from the American mainland into the Hawaiian Archipelago. But an understand-  
75 ing of exactly when the first tarweed(s) initially colonized the Hawaiian Islands and when the  
76 silverswords began to diversify has been hampered by a lack of known fossils of Madiinae.

77 In one of the earliest molecular divergence time estimation efforts, Baldwin and Sanderson  
78 (1998) estimated the maximum crown age of the silversword alliance to be 5.2 ( $\pm 0.8$ ) Ma,  
79 made possible by integrating diverse lines of evidence. Continental tarweeds are almost entirely  
80 adapted to summer-dry conditions that began to develop in western North America at Mid-  
81 Miocene, approximately 15 Ma (Baldwin 2014; Jacobs et al. 2004). If crown tarweeds began  
82 diversifying only after the onset of such summer-dry conditions, as Baldwin and Sanderson  
83 reasoned, then tarweeds are at most 15 million years old. Using a clock-like nuclear ribosomal  
84 ITS tree with an external calibration of 15 Ma, Baldwin and Sanderson were able to estimate the  
85 maximum silversword alliance crown age and thereby compute the expected minimum speciation  
86 rate under a pure-birth process. They also noted that their maximum age estimate for the  
87 silverswords of  $5.2 \pm 0.8$  Ma is remarkably consistent with the minimum age estimate of Kaua‘i  
88 of  $5.1 \pm 0.2$  Ma (as the island’s age was known nearly twenty years ago; Clague and Dalrymple  
89 1987).

90 Hawaiian paleogeographic evidence, however, did not enter into their dating estimate. At the

time, use of such data for estimating clade ages was problematical for multiple reasons. First, the complex geological history of the Hawaiian Archipelago was less well understood; today, island ages are known more accurately and precisely, but still not perfectly (Clague and Sherrod 2014). Second, despite the fact that tarweeds inhabit both North America and the major groups of Hawaiian Islands provides evidence that long-distance dispersal events must have occurred, the events themselves are unobserved in terms of timing and geographical context. Finally, the distribution of (unobserved) biogeographic events depends on a phylogenetic context, which is also unobservable and must be inferred. These sources of paleogeographic, biogeographic, and phylogenetic uncertainty exist whenever biogeography is used to time-calibrate a phylogeny, though to different degrees for different systems.

Accurately dated phylogenies are necessary to test empirical biogeographic hypotheses about island radiations. An example of such a hypothesis is the “progression rule” of island biogeography (Hennig 1966). First articulated for hotspot archipelagos by Funk and Wagner (1995), the progression rule states that clades tend to inhabit older islands first and disperse to younger islands in the order that the islands appear, leading to a phylogenetic pattern of progressive branching off of lineages representing areas of decreasing age. Adherence to this rule depends largely on ecological factors, such as whether the lineage may thrive in the context of the newly encountered community (Shaw and Gillespie 2016). Another factor is that younger islands have been biogeographically accessible for shorter periods of time compared to older islands, thus enabling fewer opportunities for a dispersing lineage to establish itself there. A related hypothesis is what we call the “diversification corollary” of the island biogeography progression rule: clades tend to experience higher rates of diversification when islands are young. The idea is that unspecialized lineages colonize new islands and then rapidly specialize and diversify as they fill available niches. This pattern was articulated by Wagner et al. (1995) to explain the Hawaiian radiation of *Schiedea* (including *Alsinidendron*; Caryophyllaceae) and is predicted under the general dynamic model of island biogeography (Whittaker et al. 2008). Additionally, Lim and Marshall (2017) found that a decline in island area associated with erosion and subsidence of older islands is correlated with a decline in the rate of species accumulation in rapidly diversifying lineages of the Hawaiian biota. Early work testing the progression rule hypothesis relied on pattern biogeography, such as area cladograms, to test for the rule’s existence in a clade (Cowie and Holland 2008; Gillespie et al. 2008; Parent et al. 2008; Funk and Wagner 1995). To our knowledge the rule’s diversification corollary has not been explicitly tested in a phylogenetic framework since it requires incorporating the timing of both lineage splitting and paleogeographic events.

The primary goal of this study is to illuminate the major biogeographic and evolutionary events underlying the silversword radiation throughout the Hawaiian Archipelago. Such understanding depends on the diversification times within the silversword alliance, and most critically among those dates, the age of the most recent common ancestor (MRCA) of living members of the clade. We estimate these unknown ages using the process-based biogeographic dating technique described in Landis (2017), but instead use the Dispersal-Extinction-Cladogenesis (DEC) model of Ree et al. (2005) to generate time-heterogeneous transition probabilities (Ree and Smith 2008; Matzke 2014). This is accomplished by simultaneously fitting our dataset to an ensemble of phylogenetic models—including diversification processes, time-stratified biogeographic processes, and processes of molecular evolution—whose complementary features induce time-calibrated node age estimates. Additionally, we adapted the uniformization method (Rodrigue et al. 2008) of stochastic mapping (Nielsen 2002) to operate on time-stratified biogeographic processes in order to understand how and when the silversword alliance ancestor(s) first colonized the Hawaiian Islands and when diversification of the crown group began. Using this framework, we also developed new statistical tests for the progression rule of island biogeography and its diversification corollary that are informed by the timing and nature of dispersal

and lineage splitting events throughout the archipelago. Finally, we discuss the potential use of process-based biogeographic dating methods when studying other island biogeographic systems, and how the method may be improved.

## 2 Methods

We estimated the timing and ordering of the silversword radiation using a fully Bayesian phylogenetic analysis. Central to our analysis was the premise that paleogeographic dynamics induce time-heterogeneous biogeographic transition probabilities (Ree and Smith 2008). For example, a dispersal event into an island has probability zero before that island formed and a non-zero probability afterwards. In a phylogenetic context, this means that the biogeographic rate of events and the geological timing of events are separately identifiable. That said, the relative divergence times and topology of a phylogeny are not adequately estimated from biogeographic data alone. We concurrently estimate those aspects of phylogeny from molecular data (Zuckerkandl and Pauling 1962; Thorne et al. 1998). By combining sources of information from molecular, biogeographic, and paleogeographic evidence, our approach jointly models these features to estimate a geologically dated phylogeny. For more details on process-based biogeographic dating, see Landis (2017).

### Silverswords and tarweeds

We include 43 species and subspecies from the clade corresponding to tribe Madieae sensu Baldwin et al. (2002), including 35 taxa from the silversword alliance plus eight outgroup taxa. The eight outgroup taxa inhabit the North American mainland, while all remaining silversword alliance taxa inhabit the Modern Hawaiian Islands. The silversword alliance is composed of three genera: *Argyroxiphium*, *Dubautia*, and *Wilkesia*. For molecular data, we obtained the same 647 bp multiple sequence alignment of the nuclear ribosomal internal transcribed spacer region (ITS) as used in Baldwin and Sanderson (1998). This dataset was chosen because it is highly congruent with phylogenetic evidence from nuclear chromosomal rearrangements (Carr 2003; Carr and Kyhos 1986), in contrast to chloroplast DNA trees, which are highly incongruent with ITS and chromosomal structural data as a result of chloroplast capture (Baldwin 1997; Baldwin et al. 1990; B. G. Baldwin and W. A. Freyman, unpubl. data). Use of the same dataset analyzed by Baldwin and Sanderson (1998) also facilitates a comparison of the performance of our methods with those of the most detailed previous study of the age and rate of diversification of the silversword alliance. Hawaiian species ranges were coded according to Wagner et al. (2005), except we omitted the youngest island from the ranges *Dubautia laxa* subsp. *hirsuta* and *D. plantaginea* subsp. *plantaginea*. Reducing the state space in this way improves the computational efficiency of the method, as described in Webb and Ree (2012). Omitting old islands might cause some lineages to appear artificially young during inference, so we opted to omit young islands.

### Model

#### Geographical areas and paleogeographical uncertainty

The Hawaiian Islands are a Pacific archipelago located far from any continental flora. Of particular interest, the islands form an extensive chain in the North Pacific, from southeast to northwest, in sequence from youngest to oldest. The strict ordering of island ages has resulted from the relationship between the volcanic Hawai‘i hotspot, which produces newborn islands during eruption, and the steady northwesterly drift of the Pacific Plate over the hotspot (Clague and Sherrod 2014). Although the difference in neighboring island ages is semiregular, on the

order of one to two million years, no island's age is known perfectly (without error). One component of the error may be caused by estimation error in dating the rock formations—an error term that will likely diminish with advances in geological methods—but a second component of uncertainty emerges from the fact that the date of a formation only provides a minimum bound on the island age (i.e., an island whose oldest estimated surfacing date is, say, 5 Ma must be at least that old, but it could be older). Introducing further uncertainty, we are interested in the maximum age at which the island was habitable in order to influence the dispersal rate of species into the island. Each island was formed over several stages of volcanic activity, where biogeographically relevant features, such as habitability and rock volume, vary between stages. For this study, we only considered the island formation times. Figure 1 provides the island age ranges we adopted, following the dates proposed by Lim and Marshall (2017), which marginally increased the minimally observable age estimates presented by Clague and Sherrod (2014). Definitions for island growth and decay are defined later alongside the progression rule and the diversification corollary.

Because we rely on the island ages to inform our divergence time estimates, we must model the island age uncertainty in order to correctly propagate estimation error. To do so, we modeled the island ages as uniform random variables bounded by the ages provided in Figure 1, i.e. over the intervals where island "growth starts". Our "relaxed rock" approach integrates over all combinations of tree topologies, divergence times, and island ages using MCMC, just as one integrates over divergence times and fossil taxon sampling times when applying the fossilized birth-death process (Heath et al. 2014).

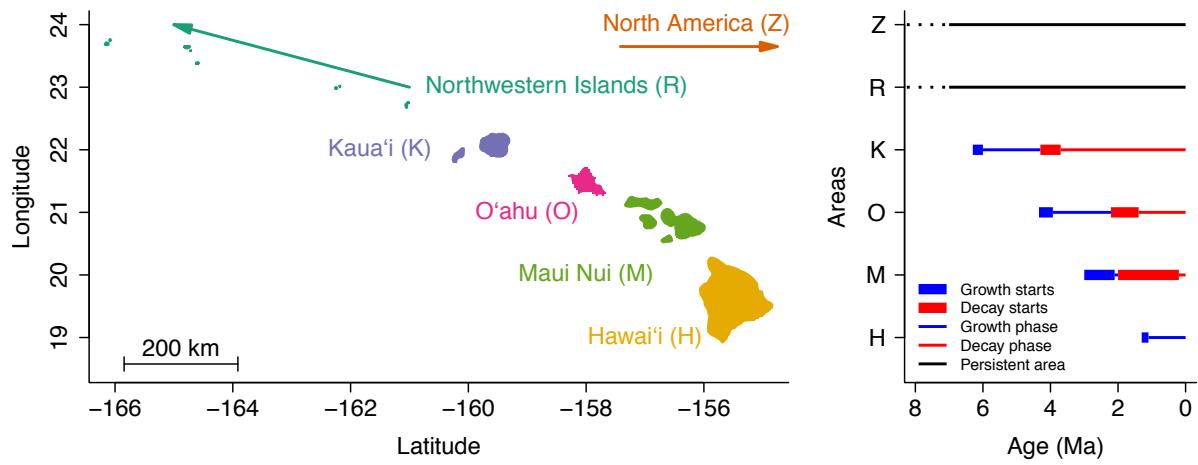


Figure 1: The Hawaiian Archipelago. The left panel shows the six biogeographic areas used in this study (in ascending order of age): Hawai'i (H), the Maui Nui complex (M), O'ahu (O), Kaua'i and Ni'ihau (K), the Northwestern Hawaiian Islands (R) from Nihoa to Kure Atoll, and the North American mainland (Z). Each line in the right panel corresponds to the paleogeographic history of a particular area. Blue lines indicate the time interval during which an island experiences net growth (blue) or net decay (red). Thick lines indicate the range of ages during which the growth or decay phases began. Islands are only inhabitable after the growth phase begins. We do not consider the growth and decay phases for two areas, R and Z.

## 206 Paleogeography-dependent range evolution

207 Long-distance dispersal events are rare relative to short-distance dispersal events as evidenced  
208 by estimates of colonization frequency of increasingly remote islands (Carlquist 1974). For

209 the silversword alliance radiation, the distance between the North American mainland and the  
 210 Hawaiian Islands is greater than the distances among the islands by more than an order of  
 211 magnitude. This distance is a compelling reason to assume that the direct ancestor of living  
 212 members of the silversword alliance colonized the Hawaiian Archipelago only once—something  
 213 that seems exceedingly likely, but is not necessarily true. With this in mind, we parameterized  
 214 dispersal rates between islands to correspond to their relative coast-to-coast distances, meaning  
 215 that the data inform the magnitude of the dispersal penalty (Webb and Ree 2012; Landis et al.  
 216 2013).

217 Because of the linear direction of island emplacement, we can assume that the relative dis-  
 218 tances between islands or island areas have remained essentially constant over time in terms of  
 219 their sequential order (Carson and Clague 1995). Accurate paleogeographical distances between  
 220 islands were not available, so we used modern distances between all islands for simplicity. Dis-  
 221 tances between islands were measured coast-to-coast as the crow flies. To model the effect of  
 222 distance on dispersal, we first define the relative distances between areas as  $g_{ij}$ , which encodes  
 223 the geographical distances between each area pair  $(i, j)$  divided by the mean distance over all  
 224 area pairs.

Then we model the dispersal rates with

$$d_{ij}(k) = \delta \times o_j(k) \times g_{ij}^{-\beta}$$

225 where  $\delta$  is a base dispersal rate,  $o_j(k)$  equals 1 if island  $j$  exists during epoch  $k$  and equals 0  
 226 otherwise, and  $\beta > 0$  is a distance scaling parameter to be estimated. Note, the relative distance  
 227 between any pair of areas equals 1 when  $\beta = 0$ .

228 By combining  $d_{ij}(k)$ , the dispersal rates, with  $e$ , the instantaneous extirpation rate, we  
 229 construct the anagenetic dispersal-extirpation rate matrix,  $Q_{DEC}(k)$ , for each epoch  $k$  (Ree and  
 230 Smith 2008). Ranges are constrained to be one or two areas in size to reduce the state space  
 231 of the model (Webb and Ree 2012). Additionally, the original formulation of DEC results  
 232 in extirpation rates that are biased towards zero when fitted to empirical datasets (Massana  
 233 et al. 2015). Empirical datasets contain no extant taxa with size zero ranges (null ranges),  
 234 resulting in ascertainment bias. To correct for this, we use conditioned transition probabilities,  
 235  $P'_{ij} = P_{ij}/(1 - P_{i0})$ . Cladogenetic events results in an allopatric or sympatric pattern (Ree et al.  
 236 2005) while treating the relative probability of patterns as an estimated parameter. Based on the  
 237 results from previous phylogenetic and biogeographic analyses (Baldwin et al. 1991), we forced  
 238 a mainland root state (Z). Combined, this lets us compute the likelihood of the range data given  
 239 a phylogeny, range evolution parameters, and a (relaxed) paleogeographic hypothesis.

240 While we assume that a full-featured model most realistically portrays the biogeographic  
 241 system, and thus favors more realistic evolutionary reconstructions, we would better understand  
 242 which model features improve the results by contrasting such results to those of simpler models  
 243 that are feature-poor. Two geography-aware models were considered: the full model allowed  
 244 each modern island to appear independently in sequence (+G4), and the hotspot-naive model  
 245 assumed that all four modern islands appeared in unison with the formation of Kaua'i (+G1).  
 246 As a point of contrast, we also considered a geography-naive model, which forced all areas to  
 247 be present at all times and set the distances between all areas to be equal (-G). In essence,  
 248 each model variant reconfigured how the dispersal rates between areas were computed. It is  
 249 important to note that the -G model is time-homogeneous, so it contains no mechanism for the  
 250 biogeographic process to inform the absolute timing of divergence events.

## 251 Molecular evolution and diversification processes

252 Range evolution is modeled simultaneously with the molecular evolution and diversification pro-  
 253 cesses, allowing the biogeographic processes to inform the clade's distribution of divergence times

254 (Landis 2017). That is, we do not first infer the dated molecular phylogeny then subsequently  
 255 model range evolution using an empirical distribution of trees.

256 Molecular variation is modeled by the HKY85 substitution process (Hasegawa et al. 1985).  
 257 Site-rate heterogeneity is gamma-distributed (Yang et al. 1995a) with four rate categories and  
 258 a uniform prior on the shape and scale. Branch-rate heterogeneity is modeled under an uncor-  
 259 related lognormal clock model (Drummond et al. 2006) with 32 discrete rate quantiles, where  
 260 the mean clock rate has a uniform prior over orders of magnitude and the standard deviation is  
 261 distributed by an exponential hyperprior with an expected value of one.

262 Diversification is modeled by a constant rate birth-death process (Nee et al. 1994). Tree  
 263 topology and divergence times are estimated as random variables. Recognizing that divergence  
 264 time estimates are sensitive to modeling assumptions, we analyzed our data under a variety of  
 265 birth and death rate priors, and a variety of taxon sampling scenarios (explained in SI). Our  
 266 presented results assume *Madia* lineage-wide sampling probabilities ( $\rho = 0.61$ ) and moderate  
 267 expected prior birth and death rates (0.10). Pectinate backbone constraints were applied for the  
 268 five oldest nodes in the phylogeny. We generated and applied three secondary node calibrations  
 269 (Table 1) by extending recent work by Barreda et al. (2015) to date the radiation of Asteraceae  
 270 (SI).

Clade	mean age	minimum age	maximum age
Madiinae	8.97	3.79	14.14
<i>Arnica</i> +Madiinae	10.75	4.91	16.59
<i>Hulsea</i> + <i>Arnica</i> +Madiinae (root)	15.99	9.13	22.85

Table 1: Secondary node calibrations. Ages are reported in millions of years. Node age cali-  
 brations correspond to the 95% highest posterior densities (HPDs) from the expanded Barreda  
 et al. (2015) analysis.

## 271 Analysis

### 272 Bayesian inference using RevBayes

273 This study relies on Markov chain Monte Carlo (MCMC) to estimate the joint posterior dis-  
 274 tribution of parameters for the molecular substitution process, the diversification process, the  
 275 range evolution process, and paleogeographic features. All phylogenetic modeling was completed  
 276 in RevBayes (Höhna et al. 2016). Analysis scripts and data files are available through the online  
 277 repository located at [https://github.com/mlandis/biogeo\\_silversword](https://github.com/mlandis/biogeo_silversword). A RevBayes tut-  
 278 rial for the biogeographic dating of silverswords is available at [https://revbayes.github.io/  
 279 tutorials#phylo\\_biogeo](https://revbayes.github.io/tutorials#phylo_biogeo).

### 280 Secondary diversification rate estimate

281 The birth-death process used to model the diversification of all tarweeds and silverswords violates  
 282 assumptions about uniform taxon sampling: it is fitted to a dataset that includes subspecies,  
 283 and it assumes that the silversword alliance and mainland tarweeds diversified under the same  
 284 rate-constant process. To improve empirical accuracy, we estimated a second set of diversifica-  
 285 tion rate parameters from the primary posterior distribution of dated trees. First, we pruned  
 286 away all outgroup species and redundant subspecies from each posterior tree sample so each  
 287 filtered sample represented 25 of 33 known silversword alliance species. We then estimated the  
 288 posterior birth-death process parameters from this set of species-level trees, treated as a mixture  
 289 model over trees with uniform mixture weights. As priors, we assume the diversification rate is  
 290 lognormally distributed and centered on two lineages diversifying into 33 species after 3.5 Ma  
 291 with log-standard deviation of 0.5 and a Beta(2, 2) prior on the turnover proportion.

## 292 Stochastic mapping, ancestral state estimates, and summarizing uncertainty

293 We found that stochastic mapping by rejection sampling (Nielsen 2002) was inefficient for DEC,  
294 owing to the existence of an absorbing state (the null range), the asymmetry of rates, the large  
295 state space, and the underlying epoch model. For instance, rejection sampling will fail if the  
296 null range is sampled during a stochastic mapping, i.e., once a simulated history enters the null  
297 range, it remains in that state until the branch terminates, causing the sample to be rejected.  
298 This is almost certain to occur when the branch length is long or the extirpation rate is large.  
299 Particularly in the Bayesian setting, where parameters that do not maximize the likelihood are  
300 still of interest, stochastic mapping must perform reliably for all regions of parameter space  
301 with high posterior support. To address this problem, we modified the matrix uniformization  
302 sampling method described by Rodrigue et al. (2008) for the purposes of historical biogeography  
303 (Dupin et al. 2017). Our extension accounts for the time-stratified anagenetic and cladogenetic  
304 probabilities of DEC (details in SI). Visualizations of stochastic mappings are available online  
305 through the SI and at [https://github.com/mlandis/biogeo\\_silversword](https://github.com/mlandis/biogeo_silversword).

306 Ancestral range estimates were computed by sampling internal node states, before and after  
307 cladogenesis, using a demarginalization approach (Yang et al. 1995b). Ranges were sampled  
308 regularly during MCMC, and thus under a variety of evolutionary scenarios. To summarize  
309 the range estimates, using the maximum clade credibility tree as a reference, we omitted range  
310 samples corresponding to nodes whose left and right sister subclades were not found in the  
311 reference topology. For example, if the reference topology contained the node with subclades  
312 ((A,B,C),(D,E)), a sample containing the subclade (((A,B),C),(D,E)) would be a valid match,  
313 whereas a clade containing the subclade ((A,B),(C,(D,E))) would not.

## 314 Long-distance dispersal into the Hawaiian Islands

315 How did the ancestor(s) of the silversword alliance first colonize the modern Hawaiian Islands?  
316 The most parsimonious biogeographic scenario involves the direct colonization of the modern  
317 Hawaiian Islands, which necessarily follows the formation of its oldest member, Kaua'i. That  
318 said, less parsimonious scenarios are not strictly impossible. To measure the support of the  
319 probability of four categorical colonization scenarios: *single modern* involves one dispersal event  
320 directly from North America (Z) to a modern island (Kaua'i, K; O'ahu, O; Maui Nui, M; or  
321 Hawai'i, H); *single older-single modern* describes one dispersal event to the older islands (R)  
322 then a second singular event to a modern island; *single older-multiple modern* is like the previous  
323 entry, but allows for multiple dispersal events from the older islands into the modern ones; and  
324 *multiple older/modern* requires more than one dispersal event from the mainland to any of the  
325 older or modern Hawaiian Islands. Note that a dispersal event as defined here could represent the  
326 introduction of multiple individuals of the same lineage closely spaced in time or the introduction  
327 of a single individual. Support across scenarios was measured by querying the joint posterior of  
328 dispersal times, divergence times, and tree topologies, then applying a simple recursive algorithm  
329 to label each joint posterior sample's dispersal sequence with a particular colonization scenario.

## 330 An event-based test of the progression rule of island biogeography

331 To test whether the silversword radiation obeyed the progression rule of island biogeography and  
332 its diversification corollary, we sampled stochastically mapped histories of the biogeographic pro-  
333 cess. As before, these samples incorporate all phylogenetic, biogeographic, and paleogeographic  
334 uncertainty defined by the model. For the progression rule of island biogeography, we labeled  
335 each dispersal event as a positive case if the newly colonized area is younger than its current is-  
336 land (e.g.  $M \rightarrow H$ ) and a negative case otherwise (e.g.  $H \rightarrow M$ ). Support for the diversification  
337 corollary is measured by the ratio of lineage splitting events occurring on young islands (positive  
338 cases) versus on old islands (negative cases). We define an island as young while it grows until

the point that it reaches its maximal area, and old after that threshold. Note, Hawai‘i is growing and considered young today. Applying this definition to the four modern islands, we partition each posterior island age sample into growth (young) and decay (old) phases by sampling from the “short” growth interval published by Lim and Marshall (2017). Taking the divergence time and ancestral range estimated for each node in a posterior sample, we classify each lineage splitting event as young or old by the above criteria. As a concrete example, suppose that Kaua‘i originated at 6.2 Ma and its growth phase ended at 4.1 Ma. A lineage splitting event on Kaua‘i at 5.0 Ma would be considered a positive case for the diversification corollary, while the same event at 2.1 Ma would be considered a negative-case event. Hidden lineage splitting events that left no sampled descendants are not counted, which we expect will cause us to underestimate the number of older lineage splitting events that occurred on now-old islands that were once young. If we find that the majority of our posterior density supports ratios of positive-to-negative events that are greater than one, we treat it as evidence in support for the progression rule and/or its diversification corollary.

### 3 Results

#### Dating the silversword radiation

Our full-featured biogeographic dating analysis under the +G4 model recovers the silversword alliance as monophyletic ( $p = 1.00$ ) and sister to the moderately supported clade ( $p = 0.78$ ) formed by *Anisocarpus madiooides*, *A. scabridus*, and *Carlquistia muirii* (Figure 2). Taxa within the silversword alliance fall into four highly supported clades ( $p > 0.99$ ), all of which have crown ages that likely followed the formation of O‘ahu. Two of the four supported alliance clades inhabit Kaua‘i partly or exclusively: the clade containing two *Wilkesia* species plus three *Dubautia* species and one clade of only *Dubautia* taxa. The remaining two clades are composed of taxa found only among the younger islands of O‘ahu, Maui Nui, and Hawai‘i: the *Argyroxiphium* clade (not on O‘ahu) and a second clade composed entirely of *Dubautia* species. We find some support favoring a sister relationship between the two Kaua‘i-inhabiting clades ( $p = 0.62$ ), but not enough to be certain of their exact relationship.

Assuming the +G4 model and the moderate diversification process configuration described above, the crown age of the silversword alliance is 3.5 Ma (HPD: 2.0 to 4.9 Ma). Under our refined diversification rate analysis, we estimate that the crown of the silversword alliance diversified at the mean rate of 1.07 species per lineage per million years (HPD: 0.20 to 1.91 spp/Myr).

Figure 3 presents the node age densities for five important silversword alliance clades: the silversword alliance crown group; the *Wilkesia*+*Dubautia* clade that is endemic to Kaua‘i; the *Dubautia* clade that is predominantly found on Kaua‘i (Dubautia K+); the *Dubautia* clade that is found only on O‘ahu, Maui Nui, and Hawai‘i (Dubautia OMH); and the *Argyroxiphium* clade. Although the +G1 and -G models misrepresent Hawaiian paleogeography, their results are useful for contrasting with the +G4 results. Under the geography-naive model (-G), the silversword alliance crown age is extremely responsive to the prior model settings, with the crown age often appearing before the appearance of Kaua‘i. Conditioning on paleogeography (+G4 or +G1) greatly dampens how sensitive the silversword alliance crown age estimate is to model conditions.

Modeling the individual appearances of each island (+G4) generates additional dating information that is sacrificed when assuming all modern islands appear simultaneously (+G1). This effect is most evident when the diversification model assumes low sampling probabilities and slow prior birth and death rates (Figure 3, top); While *Argyroxiphium* and *Dubautia* (OMH) only inhabit modern islands younger than Kaua‘i, these two clades’ ages are frequently older than their island ages under the +G1 model, but not under the +G4 model.

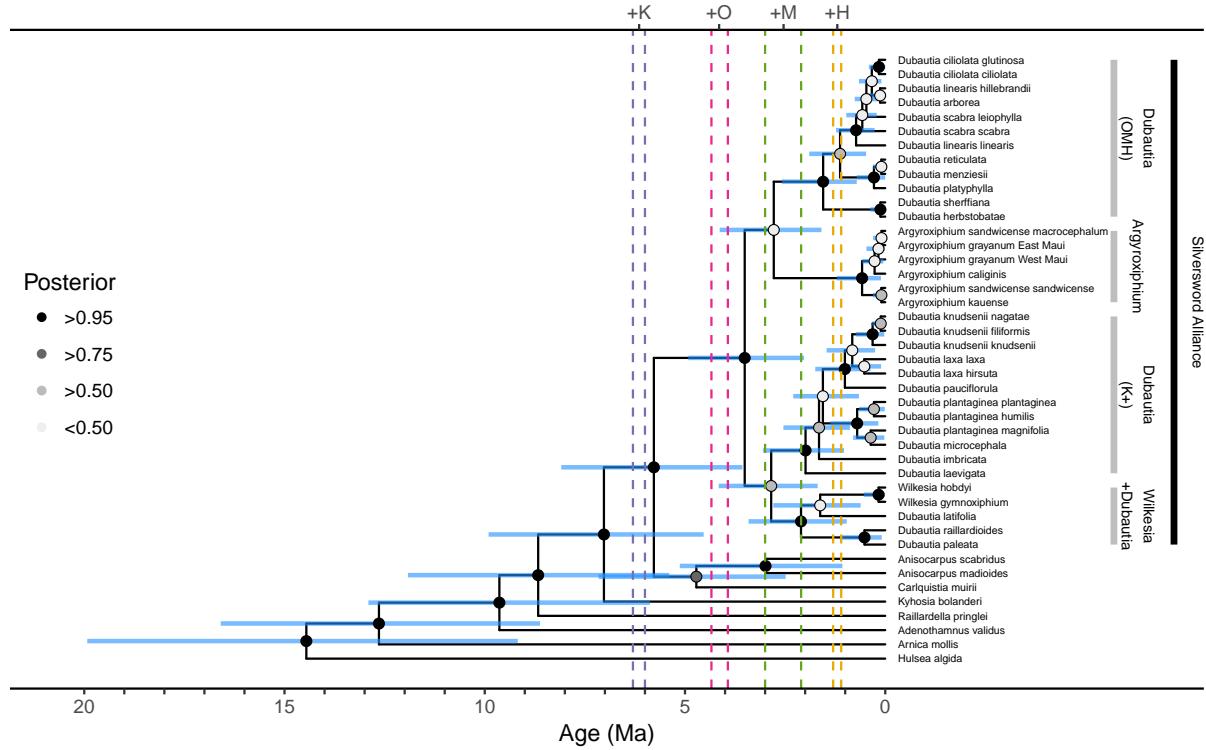


Figure 2: Maximum clade credibility tree of the silversword alliance and closely related tarweeds under the +G4 model. Vertical bars demarcate four subclades within the silversword alliance (see text). Node markers indicate posterior clade probabilities with shades from light gray to black. Node bars report the 95% highest posterior density for divergence time estimates. Vertical dashed lines bound the possible origination times per island complex (from left-to-right: Kaua‘i, O‘ahu, Maui Nui, Hawai‘i).

386 Results for the remaining sensitivity analyses are given in the SI rather than here. However,  
 387 one noteworthy result is that the divergence times are most consistent across subclades and  
 388 model settings when we assume perfect taxon sampling and birth and death rate priors that  
 389 favor exceptionally high birth and death rates (0.50). These settings induce a “tippier” tree,  
 390 where all divergence times become sufficiently young that island availability no longer restricts  
 391 dispersal patterns.

### 392 Long-distance dispersal into the Hawaiian Islands

393 Figure 4 shows that under the fully featured +G4 model, the “single modern” scenario is fa-  
 394 vored to explain how tarweed ancestors first colonized the modern Hawaiian Islands (the +G4  
 395 probabilities of Figs. 4A–D sum to  $p = 0.87$ ). Together, colonization scenarios involving a  
 396 single long-distance dispersal event into the Hawaiian Islands (Fig. 4A–F) are roughly 13 times  
 397 as probable as scenarios involving multiple events (Fig. 4G). When ignoring geography under  
 398 the -G model, we find increased support for the “multiple older/modern” scenario, decreased  
 399 support for either of the two “single older” scenarios, and decreased support for Kaua‘i as the  
 400 destination under the “single modern” scenario. Estimates under the single-island +G1 model  
 401 capture features of both the +G4 and -G analyses: +G1 is more similar to +G4 in that a single  
 402 long-distance dispersal event is strongly favored, but more similar to -G in that support for  
 403 Maui Nui as the destination is substantially increased relative to that for Kaua‘i. Lastly, the two  
 404 “single older” scenarios find the greatest support under the +G4 model, indicating that support

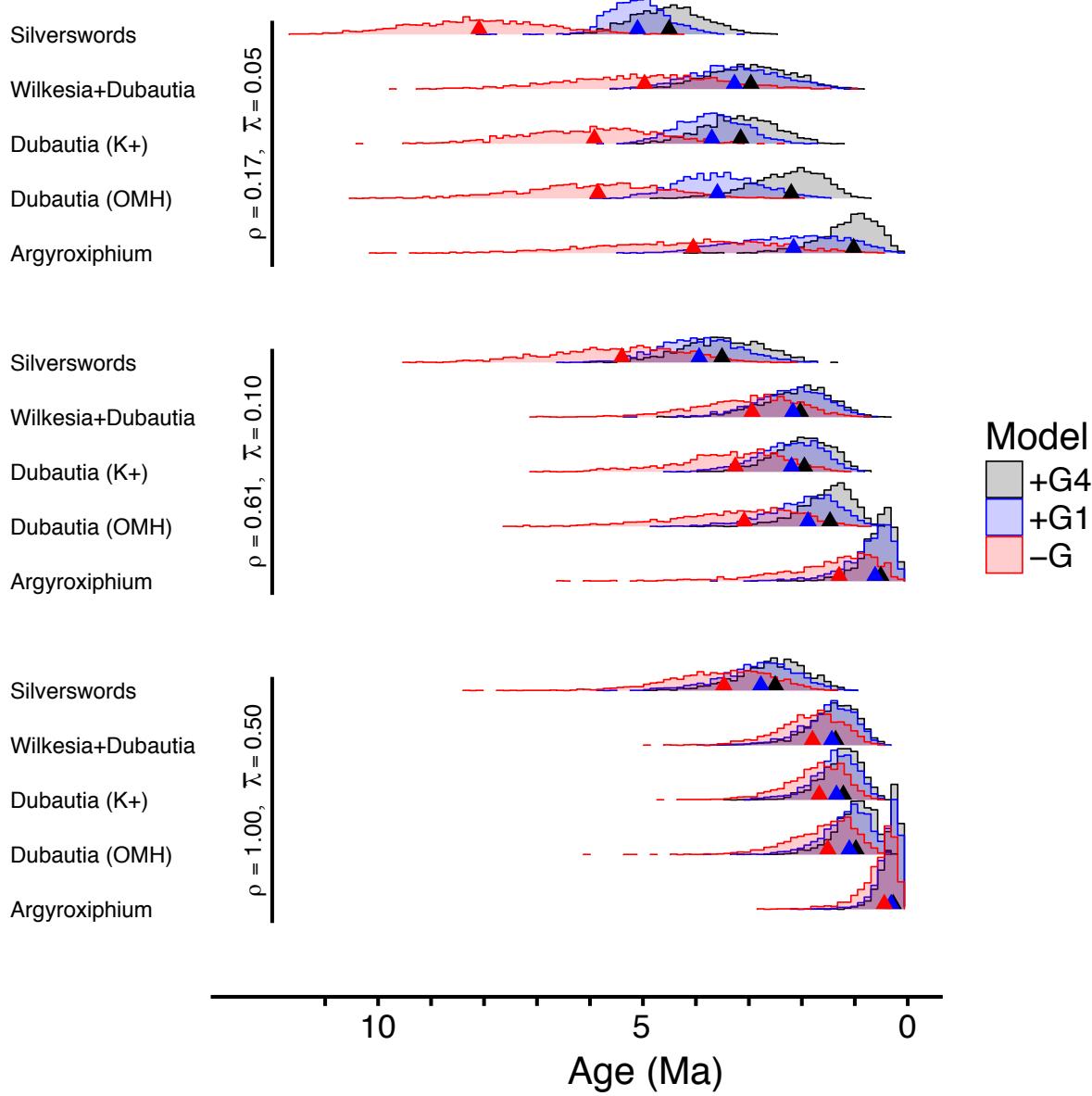


Figure 3: Silversword alliance clade ages under alternative model assumptions. Posterior clade age estimates for five highly supported clades and the three biogeographic models settings described in the text. The three panels in this figure show three of twelve diversification settings that were considered: slow birth/death rates and poor taxon sampling (top); moderate birth/death rates and medium taxon sampling (middle); high birth/death rates and perfect taxon sampling (bottom). Model +G4 assumes the Modern Hawaiian Islands originated sequentially (black), Model +G1 assumes all Modern Hawaiian Islands originated simultaneously (blue), and Model -G (red) assumes all islands always existed; See Methods for details.

for the indirect colonization of the modern Hawaiian Islands may not be independent of the ages at which younger islands appear (+G1).

#### Dating key biogeographic events in the Hawaiian radiation

Figure 5 summarizes the joint distribution of phylogenetic and ancestral range estimates under the +G4 model as previously described in the Methods section. Consistent with the results

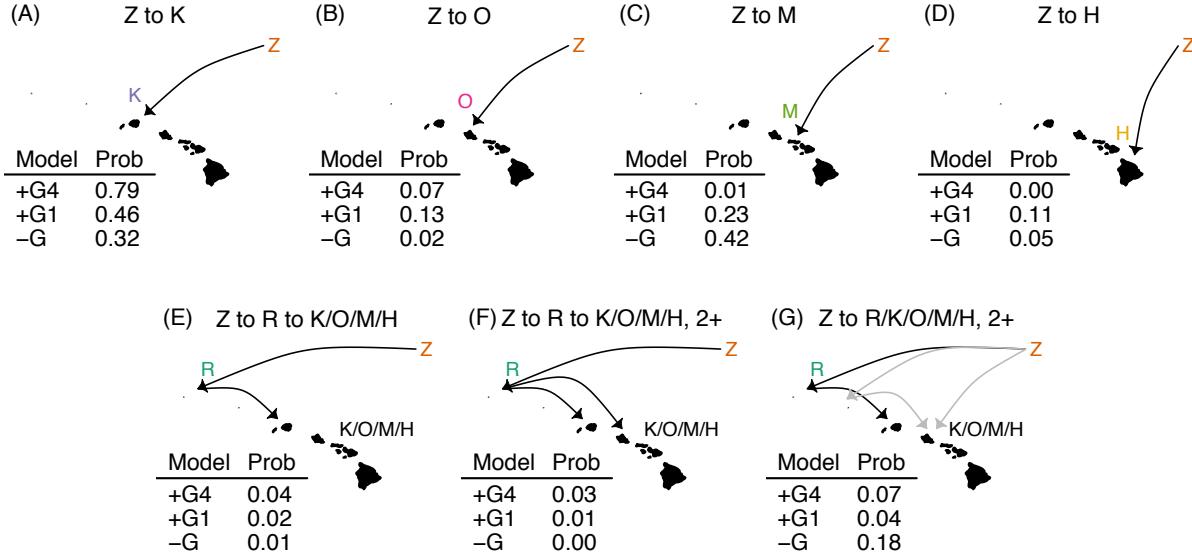


Figure 4: Hawaiian silversword colonization scenarios. Biogeographic dispersal histories were classified into several distinct evolutionary scenarios as described in the main text: (A-D) the single modern colonization scenario is represented with each of the four modern islands as destinations (panels A, B, C, D, correspond to K, O, M, H); (E) the single older-single modern scenario without regard to which modern island was the destination (K/O/M/H); (F) the single older-multiple modern scenario; and (G) the multiple older/modern scenario. Each scenario's posterior probability is given for the three models: the full model (+G4), the hotspot-naive model (+G1), and the geography-naive model (-G).

410 presented in Figure 4, the ancestral range of the silversword alliance crown group very probably  
 411 included the island of Kaua'i. The majority of biogeographic variation appears in two clades:  
 412 the *Argyroxiphium* clade and the *Dubautia* clade containing taxa on islands younger than Kaua'i  
 413 (i.e. the minimal clade including *D. arborea* and *D. sherffiana*). In the second major *Dubautia*  
 414 clade, made largely of taxa that are endemic to Kaua'i, the three dispersal events from Kaua'i  
 415 into the younger islands are relatively recent, occurring within the past one million years.

416 The ancestral range estimate summary shown in Figure 5 does not display exactly when  
 417 a particular island was first colonized nor report how those times might vary in response to  
 418 phylogenetic uncertainty. To disentangle when key clades originated, when islands originated,  
 419 and when those islands were first colonized, we present the posterior event ages in Figure 6A.

420 The silversword alliance radiation throughout the modern Hawaiian Islands must have been  
 421 precipitated by three historical events: at least one modern island must have formed, the ancestor  
 422 of living members of the silversword alliance must have first colonized the modern island chain,  
 423 and the oldest surviving silversword alliance lineages must have begun to radiate. Even if  
 424 improbable, the origination of the silversword alliance could have predated the origination of,  
 425 or their arrival upon, the modern islands. Moreover, there was likely some delay between these  
 426 critical events from the standpoints of biology, based on observations in community assembly  
 427 and the element of chance in dispersal dynamics, and of mathematics, because the expected  
 428 waiting time between dispersal events is necessarily greater than zero. Figure 6B reports the  
 429 evolutionary lag between these events, taking the oldest island complex, Kaua'i, as an upper  
 430 bound. The delay between the island origination time and the first arrival time upon Kaua'i  
 431 is nearly 1.5 million years (posterior mean KO-KA=1.4 Myr), and between the first arrival  
 432 time and the silversword alliance origination is over another million years (posterior mean KA-

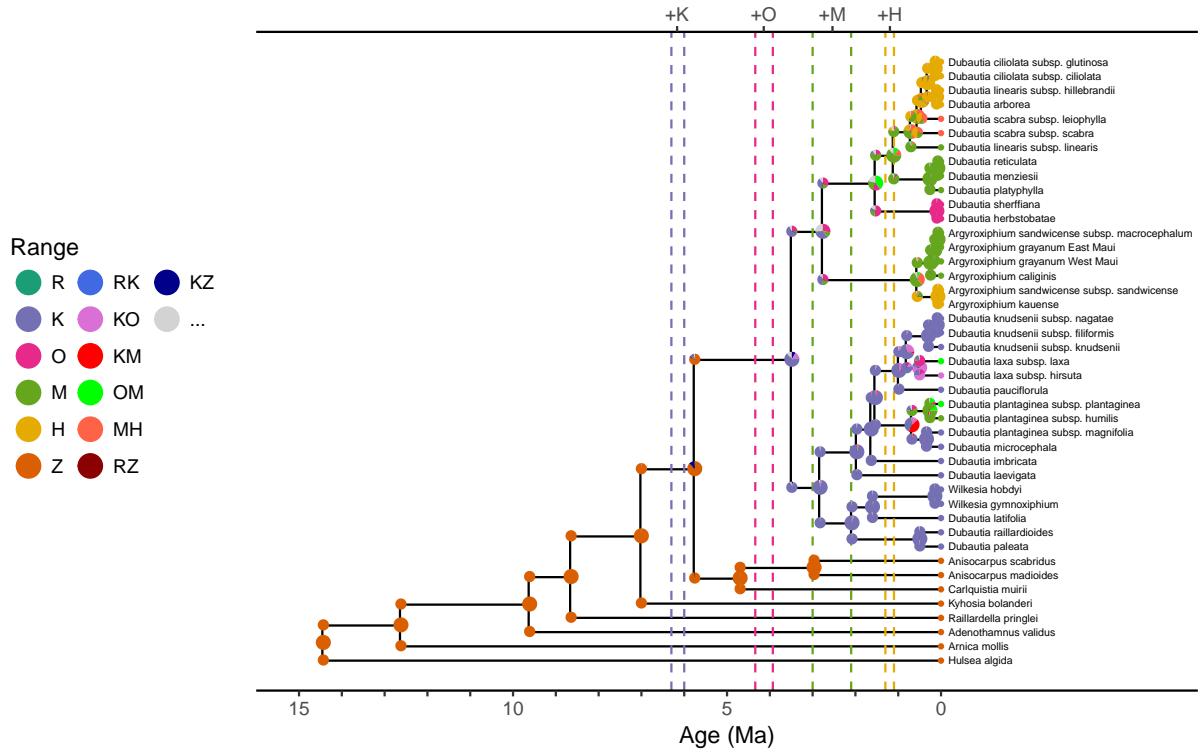


Figure 5: Ancestral range estimates of tarweed+silverswords under the +G4 model. Ancestral range estimates are plotted upon the maximum clade credibility tree. Pie charts report the range estimate probabilities before cladogenesis (node) and after cladogenesis (shoulders). The three most probable ranges are plotted per node/shoulder, with the remaining less probable ranges being binned into the range labeled ‘...’; these improbable ranges are valid in the model but not listed in the legend. Vertical dashed lines bound the possible origination times per island complex (from left-to-right: Kauai'i, Oahu, Maui Nui, Hawaii'i).

433 SO=1.2 Myr). Note, the posterior of lag separating the arrival at Kauai'i from the crown age of  
 434 the silversword alliance contains left tails that are negative, which is corroborated by the results  
 435 presented in Figure 4.

#### 436 Testing the progression rule in silverswords

437 The silversword alliance radiation presents strong positive support for the progression rule of  
 438 island biogeography ( $p > 0.99$ ) with a posterior mean of 3.9 positive dispersal events for every  
 439 negative-case dispersal event (Figure 7A,C,E). Consistent with earlier findings from Figure 4,  
 440 we find greater support for dispersal from the mainland (Z) to Kauai'i (K) than to the older  
 441 Hawaiian Islands (R) or the remaining young islands (O/M/H). There is strong support against  
 442 the progression rule's diversification corollary in the silversword alliance ( $p < 0.01$ ), however,  
 443 with 3.8 lineage splitting events occurring on older decaying islands for every lineage splitting  
 444 event occurring on younger growing islands (Figure 7B,D,E). Negative-case lineage splitting  
 445 events occurred primarily within Kauai'i (61%), followed by Maui Nui (32%) and Oahu (7%),  
 446 while positive-case lineage splitting events most frequently occurred within Hawaii'i (60%), then  
 447 Maui Nui (21%), then Kauai'i (10%), and then finally Oahu (9%).

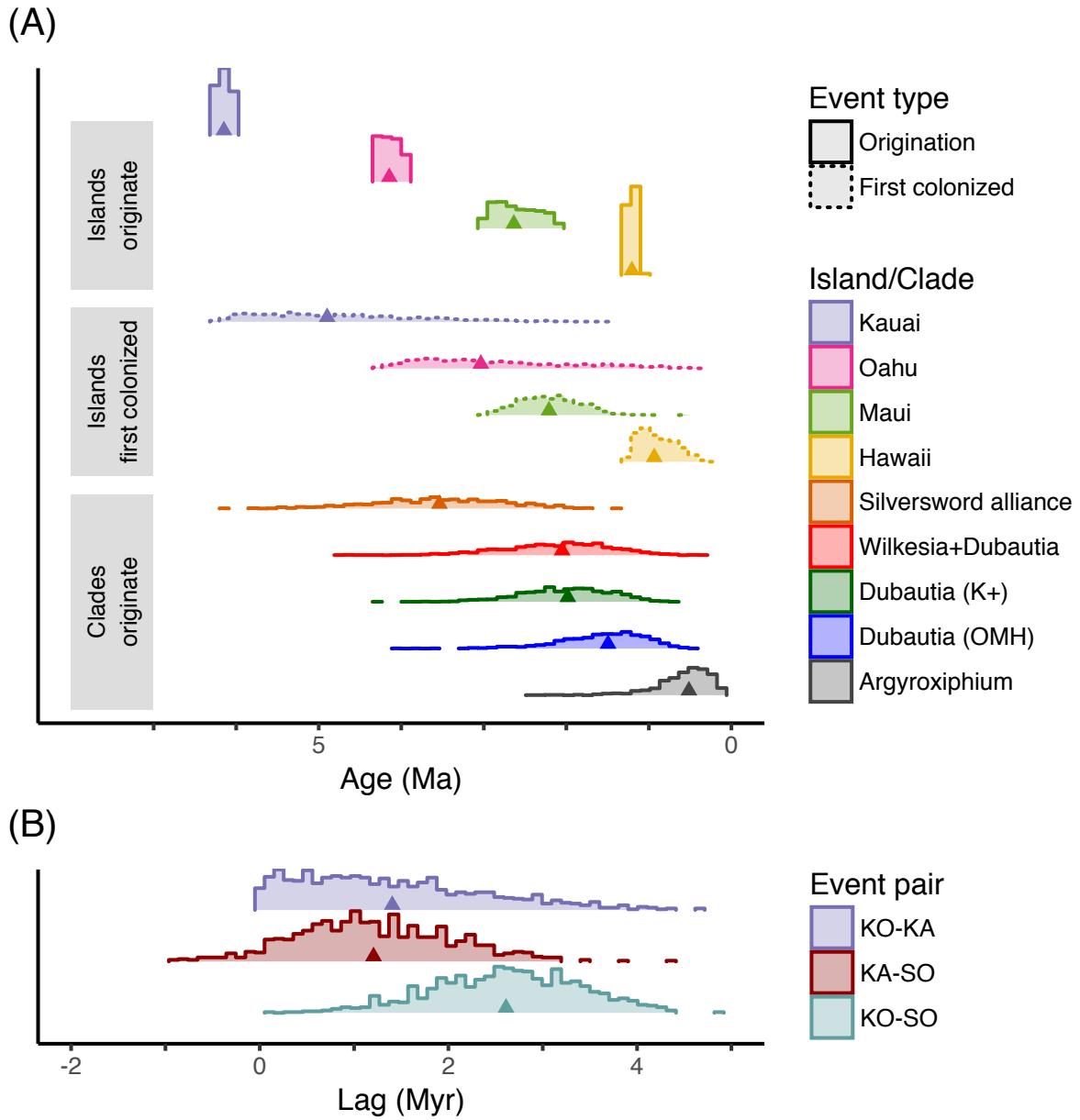


Figure 6: Age distributions of key biogeographic events in the silversword alliance radiation. (A) Histograms with dotted boundaries refer to first arrival times, while solid boundaries refer to origination times of islands and focal clades in this analyses (distinct by color). First arrival times relate to the first time any crown silversword alliance lineage arrived on a given island. Clade ages match those given for the +G4 model in the middle panel of Figure 3. Note, first arrival events always follow the origination time of the corresponding island. (B) Histograms show the posterior differences in time for pairwise combinations of the following three event ages: origination of Kaua'i (KO); the ancestors of living silversword alliance species first arrive at Kaua'i (KA); and the crown age of surviving members of the silversword alliance (SO). Note, KO-KA is always greater than zero because Kaua'i cannot be colonized before it originates. The remaining differences, KO-SO and KA-SO, may be negative if the silversword alliance began to diversify before Kaua'i formed or before the first arrival on Kaua'i, respectively. The posterior mean differences are KO-KA=1.4, KA-SO=1.2, KO-SO=2.6 in millions of years.

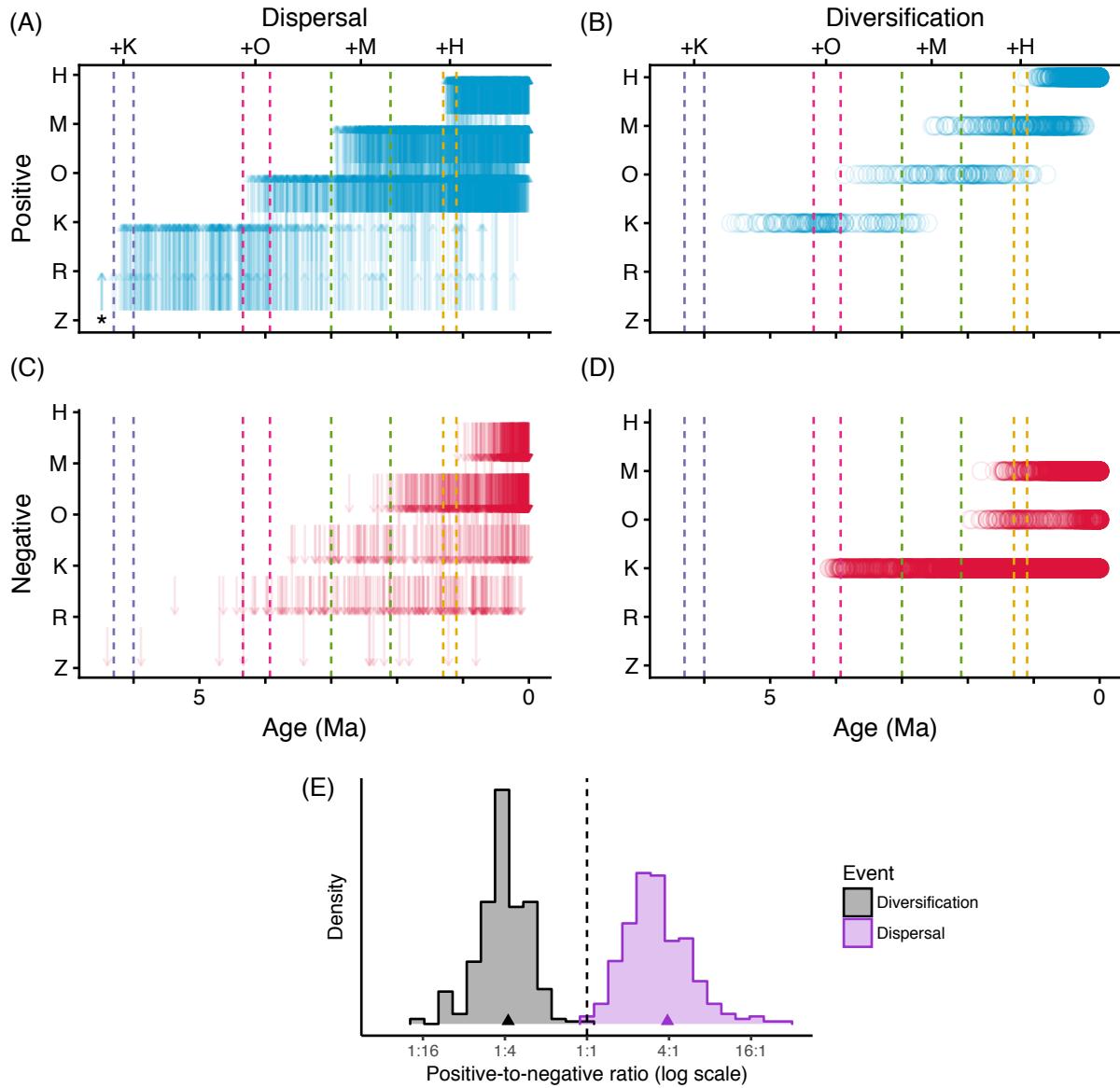


Figure 7: Posterior support for and against the progression rule of island biogeography and its diversification corollary. Dispersal events (A,C) and lineage splitting events (B,D) are classified into either positive (A,B) or negative (C,D) cases that follow or break the progression rule. Positive lineage splitting events occur on islands before the island reaches its maximal area (the older Hawaiian Islands, R, and the mainland, Z, are omitted). Positive dispersal events occur from an old area into a younger area. Dashed lines bound the possible origination times per island complex. (A) A small fraction of type-positive Z → R events occurred before 6.5 Ma, and are represented by the single arrow and asterisk. (E) Posterior estimates of the ratio of positive-to-negative cases of the progression rule for dispersal (purple) and the diversification corollary (black). Neither lineage splitting nor dispersal processes are probable at the 1:1 ratio (dashed line); the dispersal process obeys the progression rule yet lineage splitting events run opposite to the progression rule's diversification corollary.

## 4 Discussion

The silversword alliance is an especially prominent example of insular adaptive radiation for which rigorous estimation of the timing of diversification and the pattern of inter-island disper-

451 sal have been long available (Baldwin and Robichaux 1995; Baldwin and Sanderson 1998). As  
452 such, the clade is ideal for examining the potential for advancing understanding of the radiation  
453 through a new approach to biogeographic hypothesis testing. In particular, we used an integrative  
454 Bayesian phylogenetic framework (Landis 2017) incorporating refined paleogeographic  
455 information to disentangle colonization and diversification history and to test the progression  
456 rule of island biogeography (Funk and Wagner 1995) and its diversification corollary. Those find-  
457 ings provide a new perspective on the geological context of dispersal and evolutionary radiation  
458 in an insular clade, as discussed below.

459 The crown group of the silversword alliance began diversifying approximately  $3.5 \pm 1.5$  Ma.  
460 This age is younger than  $5.2 \pm 0.8$  Ma, the maximum clade age of the silversword alliance  
461 estimated by Baldwin and Sanderson (1998), whose results at the time provided early robust  
462 evidence for a major Hawaiian radiation that was contemporary with the modern high islands,  
463 rather than pre-dating the oldest high island, Kaua'i. Where our analysis uses island paleo-  
464 geography to date the clade, Baldwin and Sanderson's maximum age estimate was obtained by  
465 applying a phylogenetic niche conservatism argument to paleoclimatological data from western  
466 North America in order to bound the maximum age of continental tarweeds. The consistency  
467 between the two age estimates suggests future work might integrate both lines of reasoning to  
468 further improve age estimates for tarweeds and the silversword alliance. The relatively tight  
469 support interval for the Baldwin and Sanderson estimate ( $\pm 0.8$  Ma) is smaller than ours for at  
470 least three reasons: we modeled the uncertainty in the root age estimate itself rather than the  
471 bound, our divergence time estimates assume rate heterogeneity across lineages rather than clock  
472 constancy, and Bayesian credible intervals and frequentist bootstrap replicates are not strictly  
473 equivalent.

474 As to the pace of the radiation, we estimate that the silversword alliance crown group di-  
475 versified at a mean rate of  $1.07 \pm 0.86$  spp/Myr. Our diversification rate estimate differs in  
476 several ways from the minimum speciation rate estimate of Baldwin and Sanderson,  $0.56 \pm 0.17$   
477 spp/Myr. Part of the difference is explained by replacing the maximum age estimate (5.1 Ma)  
478 with an actual age estimate (3.5 Ma). Here, the younger crown age is partly responsible for  
479 the higher diversification rate. Complicating an exact comparison, the original estimate also  
480 assumed a pure birth process with perfect taxon sampling, and, strictly speaking, estimated the  
481 rate of new species *or* subspecies originating. Another difference is that we now obtain some  
482 internal node calibrations under the paleogeographic model, causing some lineages to appear at  
483 younger ages than they would if paleogeography was ignored (Figure 3). Our estimated diversi-  
484 fication rate is not only higher than estimated earlier for the silversword alliance but falls within  
485 the range of rates estimated for other major island plant radiations such as Hawaiian *Bidens*  
486 and Macaronesian *Echium*, and approaches the range of rates estimated for Andean *Lupinus*  
487 (see Knope et al. 2012; Lagomarsino et al. 2016).

488 Matching intuition, our analysis found it highly likely that a single tarweed lineage first  
489 colonized Kaua'i directly from the North American mainland , after which it began radiating  
490 into what we know as the silversword alliance today. Based on our analysis, it is unlikely that  
491 the Northwestern Hawaiian Islands, which arose prior to Kaua'i, played a significant role in  
492 the tarweed colonization of the Hawaiian Archipelago. Modeling the effect of higher rates of  
493 extinction on those older islands, applying a slower prior to the diversification or substitution  
494 rates, or extrinsic information pushing the silversword alliance crown age to be older could  
495 overturn this result. But, as it is, nothing requires a colonization event into the Hawaiian  
496 Archipelago before the formation of Kaua'i. Our estimate that both the crown *and* stem ages of  
497 the silversword alliance are contemporary with Kaua'i corroborates the biogeographic importance  
498 of a pre-Kaua'i gap in island formation and presence of only relatively small, widely spaced islands  
499 in the chain prior to the rise of Kaua'i (Price and Clague 2002). Based on paleogeographic  
500 reconstructions (Lim and Marshall 2017), Kaua'i would have approximated its modern area at

501 our estimated colonization time for the initial dispersal from North America, in line with the  
502 expectation that the colonizing tarweed would have found conditions favorable for establishment  
503 in montane Hawaiian settings (Carlquist 1995; Baldwin and Wagner 2010).

504 This lone long-distance dispersal event becomes an appealing candidate for use as a bio-  
505 geographic node calibration, where one might assert that the silversword alliance crown group  
506 began to diversify only after Kaua‘i formed. Baldwin and Sanderson (1998) noted that any error  
507 in an island age estimate would result in a cascade of node age estimation error throughout  
508 the phylogeny. Supposing that the age of Kaua‘i was known perfectly, there is still the issue  
509 of what density to apply to the node: the density would need to measure the delay between  
510 the appearance of the island and the colonization of the island, and between the colonization of  
511 the island and the first lineage splitting event that left sampled descendants. In other words,  
512 the biogeographic node age density should depend on the age of the island, the dispersal rate  
513 into the island, and the speciation rate on the island, but the values of those parameters are  
514 unknown and inferred through the evolutionary analysis itself. Sidestepping these complications  
515 by jointly inferring the evolutionary parameters along with the divergence times, we estimate  
516 this lag from the data directly rather than assert its effect through the prior (Figure 6B).

517 While the conspicuous disjunction between the continental tarweeds and the Hawaiian sil-  
518 versword alliance offers a singular plausible biogeographic event suitable for node calibration,  
519 weaker node calibrations could not be so easily or consistently applied to less certain biogeog-  
520 graphic events within the silversword radiation. For example, six taxa of *Dubautia* sect. *Rail-*  
521 *liardia* (the six taxa at far upper right of Fig. 2) are found on the youngest island, Hawai‘i.  
522 Suppose one was certain that these six taxa formed a clade. Their co-occurrence on Hawai‘i  
523 could be explained by a single dispersal event. The dispersal event must have occurred after  
524 Hawai‘i originated, thereby informing the age of the clade, which could justify the use of a bio-  
525 geographic node calibration. But if we cannot be certain of the monophyly of the six taxa, then  
526 anywhere from one to six dispersal events may be needed to explain their occurrences, and the  
527 placement of those hypothetical events would need to be defined over the set of relevant clade  
528 topologies—where sets defining random treespace grow rapidly with the number of taxa. While  
529 node calibrations are not easily applied in cases such as this, process-based biogeographic dating  
530 methods inherently marginalize over all defined phylogenetic and biogeographic scenarios.

531 We found some effect for this subtler dating information when examining crown ages for  
532 the four major silversword alliance subclades. Three models were used: one model ignoring  
533 geography (-G), one model that reflects our best translation of paleogeography (+G4), and  
534 one model that ignored finescale paleogeographic knowledge (+G1). If the divergence times for  
535 the silversword alliance and the four subclades therein are equal when assuming +G1 or +G4,  
536 then the exact ages of appearance for O‘ahu, Maui Nui, and Hawai‘i would be inconsequential  
537 to dating the clade. However, we found that the ages estimated for the subclades that are  
538 endemic to the younger islands are older under +G1 than under +G4, indicating that fine scale  
539 phylogenetic, biogeographic, and paleogeographic interactions generate information that may  
540 be extracted through process-based biogeographic dating methods. This suggests that other  
541 datasets may contain similarly diffuse information about clade ages, a feature overlooked by  
542 traditional node calibration based frameworks.

543 Using the posterior distributions of lineage splitting and dispersal events obtained from our  
544 stochastically mapped biogeographic histories, we classified the events as evidence in favor (old-  
545 to-young) or against (young-to-old) the progression rule and its diversification corollary, and  
546 we measured the probability and magnitude of support for and against the progression rule  
547 in island biogeography (Funk and Wagner 1995). While we found strong support ( $p > 0.99$ )  
548 for the dispersal process following the progression rule, the diversification process does not  
549 follow the progression rule’s diversification corollary ( $p < 0.01$ ). The negative signal for the  
550 diversification process is fueled by two of the silversword alliance subclades that have been

551 diversifying without rest in Kaua‘i for millions of years. At a glance, the number of speciation  
552 events per unit time (i.e. the rate) remains remarkably steady within Kaua‘i, even as Kaua‘i  
553 declines in area. That finding cannot be explained by differences in taxonomic judgment about  
554 species boundaries in silversword alliance lineages on Kaua‘i versus the younger islands; species of  
555 the silversword alliance on Kaua‘i are in general even more divergent genetically than on younger  
556 islands (Carr and Kyhos 1986; Witter and Carr 1988) and are highly distinctive morphologically  
557 and ecologically (Carr 1985; 1999). Our result may instead reflect ecological factors associated  
558 with the extensive, deep erosional dissection of Kaua‘i that has accompanied its loss of area. To  
559 some extent, such activity may have offset habitat loss associated with reduction in island size  
560 by creating habitat heterogeneity (see Lim and Marshall 2017) and opportunities for isolation at  
561 finer geographic scales that have facilitated speciation, as predicted by (Whittaker et al. 2008)  
562 for islands at a comparable developmental stage (“maturity”) within oceanic archipelagos. Such  
563 considerations may be reflected by the relatively high number of silversword alliance species of  
564 limited geographic distribution on Kaua‘i (Carr 1999).

565 While we see the results of this event-based test of the progression rule as an advance in  
566 the study of island biogeography, it has limitations. One challenge arises in objectively defining  
567 when an island is young or old. This is simple for directional events, like dispersal, where for  
568 any pair of areas one is older than the other. Whether a lineage splitting event occurs on a  
569 young or an old island is not so clear; we used the time when an island’s growth rate turned  
570 negative to demarcate young from old, but, as discussed above, other ecological factors may to  
571 some extent counteract loss of island size in influencing speciation rate. As another example,  
572 the ratio tests consider the proportions of positive and negative events within each stochasti-  
573 cally mapped evolutionary history, then ask whether the ratio is generally larger, smaller, or  
574 equal to the balanced ratio of one-to-one. But those negative lineage splitting events that took  
575 place in Kaua‘i over the past four million years may drown out evidence that some subclades  
576 positively adhere to the progression rule’s diversification corollary—namely the two subclades  
577 inhabiting only islands younger than Kaua‘i. Our analysis also did not consider possible extinc-  
578 tion events on Kaua‘i (and elsewhere), where loss of higher elevation habitat through erosion  
579 and subsidence, for example, may have resulted in a bias toward loss of earlier diverging lin-  
580 eages. This bias might be eliminated by reformulating the DEC biogeography model within  
581 the State-Dependent Speciation and Extinction (SSE) framework (e.g. Goldberg et al. 2011).  
582 Such an approach could account for both cladogenetic events as well as extinction during the  
583 diversification process (Goldberg and Igić 2012; Freyman and Höhna 2017) and incorporate the  
584 effects of island ontogeny (or other paleogeographic features) on speciation and extinction rates  
585 (Lim and Marshall 2017).

586 Considering the finer-scale features of our reconstruction, the novel finding of a consider-  
587 able lag between island colonization and diversification of the silversword alliance (Figure 6B)  
588 is especially intriguing in light of the additional finding here of strong evidence against diversi-  
589 fication during the island growth phase, at least on the oldest high island, Kaua‘i (Figure 7D).  
590 Although an undetected extinction bias toward early diverging lineages may partially explain  
591 these results, there remains strong evidence that diversification of the silversword alliance on  
592 Kaua‘i has continued apace as the island has diminished considerably in size through erosion  
593 and subsidence. The importance of new opportunities for speciation during the later stages of  
594 island development that may arise from such processes as erosional dissection of the terrain into  
595 more complex and isolated habitat space warrants more study and may help to explain why  
596 Kaua‘i contains higher species richness of the silversword alliance and of endemic angiosperms  
597 in general than any younger island of the chain (Sakai et al. 2002; Wagner et al. 2005).

598 Our work shows that a variety of biogeographic hypotheses may be tested by defining cat-  
599 egorical hypotheses, then recording the frequency of events from the posterior distribution of  
600 stochastically mapped biogeographic histories (Dupin et al. 2017). Because our stochastic map-

pings are are fully Bayesian, they exactly characterize our confidence in the variety of biogeographic scenarios that are probable under the model. The fully Bayesian approach reports our uncertainty in both the biogeographic history *and* in the evolutionary and paleogeographic conditions that could have plausibly generated that history, thus guarding against a false sense of precision regarding past events. These estimates are subtly distinct from maximum likelihood settings where histories are typically simulated under the single point estimate of parameters with the highest probability, rather than over the range of model parameters with high probability (i.e. those with high confidence/credibility). That said, obtaining Bayesian stochastic mappings over a broad range of parameters posed some technical challenges. Rejection sampling approaches for stochastic mapping were, for all practical purposes, incompatible with posterior samples where the rate of area loss was not small and/or branch lengths were long; nearly all simulated stochastic mappings under the biogeographic process lead to the null range (an absorbing state) under these settings. To circumvent this issue, we extended the uniformization sampling method (Rodrigue et al. 2008) to accommodate cladogenetic events and the time-heterogeneous rate matrices of the epoch model.

Although some of the coarse-scale features of our reconstruction may not surprise researchers of Hawaiian biogeography in general or researchers of the silversword radiation in particular—e.g. that the silversword alliance is monophyletic and younger than Kaua‘i, that one ancestral lineage founded the radiation, that they preferentially colonized younger islands in accordance with the progression rule—our framework greatly refines our ability to quantify exactly the location and timing of evolutionary events. This level of detail brings the next generation of biogeographic questions into reach: What geographical and ecological factors determine the periods of delay between island formation, island colonization, and radiation within the island? And how does the spatiotemporal distribution of habitat availability drive the evolution of novel ecological adaptations? By advancing the methodological framework to study these questions, we come closer to understanding the phenomenon of adaptive radiation as it behaves in nature. We also anticipate that enhanced phylogenetic resolution from ongoing phylogenomic studies of the silversword alliance (B.G. Baldwin and W.A. Freyman, in prep.) will provide additional answers to these questions.

The Hawaiian silversword alliance is representative of many island biogeographic systems: fossils are few or absent, island ages are uncertain, comprehensive genetic sampling is limited, but evolutionary hypotheses are plentiful. Recognizing these commonalities, we developed our inference strategy to be easily translated into other island biogeographic systems, even with systems that are not as well-behaved or well-understood as the Hawaiian silverswords. Our method, for instance, is directly relevant to the study of other diverse lineages of Hawaiian flora and fauna, including the honeycreepers (Lerner et al. 2011), *Psychotria* (Nepokroeff et al. 2003), mints (Lindqvist and Albert 2002), lobelioids (Givnish et al. 2009), drosophilid flies (Lapoint et al. 2013), hyposmocomid moths (Haines et al. 2014), and many other remarkable clades that warrant similar analyses to assess the generality of our findings regarding the progression rule of biogeography and the diversification corollary. But, also, the relaxed rock paleogeographic model we introduced readily accommodates origin sequences for island systems far more complex than that of the Hawaiian Archipelago, such as the Galápagos Islands (Geist et al. 2014) or the Indo-Australian Archipelago (Lohman et al. 2011). Following the pioneering work of Sanmartín et al. (2008), a joint analysis that pools biogeographic evidence across multiple clades could, in principle, allow one to estimate otherwise uncertain paleogeographic features, such as area age, availability, and connectivity. As phylogenomic data become available for the many insular lineages that currently lack phylogenetic resolution, joint models of biogeography and diversification will advance further the refinement and understanding of biogeographic events and diversification times.

For many biogeographic systems, even minor amounts of phylogenetic, biogeographic, and

651 paleogeographic uncertainty can obscure our intuition about historical events. In many cases,  
652 the perception of such uncertainty is daunting enough to prevent further investigation, because  
653 it clouds our sense of what is tractable: it becomes unclear what features of a clade's history  
654 can be reconstructed and at what level of detail can hypotheses be posed and tested. What we  
655 show in this work is that by designing our inference methods to embrace these inherent sources  
656 of uncertainty, we can still form and test biogeographic hypotheses against a range of plausible,  
657 but ultimately unknowable, evolutionary histories, leading us to better understand how species  
658 diversify in space and time.

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## 665 Contributions

666 M.J.L., W.A.F., and B.G.B. designed the study. M.J.L. and W.A.F. developed the methods  
667 and conducted the analyses. M.J.L, W.A.F., and B.G.B. interpreted the results and wrote the  
668 manuscript.

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## 673 Data archival

674 Data and scripts used for this study are available at [https://github.io/mlandis/biogeo\\_](https://github.io/mlandis/biogeo_silversword)  
675 [silversword](https://github.io/mlandis/biogeo_silversword). Input and output files are hosted on Dryad at [https://datadryad.org/resource/](https://datadryad.org/resource/doi:10.5061/dryad.rj10fh0)  
676 [doi:10.5061/dryad.rj10fh0](https://datadryad.org/resource/doi:10.5061/dryad.rj10fh0).

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