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How old is the Hawaiian biota? Geology and phylogeny suggest recent divergence

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This study quantifies long-term landscape changes in the Hawaiian archipelago relating to dispersal, speciation and extinction. Accounting for volcano growth, subsidence and erosion, we modelled the elevations of islands at time intervals of 0.5 Myr for the last 32 Myr; we also assessed the variation in the spacing of volcanoes during this period. The size, spacing and total number of volcanic islands have varied greatly over time, with the current landscape of large, closely spaced islands preceded by a period with smaller, more distantly spaced islands. Considering associated changes in rates of dispersal and speciation, much of the present species pool is probably the result of recent colonization from outside the archipelago and divergence within contemporary islands, with limited dispersal from older islands. This view is in accordance with abundant phylogenetic studies of Hawaiian organisms that estimate the timing of colonization and divergence within the archipelago. Twelve out of 15 multi-species lineages have diverged within the lifetime of the current high islands (last 5 Myr). Three of these, and an additional seven (mostly single-species) lineages, have colonized the archipelago within this period. The timing of colonization of other lineages remains uncertain.

Keywords: dispersal; Hawaii; island biogeography; molecular clock; phylogeny; speciation

1. INTRODUCTION

Evolutionary biologists accept the idea that older, now eroded islands, contributed to the present Hawaiian biota; however, the degree of this contribution has remained uncertain. Previous studies have delimited the original shorelines of submerged islands (Moore *et al.* 1994), estimated their ages and maximum elevations (Clague 1996), and speculated on the potential for older islands to serve as biological sources for the current high islands (Carlquist 1980; Carson 1983; Carson & Clague 1995), leading to the first molecular clock estimates confirming the origins of Hawaiian taxa on older islands (Beverley & Wilson 1985; Givnish *et al.* 1995). Assuming that processes of dispersal and speciation have been going on continuously, long before the present high islands arose, suggests a gradual rate of species accumulation. However, biological rates vary with geographical properties, such as island size, number and spacing (MacArthur & Wilson 1967; Heaney 1986; Losos & Schluter 2000), which have varied considerably over time. By creating a detailed geological model to examine this variation and by examining a wealth of phylogenetic studies of Hawaiian organisms, we conclude that many lineages arrived or diversified recently, counter to the assumption of slow accumulation.

The Hawaiian chain is characterized by the growth of shield volcanoes that go through a life cycle with well-defined stages. Volcanoes form over a stationary hot spot and are then removed from the hot spot by the motion of the Pacific tectonic plate, producing a linear array of volcanic summits increasing in age to the northwest (Wilson 1963). After reaching their maximum height volcanoes rapidly subside within *ca.* 1 Myr (Moore & Clague 1992), then erode down to sea level over several million years. Finally, as all volcanic rock above the surface disappears, atolls may form (Darwin 1837) with small coralline islands. To reconstruct the changing height of each volcanic peak over time, we estimated its original elevation and then derived growth, subsidence and erosion rates. In addition, we determined the degree of variation in the spacing of volcanoes over time. The resulting model informs testable hypotheses about the histories of evolutionary lineages in the Hawaiian Islands.

2. MATERIAL AND METHODS

We used Geographic Information Systems technology to analyse several features (figure 1) in order to determine rates of growth, subsidence and erosion, and to assess the degree of spacing of volcanoes in the Hawaiian chain. Sea level change is not considered here as it varies by slightly more than 100 m, while the processes modelled here represent more substantial change.

(a) *Original height*

As volcanoes form, lava deposited underwater forms a steeper slope than that deposited subaerially (above the sea surface) (Moore 1987; Mark & Moore 1987). While rapid subsidence after formation submerges this break-in-slope, it has been accurately located in sonar surveys to estimate the maximum shorelines of islands throughout the archipelago (Moore *et al.* 1994). Clague (1996) estimated the positions of summits by examining the locations and shapes of seamounts, atolls and rocky islets, and derived theoretical heights and ages for each. We used the same summit positions and ages, with a few adjustments based on a slightly different interpretation of bathymetry. In the relatively uneroded main islands, slopes measured along the shortest distance from the summit to the maximum shoreline average an angle of 7°. Therefore, the original elevation of an eroded island

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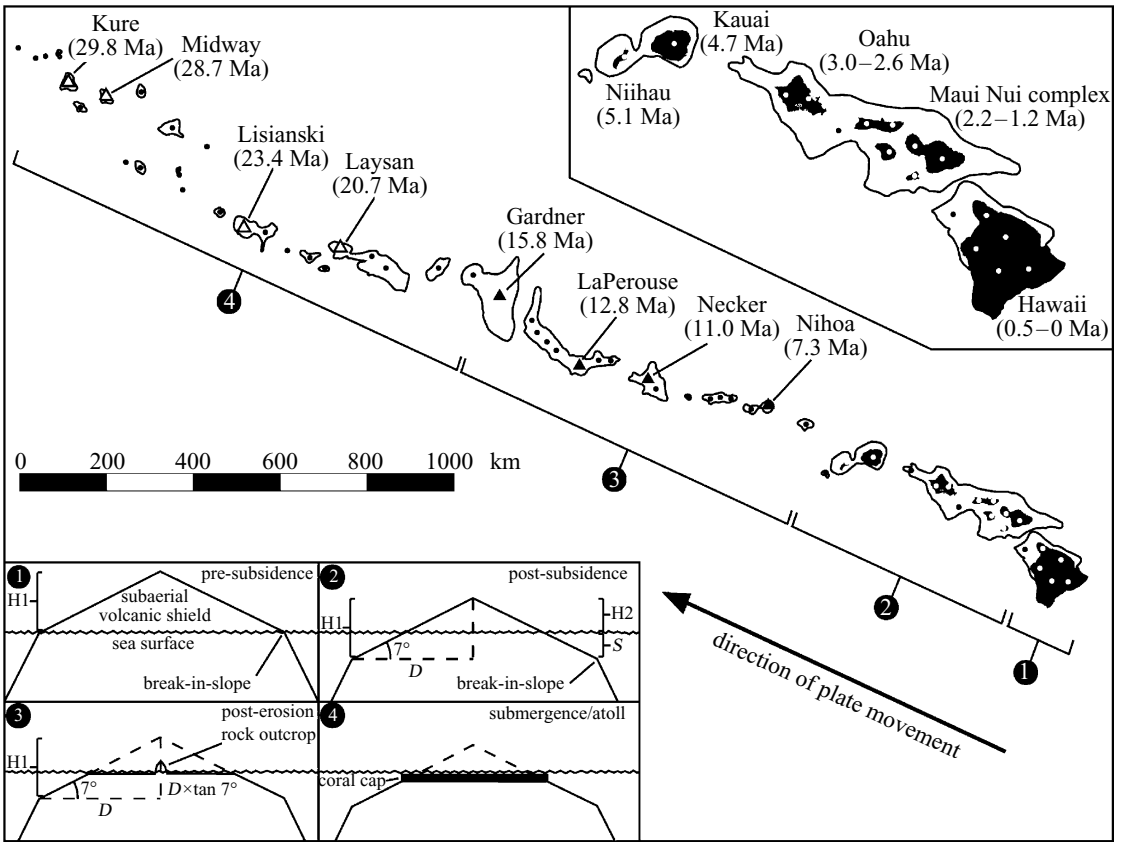

Figure 1. Features of the Hawaiian ridge, life stages of volcanoes, and estimates of height over time. Main islands are detailed in the inset. Ages are given in parentheses for selected volcanic peaks; for islands with multiple volcanoes, the range of ages is given (Clague 1996). The numbered sequence of boxes depicts life stages of islands and associated features used to estimate life histories. (1) The break-in-slope, marking the maximum shoreline of a volcano as it formed, is depicted by a black outline on the map (Moore *et al.* 1994). Ages on the map pertain to the formation of this feature for major volcanoes (Clague 1996). (2) The depth of the break-in-slope (*S*) indicates the amount of subsidence that has occurred since shield formation; the present elevation of an uneroded volcano (H2) is then added to determine its original height (H1). The original height can also be calculated by using the distance from summit to shore (*D*) and assuming a 7° angle. Summits of the main islands (which have not eroded substantially) are shown as white dots on the map over the island areas shown in black. (3) Slower subsidence and erosion reduce volcanic peaks to sea level. Four rocky islets (filled triangles on the map) are near the end of this stage, with the amount of erosion (*E*) estimated. (4) Finally, with no more rock above sea level, only seamounts (black dots) and small coralline islands (open triangles) remain.

can be estimated from this distance assuming a 7° angle. The conservative 5° slope previously used (Clague 1996) is probably an underestimate; a better fit is obtained with the 7° estimate. Confidence of 95% for a given height estimated from a 7° slope is *ca*. 36% of the estimate (for example: 1000 ± 360 m, 2000 ± 720 m, 3000 ± 1080 m, etc.).

(b) *Growth rate*

Volcanoes of the Hawaiian ridge are estimated to reach maximum elevation within *ca*. 0.5 Myr of emergence (Moore & Clague 1992). As age estimates relate to the lavas at the end of this growth stage (Clague 1996), we define this stage as the 0.5 Myr before the estimated age and derive a linear growth rate from the estimated maximum elevation.

(c) *Subsidence rate*

The initial subsidence (measured as the depth of the break-in-slope) varies between 1000 and 1500 m in the main islands. The amount a summit subsides after formation is a function of the volume of material overlaying the crust in the region, so larger, or clustered, volcanoes subside more than smaller, or isolated, volcanoes. We measured the area (in km^2) of subaerial deposits within a 100 km radius of each volcanic summit (the approximate radius of the zone of active subsidence; Moore (1987)) as a surrogate for regional mass. Using known amounts of subsidence from the main islands, we derived an equation to extrapolate an amount of subsidence for volcanoes from which it has not been measured. Examinations of dated coral reefs and volcanic features suggest that the rapid stage of subsidence lasts *ca*. 1 Myr after formation (Moore & Clague 1992). We therefore used the estimated amount of subsidence for each volcano divided by 1 Myr to yield a rate of subsidence.

(d) *Erosion rate*

After rapid subsidence has slowed, erosion plays a larger part in the reduction of a volcanic shield. For the four rocky islets (figure 1), the estimated elevation after initial subsidence, minus the current elevation, approximates the amount of erosion that has occurred. Using the ages of these, we obtained an average rate of erosion for each, which varies according to its estimated height at the end of the subsidence stage (under the assumption that larger volcanoes will generate orographic precipitation and therefore erode more quickly). We derived an equation to extrapolate an erosion rate for each volcano based on its esti-

mated post-subsidence elevation. While the assumption of a constant rate is probably inaccurate (especially considering the occurrence of sporadic massive landslides; Moore *et al.* 1994), there are too few data to determine how this rate may change over time.

(e) *Life history reconstruction*

We reconstructed each volcano's life history by applying the estimated rates for each period in its life cycle according to its estimated age and original height. Each volcano's height was estimated at intervals of 0.5 Myr beginning 32 Myr ago (Ma) (before which time there were no summits above the surface; Carson & Clague 1995), as that represents the upper time limit for the dispersal and evolution of biota. For each time-frame, we examined the distribution of peaks of different sizes.

(f) *Volcano spacing*

We used two methods to determine the spacing of volcanoes. The distance between their maximum shorelines represents the minimum possible distance between them. If the original subaerial surfaces of two volcanoes directly abut, they were joined above the surface before subsidence, thus the effective distance between them is 0. Using this measure, we estimated the distance between each volcano and the next older volcano (the most likely source for dispersal; Carson & Clague 1995). Another measure of the distance between two volcanoes is the distance between their summits. As a volcano subsides and erodes, the area remaining above the surface is centred on the summit. In addition, upland species will be restricted to this area, so that their dispersal distance will be that between two summits.

3. RESULTS

Our model reveals the dynamic nature of the Hawaiian archipelago (figures 2 and 3). During the period from 32 to *ca*. 18 Ma, a few peaks briefly exceeded 1000 m, though at any given point in time most islands were small (figure 2*a*). Gardner, which formed around 16 Ma was the most substantial island to have predated the present high islands and was probably comparable to the present island of Hawaii (greater than 4000 m elevation, greater than 10 000 km^2 area). After its formation, a series of mid-sized volcanoes formed, culminating with Necker at *ca*. 11 Ma. During the period between 18 and 8 Ma (the first 'peak period') there were multiple peaks over 1000 m (some greater than 2000 m) at any given time contributing to a substantial archipelago. The formation of smaller islands after Necker and before Kauai resulted in a diminished archipelago. When Kauai formed, few (if any) older islands had peaks over 1000 m. Since the formation of Kauai, larger volcanoes formed so that for the last 3 Myr there have been multiple peaks over 1000 m continuously (the second peak period) and more area than has existed at any time in the last 32 Myr. Despite the assumptions and uncertainties of the model, it is clear that there were generally smaller volcanoes that formed for several million years before Kauai and that larger islands which formed prior to those had probably diminished when Kauai formed.

Spacing of volcanoes has also varied during the time-period examined. There were three instances when more than three volcanoes connected above the surface: one during the first peak period (St Rogatien through LaPerouse) and two during the second (Oahu through Maui, and the volcanoes of the island of Hawaii) (figure 2*b*). There were also two periods in which volcanoes that formed were more distantly spaced: 27–28 and 5–7 Ma (just before the formation of Kauai). Both methods of measure indicate a pattern of proximity during peak periods and distant spacing during the intervening period (figure 2*b*,*c*).

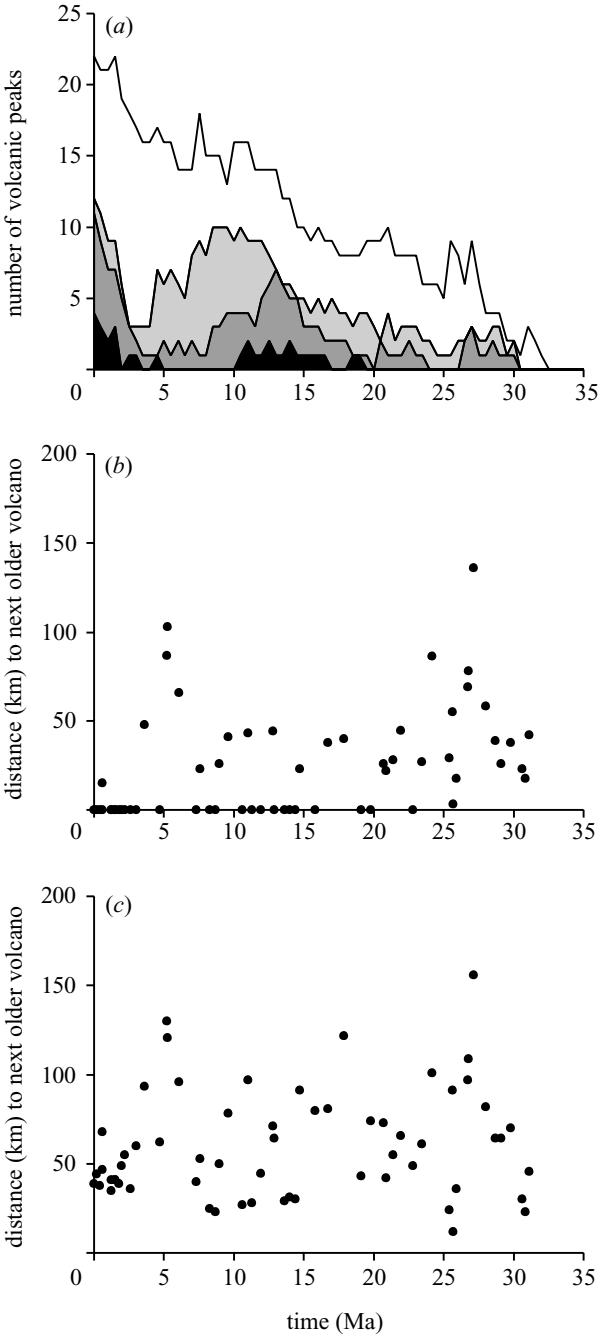

Figure 2. Variation in size and spacing of volcanoes. (*a*) Distribution of peak heights over time (black areas: $>$ 2000 m; dark grey shaded areas: 1000–2000 m; light grey shaded areas: 500–1000 m; white areas: $<$ 500 m). (*b*) Distance between maximum shorelines of volcanoes. (*c*) Distance between summits of volcanoes.

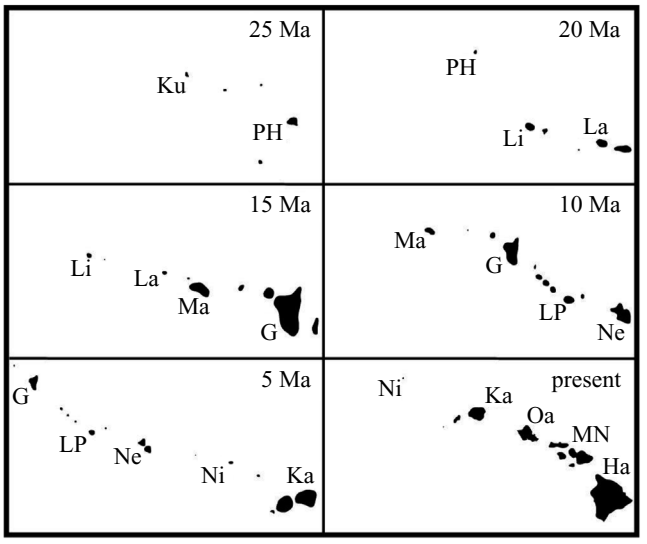

Figure 3. Island configurations at 5 Myr intervals. We adjusted a rough digital elevation model of the estimated pre-erosion surface according to height estimates for different points in time. Ku, Kure; PH, Pearl and Hermes; Li, Lisianski; La, Laysan; Ma, Maro; G, Gardner; LP, LaPerouse; Ne, Necker; Ni, Nihoa; Ka, Kauai; Oa, Oahu; MN, Maui Nui; Ha, Hawaii.

4. DISCUSSION

Colonization from outside the archipelago most probably occurred when substantial islands with diverse habitats were available. A volcanic island's area and range of habitats are closely related to its height, so the two peak periods probably presented the best opportunities for colonization. Juvik (1998) estimated the frequency of colonization for different groups of organisms using the time since the formation of Kure and estimated numbers of colonists that led to the present biota: once in 98 000 years for plants, once in 68 000 years for insects and less than once in 1 Myr for birds. These should be considered *net* rates, however, since many lineages (the progeny of colonization events), even if resident for millions of years, have undoubtedly become extinct within this period. The *actual* colonization rate is certainly higher but cannot be estimated due to an unknown extinction rate for lineages.

The most likely source for the biota of an emerging island is the next oldest island that has not yet eroded away (Carson 1983; Carson & Clague 1995; Givnish *et al.* 1995). Because immigration rate relates to distance (MacArthur & Wilson 1967) and the available range of habitats (on target and source islands), it is possible to speculate on the relative rate of transfer of biota from older to younger islands, based on palaeogeography. We expect high rates of transfer when high islands are numerous and closely spaced; therefore the two peak periods were the most favourable times for the transfer of biota from older to younger islands. Conversely, we expect low rates of transfer when high islands are few and widely spaced. When Kauai (the oldest present high island) formed, there were relatively small islands available as a source, and the largest of these (Nihoa, Necker, LaPerouse and Gardner) were distant compared with the spacing of the present high islands (figure 2). Thus, there may have been a 'bottleneck' whereby a limited amount of the biota that existed during the first peak period was transferred to the islands of the present peak period. Additionally, while higher elevation habitats (greater than 1500 m) occurred during the first peak period, they had probably vanished entirely by the time Kauai formed, and with a climate that was probably warmer at that time source islands were even less likely to contain cool upland habitats. Contemporary species living in montane habitats probably arrived from outside the Hawaiian archipelago or evolved after the formation of Kauai. Examples include species of the silversword alliance, *Geranium*, *Viola* and *Tetramolopium* (table 1). Lowland and coastal taxa may have experienced a less severe bottleneck, since low elevation islands were more numerous and less distantly spaced than high islands.

In the Hawaiian Islands, the descendants of original colonists form distinct lineages. While many lineages consist of a single species, several well-studied lineages have diversified considerably and account for the majority of species diversity (Carlquist 1980; Wagner *et al.* 1990). Assuming the degree to which a lineage diversifies is a function of the area and range of habitats available (Heaney 1986; Losos & Schluter 2000), the two peak periods presented the best opportunities for speciation. With the previously discussed bottleneck limiting the transfer of biota to the present high islands, the present species pool would then be a result of divergence of limited transfers (from older islands) and recent colonists (from outside). Hence, we propose that much of the present species pool is in lineages that arrived or diversified rather recently.

To test this theory we surveyed the literature and assembled estimates (most of which use a molecular clock) of the timing of arrival and diversification of Hawaiian taxa. Two types of estimates are available. The first type is the age of the **m**ost **r**ecent **c**ommon **a**ncestor (MRCA) of multi-species lineages of Hawaiian organisms. This marks when historically known taxa began to diverge from one another, but does not necessarily indicate the time of colonization. It is possible that a given lineage colonized older islands long ago and that a single transfer to the present high islands diversified into the known taxa more recently. A second type of estimate is that of the age of the MRCA of Hawaiian taxa and an outside relative. In most cases, the closest outside relative is not known or has gone extinct, and thus many estimates of the MRCA are based on a more distant relative. The age of divergence from an outside relative is therefore probably older than the actual time of colonization. Thus, any such age estimate marks the upper time limit of colonization and any subsequent divergence within the islands. Both types of estimate are numerous in the Hawaiian Islands compared with other regions. When available, the first type of estimate was preferred; otherwise, the second type was used (table 1).

For multi-species lineages, 12 out of 15 have diverged since the formation of Kauai. Of these 12 lineages, three have diverged from outside relatives (and thus colonized) since 5 Ma while, for the rest, the possibility remains that they arrived in the archipelago earlier and diversified from a single transfer event. For single-species lineages and those that have an unknown number of species, all seven have diverged from outside relatives (and thus colonized)

Table 1. Age estimates for MRCAs of lineages of Hawaiian organisms.[a]

lineage	type of organism	no. of species	age (Ma)	method	source
Hawaiian fruitflies (Drosophilidae)	insect	*ca*. 1000	26	IC	Russo *et al.* (1995)
Hawaiian lobelioids (Campanulaceae)	plant	125	15	IC	Givnish *et al.* (1996)
Megalagrion damselflies (Coenagrionidae)	insect	23	9.6	IC	Jordan *et al.* (2003)
Silversword Alliance (Asteraceae)	plant	28	5.1	IC	Baldwin & Sanderson (1998)
Laysan duck, *Anas laysanensis* (Anatidae)	bird	1	< 5	EC	Fleischer & McIntosh (2001)
Hawaiian crows, *Corvus hawaiiensis* + other spp.? (Corvidae)	bird	1+?	< 4.2	EC	Fleischer & McIntosh (2001)
Hawaiian honeycreepers, Drepanidinae (Fringillidae)	bird	*ca*. 50	4–5	IC	Fleischer *et al.* (1998)
Viola spp. (Violaceae)	plant	6	3.7	BS, LD	Ballard & Sytsma (2000)
flightless Anseriformes, 'moa-nalos' (Anatidae)	bird	4	< 3.6	EC	Sorenson *et al.* (1999)
Hawaiian thrushes, *Myadestes* spp. (Muscicapidae)	bird	5	< 3.35	EC	Fleischer & McIntosh (2001)
Kokia spp. (Malvaceae)	plant	4	< 3	EC	Seelanan *et al.* (1997)
flightless rails, *Porzana sandwicensis* + other spp.? (Rallidae)	bird	1+?	< 2.95	EC	Fleischer & McIntosh (2001)
Geranium spp. (Geraniaceae)	plant	6	2	BS	Funk & Wagner (1995)
Hesperomannia spp. (Asteraceae)	plant	4	1.81–4.91	EC	Kim *et al.* (1998)
flightless ibises, *Apteribis* spp. (Plataleidae)	bird	2	< 1.6	EC	Fleischer & McIntosh (2001)
Hawaiian duck, *Anas wyvilliana* (Anatidae)	bird	1	< 1.5	EC	Fleischer & McIntosh (2001)
flightless rails, *Porzana palmeri* + other spp.? (Rallidae)	bird	1+?	< 1.05	EC	Fleischer & McIntosh (2001)
Hawaiian geese, *Branta* spp. (Anatidae)	bird	3	< 1	EC, LD	Fleischer & McIntosh (2001)
Hawaiian black-necked stilt, *Himantous mexicanus knudsenii* (Recurvirostridae)	bird	1	< 0.75	EC	Fleischer & McIntosh (2001)
Hawaiian hawk, *Buteo solitarius* (Accipitridae)	bird	1	< 0.7	EC	Fleischer & McIntosh (2001)
Tetramolopium spp. (Asteraceae)	plant	11	0.6–0.7	EC, LD	Lowrey (1995)
Metrosideros spp. (Myrtaceae)	plant	5	0.5–1.0	LD	Wright *et al.* (2001)

[a] For lineages with an age estimate for the MRCA of Hawaiian taxa and an outside relative (second type of estimate), the age given is the maximum possible age of colonization and any subsequent divergence, and is denoted by a '<'. For three bird lineages, only one species was analysed, even though the lineage may contain additional extinct species that have not been sampled. 'method' refers to the method of age estimation: IC: internally calibrated molecular clock (as described in Fleischer *et al.* 1998); EC: externally calibrated molecular clock; BS: basal split in phylogeny between two islands of known age; LD: very low level of sequence divergence. The estimate by Fleischer *et al.* (1998) for Hawaiian honeycreepers supersedes previous estimates by Sibley & Ahlquist (1982) and Johnson *et al.* (1989), which suggest older origins for the group. For lobelioids, the estimate by Givnish *et al.* (1996) supersedes Givnish *et al.* (1995). The estimate by Russo *et al.* (1995) for drosophilids supersedes estimates by Beverley & Wilson (1985), Thomas & Hunt (1991) and DeSalle (1992), but agrees with the notion of an ancient origin for the group. There remains the possibility that the drosophilids are the result of two colonization events from outside, one for the 'drosophiloids' and one for the 'scaptomyzoids'; if so, then the dates of the MRCAs for these lineages are 11.0 and 10.9 Ma, respectively (Russo *et al.* 1995). For a recent review on this question, see Davis (2000).

since 5 Ma. Additional plant lineages exhibit very low levels of sequence divergence between taxa in the Hawaiian Islands (despite including many species or considerable morphological diversity), indicating rapid divergence from a recent colonization or single transfer event: Alsinoidae (32 species, two endemic genera; Soltis *et al.* 1996), *Bidens* (19 species; Ganders *et al.* 2000), and *Pittosporum* (11 species; Gemmill *et al.* 2002). Five additional single-species bird lineages (common moorhen, Hawaiian coot, black-crowned night heron, short-eared owl and Old World white-tailed eagle) are morphologically or genetically very similar to outside taxa, indicating recent arrival (Fleischer & McIntosh 2001). Therefore, there is no evidence that any endemic bird lineage colonized the archipelago prior to the formation of Kauai.

The Hawaiian biota, regardless of the timing of colonization, has been shaped by recent speciation. It is, however, possible that our view of Hawaiian lineages is skewed by the limitation of our knowledge to those that have existed more recently, thus subjecting us to the 'pull of the recent' (Raup 1972). However, the fact that large radiations have been the preferred subjects of phylogenetic studies augments the significance of the apparent lack of old lineages. Even within lineages believed to have begun diverging before the formation of the current high islands, it is probable that relatively few (but at least two) transfer events from former high islands, followed by rapid divergence, led to the current set of species. This scenario is not unlike mass extinction events in which the majority of species are extirpated and a handful of survivors diverges rapidly to fill empty niche space (Simpson 1944). In this case, the survivors are those members of the biota of older islands that dispersed to the current high islands and subsequently diversified. In remote archipelagos, geological and climatic

changes occur more rapidly than dispersal and speciation can respond, so their biotas are in a state of dynamic disequilibrium (Heaney 1986). Because the landscape of the Hawaiian archipelago is more dynamic than previously thought, only rapid speciation can account for its rich and unique biota.

Note added in proof. A new phylogeny of a lineage consisting of three endemic plant genera of the Lamiaceae indicates that they diverged from an outside relative (and thus colonized) between 2.6 and 7.4 Ma, representing a recent radiation in the second largest Hawaiian plant lineage (60 spp.). This is an externally calibrated molecular clock estimate (Lindqvist & Albert 2002).

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