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Origin and evolution of Hawaiian endemics: new patterns revealed by molecular phylogenetic studies

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The current high islands of the Hawaiian archipelago are among the most remote land masses in the world. They lie 3500 km from California, the nearest continental source, and approximately 2300 km from the Marquesas, the nearest islands (Fig. 4.1). They are the southernmost islands in the Hawaiian Ridge, formed successively over a ‘hot spot’ that has allowed magma to penetrate the Pacific Plate. The plate has moved gradually north and northwestwards over the past 85 Ma, leaving the previously formed islands to gradually erode and subside (Clague, 1996). The current high islands (Fig. 4.1, inset) range in age from Kauai/Niihau (5.1–4.9 Ma), to Oahu (3.7–2.6 Ma), to Maui Nui (2.2–1.2 Ma), during the Pleistocene comprising several islands – West Maui (1.3 Ma), East Maui (0.75 Ma), Molokai (1.76–1.90 Ma), Lanai (1.28 Ma) and Kaho’olawe (1.03 Ma) – and Hawaii (0.5 Ma to present) (Price & Clague, 2002).

Important for the establishment and evolution of the extant Hawaiian flora is the historic pattern of island formation within the archipelago. For example, islands with elevations greater than 1000 m did not exist from 30 to 23 Ma and from *c.* 8 to 5 Ma when the current high islands began to emerge (Clague, 1996; Price & Clague, 2002; Clague *et al.*, 2010). These gaps likely precluded colonisation of the current high islands by taxa on the older islands, although some may have persisted long enough to disperse to the current high islands (Clague *et al.*, 2010). As a result of the history of the islands’ formation and data from recent molecular studies, the processes of colonisation and diversification are generally assumed to have taken place within the past *c.* 5 Ma, as a result of long-distance dispersal (Price & Clague, 2002; Price & Wagner, 2004; Cowie & Holland, 2006).

Hawaii’s flowering plants are *c.* 90% endemic, and its fern flora is 70% endemic, one of the highest percentages in the world. They arose from an estimated 263–270

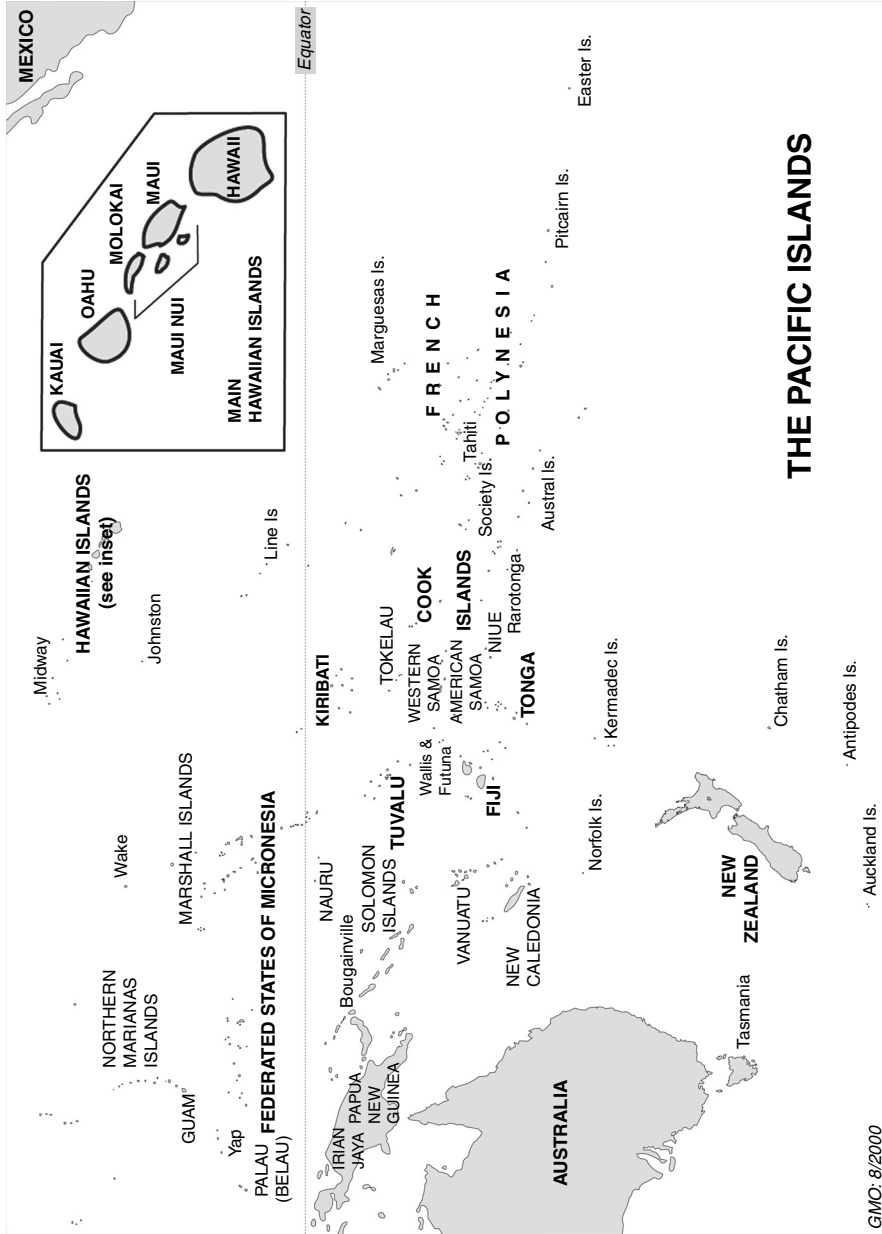


Figure 4.1 The Pacific islands, Australia, New Guinea, New Zealand and Mexico. Inset: the main Hawaiian Islands. Used by permission, C. Gemmill.

original colonists which have given rise to approximately 1030 species of flowering plants and 162 species of ferns for a total of 1192 species of vascular plants (Palmer, 2003; Price & Wagner, 2004). As a result the diversification and spread of genera within and between islands, the factors influencing their radiations, the sources of colonists and the morphological and genetic diversity of Hawaiian plants have been of interest from both evolutionary and biogeographic perspectives as the islands offer an unusual opportunity for separating these factors from the more complex interactions responsible for the creation of continental floras (Fosberg, 1948; Carlquist, 1970, 1974; Wagner *et al.*, 1995).

Wagner *et al.* (1990, 1999) listed the predominate source of the Hawaiian flora as Malesia (the region including the Malay Peninsula, Indonesia, the Philippines and New Guinea) with other relatives in Australia, New Zealand and the Pacific. However, recent work has shown that boreal, temperate and tropical regions of the Americas, Asia and Africa have also served as the source of Hawaiian genera. Dispersal has been largely by birds, with fruits carried either externally or internally, but also by wind and water (Carlquist, 1970, 1974; Wagner *et al.*, 1995; Ballard & Sytsma, 2000; Price & Wagner, 2004). Wagner and Funk (1995) brought together much of the information available at that time on Hawaiian plant and animal groups. The overarching question they attempted to answer was: Do lineages of plants and animals follow biogeographic patterns similar to the geologic pattern of island formation? That is, are the basal taxa on the oldest islands and do they move in a regular pattern to younger islands (the Progression Rule)? The largely morphological data were analysed using a consistent cladistic approach. Authors of the individual chapters also discussed the speciation and radiation of various lineages, the likely age of colonisations, habitat shifts and back-colonisations.

Molecular studies since Wagner and Funk (1995) have expanded the scope beyond the patterns within the islands themselves to phylogenetic relationships across broad geographical regions. These studies have revealed new sources of colonists, clarified the number of colonisation events, added information on the age of several lineages and revealed a role for the Hawaiian Islands within the Pacific that were not previously known. Additional data on hybridisation and polyploidy have also contributed to our understanding of the origin and evolution of the Hawaiian flora. A selection of these studies is presented below to illustrate the main findings.

Geographic sources of colonists

The endemic Hawaiian flora is the product of colonisation from a variety of geographic sources (Wagner *et al.*, 1990; 1999). Fosberg (1948) and Carlquist (1970) suggested that the majority of species lineages were derived from ancestors in the

tropical Western Pacific, but believed that other areas were to be expected from the Americas and perhaps more distant sources. Contributions by Lowrey, and Baldwin and Robichaux in Wagner and Funk (1995), using molecular data, identified New Guinea and western North America, respectively, as sources of Hawaiian *Tetramolopium* and the silversword alliance, both in the family Compositae, while geographical relationships of other genera often remained unconfirmed pending further study. Molecular studies since that time have revealed that the ancestors of the Hawaiian flora came from other areas separated from the Hawaiian Islands by great over-water and climatic distances. Among the most unusual of these are colonists from Africa and the Arctic or boreal regions. Additional colonisations have also been reported for taxa originating in western North America, Australia, New Zealand and Asia. For some of these taxa the area of origin may change with the addition of more outgroup taxa, as even now differing interpretations are possible in some cases. Regardless, it is clear that the Hawaiian flora is the product of colonisations from geographically diverse ancestors.

Africa

An unexpected source of direct colonisation to the Hawaiian Islands was revealed for the endemic genera *Hesperomannia* and *Kokia*. *Hesperomannia* (Fig. 4.2) was shown, unequivocally, to be derived from an African/Madagascan ancestor (Kim *et al.*, 1998). Although this was unexpected for a Hawaiian group, both the nuclear and chloroplast data confirmed its placement in the Compositae tribe, Vernoniaeae, rather than in the South American tribe, Mutisieae, where it had previously been placed. Furthermore, phylogenetic study of Old and New World Vernoniaeae (Keeley *et al.*, 2007) continues to support the placement of *Hesperomannia* near the base of the phylogeny. The three species of *Hesperomannia* form a monophyletic group nested within a clade of African/Madagascan taxa. Kim *et al.* (1998) estimated that the time of divergence between the African ancestor and *Hesperomannia* at 17–26 Ma \pm 1–3.43 Ma depending on gene region used for dating. They postulated the ancestor of *Hesperomannia* arrived in the archipelago when one of the northwestern Hawaiian Islands was still above water.

However, it is also possible that the ancestor of *Hesperomannia* was growing somewhere else during this period and arrived in Hawaii more recently. The estimated divergence among the extant species of *Hesperomannia* suggests that their radiation occurred between 1.8 and 4.9 Ma (Kim *et al.*, 1998; Price & Wagner, 2004), within the time frame of the current high islands. The only other taxon currently proposed to have an African origin (Table 4.1) is *Kokia*. Seelanan *et al.* (1997) used nuclear chloroplast sequences in a worldwide study of the cotton genus *Gossypium*. In the course of their study it was discovered that the African/



Figure 4.2 Endemic Hawaiian genera: (a) *Cyrtandra lessoniana* Gard, (b) *Hesperomannia arborescens* A. Gray, (c) *Argyroxiphium sandwicense* DC., (d) *Clermontia parviflora* Gaud. ex A. Gray, (e) *Melicope clusiifolia* (A. Gray) T. G. Hartley & B. C. Stone, (f) *Phyllostegia ambigua* (A. Gray) Hillebr. All photos by G. Carr except (c) by V. Funk. For colour figure see www.cambridge.org/9780521118088

Madagascan genus *Gossypoides* was sister to the Hawaiian genus *Kokia* and that the monophyletic *Gossypium* was the sister of the *Kokia* + *Gossypoides* clade. Using molecular clocking methods it was estimated that *Gossypium* diverged from its sister clade, *Kokia* + *Gossypoides*, approximately 12.5 Ma. The small amount of sequence difference between *Kokia* and *Gossypoides* resulted in a divergence between these two genera well within the age range of the modern high islands of Hawaii. It was thought that the ancestor of *Kokia* was most likely dispersed over water directly from Africa/Madagascar as there are no known stopping places between these two regions (Seelanan *et al.*, 1997). The origin of *Kokia* may need

Table 4.1 Genera, number of species, estimated age and area of origin of Hawaiian endemics.

Name	No. of species	Age (Ma)	Geographic origin	Type of data	Reference
Araliads: <i>Tetraplasandra</i> , <i>Reynoldsia</i> , <i>Munroidendron</i> (Araliaceae)	9	no date	Pacific or palaeotropics	ITS, 5S-NTS, morphology	Costello & Motley, 2007
<i>Bidens</i> (Compositae)	19	no date	Western North America-Meso- America	ITS	Kimball & Crawford, 2004
<i>Broussaissia arguta</i> (Hydrangeaceae)	1	no date	Asia	matK, rbcL	Hufford <i>et al.</i> , 2001
<i>Chamaesyce</i> (Euphorbiaceae)	27	no date	North America – Mexico	ITS, trnL-F, trnH- psbA, ndhA intron, nuclear DEADX9	Yang <i>et al.</i> , 2009
<i>Cheirodendron</i> (Araliaceae)	5	no date	uncertain	ITS	Plunkett & Lowry, 2001
<i>Cuscuta sandwichiata</i> (Convolvulaceae)	1	no date	North America (possibly)	26S	Neyland, 2001; Stefanovic <i>et al.</i> , 2007
<i>Cyrtandra</i> (Gesneriaceae)	58	no date	Asia-Pacific	ITS	Cronk <i>et al.</i> , 2005
<i>Euphorbia</i> (Euphorbiaceae)	1	no date	Australia, Melanesia	ITS, <i>ndhF</i>	Steinmann & Porter, 2002
<i>Geranium</i> (Geraniaceae)	7	2	Western North America	rbcL	Pax <i>et al.</i> , 1997
<i>Gossypium tomentosum</i> (Malvaceae)	1	1–2	Meso-America	DNA restriction site	DeJooode & Wendle, 1992
<i>Gunnera</i> (Gunneraceae)	2	no date	North America or the Americas	ITS, morphology	Wanntorp & Wanntorp, 2003
<i>Hedyotis</i> (Rubiaceae)	20	no date	uncertain	ITS	Motley <i>et al.</i> , 1998
<i>Hesperomannia</i> (Compositae)	3	17–26 (+1–3.43) 20.5 / 3.36	Africa	ITS, <i>ndhF</i>	Kim <i>et al.</i> , 1998; Price & Wagner, 2004

<i>Hillebrandia sandwicensis</i> (Begoniaceae)	1	15	Australasia or the tropics	18S, rbcL, ITS	Clement <i>et al.</i> , 2004
<i>Kandloa</i> (Leguminosae)	1	no date	uncertain	nr 5.8S; ITS	Hughes <i>et al.</i> , 2003
<i>Kokia</i> (Malvaceae)	4	3	Africa or tropics	ITS, ndhF	Seelanan <i>et al.</i> , 1997
<i>Korthalsella</i> (Santalaceae)	6 (or 2)	no date	Australasia	ITS, trnL-F; 18S, rbcL	Molvray <i>et al.</i> , 1999
<i>Labordia</i> (Loganiaceae)	16	no date	Asia-Pacific	morphology, hybridisation studies, chromosome number	Motley & Carr, 1998
Lobelids: <i>Brighamia</i> , <i>Clermontia</i> , <i>Cyanea</i> , <i>Delissea</i> , <i>Lobelia</i> , <i>Trematolobelia</i> (Lobeliaceae)	126	13	Asia-Polynesia or Africa	rpl16, rbcL, psbA- trnH, trnL-trnF, trmT-TrnL, trnV- trnk, atpB-rbcL	Givnish <i>et al.</i> , 2009
<i>Lysimachia</i> (Myrsinaceae)	15	no date	Southeast Asia	trnL-F, ITS	Hao <i>et al.</i> , 2004
<i>Melicope</i> (Rutaceae)	47	no date	Austral region	ITS, trnL-F, trnE-T, trmH-psbA	Harbaugh <i>et al.</i> , 2009b
<i>Metrosideros</i> (Myrtaceae)	1–3	3.9 (1.4–6.3)	Pacific	ITS, ETS; trnS- trnG spacer, trnG intron, trnD-trnE- trn-trnT spacers, rpl16 spacer; microsatellites	Wright <i>et al.</i> , 2001; Percy <i>et al.</i> , 2008; Harbaugh <i>et al.</i> , 2009c
Mints: <i>Stenogyne</i> , <i>Haplostachys</i> , <i>Phyllostegia</i> (Labiatae)	60	5 (2.6–7.4)	Western North America	rbcL, trnL, ITS 5.8 S	Lindqvist & Albert, 2002; Lindqvist <i>et al.</i> , 2003
<i>Pittosporum</i> (Pittosporaceae)	10	no date	Melanesia	ITS	Gemmil <i>et al.</i> , 2002; Cayzer <i>et al.</i> , 2000
<i>Plantago</i> (Plantaganaceae)	6	no date	North America	ITS, ETS, ndhF, rpl32 & rpl32-trnL	Dunbar-Co <i>et al.</i> , 2008; Wagner, pers. comm.

Table 4.1 (cont.)

Name	No. of species	Age (Ma)	Geographic origin	Type of data	Reference
<i>Pritchardia</i> (Palmae)	23	no date	South Pacific (New Zealand, Australia, Papua New Guinea and neighbouring islands)	supertree	Baker <i>et al.</i> , 2009; Bacon, pers. com.
<i>Psychotria</i> (Rubiaceae)	11	no date	Austral	ITS, ETS	Nepokroeff <i>et al.</i> , 1999, 2003
<i>Rhus sandwicensis</i> (Anacardiaceae)	1	13.5 + -3	Asia	ITS, ndhF, trnL-F	Yi <i>et al.</i> , 2004
<i>Rubus hawaiiensis</i> (Rosaceae)	1	no date	Western North America	ITS, ndhF	Alice & Campbell, 1999
<i>Rubus macraei</i> (Rosaceae)	1	no date	Western North America	ITS, ndhF	Alice & Campbell, 1999
<i>Santalum</i> 1st dispersal (Santalaceae)	2	1.0–1.5	Australia	ITS, ETS, trnK	Harbaugh & Baldwin, 2007; Harbaugh, 2008
<i>Santalum</i> 2nd dispersal (Santalaceae)	2	411–616 KY	Australia	ITS, ETS, trnK	Harbaugh & Baldwin, 2007; Harbaugh, 2008
<i>Scaevola glabra</i> (Goodeniaceae) endemic tetraploid	1	no date	Australia	ITS, LFY, NIA, G3PDH	Howarth <i>et al.</i> , 2003; Howarth & Baum, 2005
<i>Scaevola</i> (Goodeniaceae) endemic diploid clade	8	no date	Australia	ITS, LFY, NIA, G3PDH	Howarth <i>et al.</i> , 2003; Howarth & Baum, 2005
<i>Scaevola taccada</i> (Goodeniaceae) indigenous	1	no date	Australia – Polynesia	ITS, LFY, NIA, G3PDH	Howarth <i>et al.</i> , 2003; Howarth & Baum, 2005

<i>Schiedea</i> (Caryophyllaceae)	34	no date	Arctic	matK, trnL-F, and rps16	Nepokroeff <i>et al.</i> , 1999, 2003; Harbaugh <i>et al.</i> , 2009a
<i>Sicyos</i> (Cucurbitaceae)	14	no date	Australia	nuclear & chloroplast	Sebastian <i>et al.</i> , 2009
<i>Silverswords: ArgYROXiphium, Dubautia, Wilkesia</i> (Compositae)	30	5 (+0.8)	Western North America	ITS, ETS, trnK, APETALA-1, APETALA-3/TMS6	Synthesised in Carlquist <i>et al.</i> , 2003
<i>Silene</i> (Caryophyllaceae)	7	no date	uncertain: Americas or Mediterranean	rps 16 intron, ITS, intron 23 of RPB2	Eggens <i>et al.</i> , 2007
<i>Tetramolopium</i> (Compositae)	11	>1	Australasia	rbcl	Lowrey <i>et al.</i> , 2005; Lowrey, pers. comm.
<i>Vaccinium</i> (Ericaceae)	3	no date	Arctic, Boreal	ITS, matK, ndhF	Powell & Kron, 2002
<i>Viola</i> (Violaceae)	9	3.7 (upper limit)	Arctic, Beringia	ITS	Ballard & Sytsma, 2000; Havran <i>et al.</i> , 2009

further examination, however, as the African connection is found only in the sister group to *Kokia*, while the other outgroups show a more general tropical to subtropical distribution.

Arctic-boreal

Ballard and Sytsma (2000) identified the Arctic (Northern Pacific) *Viola langsdorffii* Fisch. ex Ging. as the sister to Hawaiian *Viola*, contrary to the prior view that they were descended from South American species. Using nuclear and chloroplast data (Table 4.1) to look at the relationships among *Viola* taxa in South and Central America, North America and Mexico, Asia and Europe, as well as the Hawaiian Islands, they also showed that Hawaiian species were derived, rather than basal as had been proposed based on their woody habit. They argued that a mid-Pliocene dispersal would have involved a *V. langsdorffii* already adapted to cold tundra and bogs. Although there is no tundra in Hawaii, Hawaiian violets are restricted to high elevation habitats, commonly bogs and other moist sites. The data provided an upper limit of 3.7 Ma for successful colonisation of Kauai (the oldest high island) and subsequent radiation of species within the islands.

A more recent study (Havran *et al.*, 2009), however, suggests that the original site of colonisation was likely the Maui Nui complex, thus estimating an age of 1.2–2 Ma. Ballard and Sytsma (2000) also documented the routes of migratory birds, identifying 260 species that visit Hawaii with approximately 39% coming from the Arctic and North Pacific in contrast to Australasia and the South Pacific where only about 20% of the migratory birds are found. They further suggested that the low numbers of species from Arctic ancestors may be the result of poor survival of cold-adapted species to tropical conditions or to misidentification of the source of ancestors of Hawaiian taxa.

Similarly, the three Hawaiian *Vaccinium* species (section *Macropelma* (Klotzsch) Hook. f.) were also shown to have a boreal origin (Powell & Kron, 2002). Chloroplast and nuclear DNA phylogenies showed that Hawaiian *Vaccinium* formed a monophyletic group; they had previously been placed in the wrong section. Instead of being South Pacific in origin, as had been hypothesised, the Hawaiian species were shown to be derived from within the Arctic-boreal section *Myrtilus* Dumort. *Vaccinium cereum* (L.f.) Forster (section *Macropelma*), from the Society Islands, showed affinity with the Hawaiian species based on chloroplast DNA, but this was in conflict with relationships determined by morphology and nuclear sequence data which showed Arctic origins. As a result a hybrid origin was hypothesised for this species, but the manner in which such a hybrid could be formed was not resolved.

Schiedea is the largest radiation in the Hawaiian Islands (34 species) with a purported Arctic origin (Wagner *et al.*, 2005). This study showed a single introduction

with several different radiations within the islands. The most closely related genera are the monotypic *Honckenya* and *Wilhelmina*, which have distributions that are circumboreal and Alaskan to northeastern Asian, respectively. The authors postulated that the first colonist may have been on an island older than the current high islands (Wagner *et al.*, 2005).

Western North America

The most thoroughly documented case of a Hawaiian species group derived from a western North American ancestor is that of the silversword complex, containing 30 species in the genera *Argyroxiphium*, *Dubautia* and *Wilkesia*. The origin and evolution of this group has been extensively investigated over the past 30 years by Sherwin Carlquist (Santa Barbara Botanic Garden), Bruce Baldwin (University of California, Berkeley), Gerald Carr (University of Hawaii, Manoa) and Robert Robichaux (University of Arizona) culminating in the publication of *Tarweeds and Silverswords* (Carlquist *et al.*, 2003). Phylogenetic data from nuclear and chloroplast DNA and nuclear homeotic genes (Table 4.1) along with data from crossing experiments, cytology, chemistry and anatomy were synthesised by Baldwin (2003) as part of this extensive treatment. The information from molecular work, as well as that by the other contributors, confirmed earlier hypotheses that the Hawaiian silverswords were monophyletic and derived from a single colonisation event (Carlquist *et al.*, 2003). In addition, the origin of the group from the primarily Californian 'Madiæ' lineage in the Madiinae (Heliantheae) was confirmed and the ancestors identified from among extant taxa, a most remarkable finding (Baldwin, 2003). The lineage is one of the largest and best understood of the Hawaiian taxa exhibiting adaptive radiation. Hybridisation and polyploidy, discussed below, were also important in the establishment and speciation of the silverswords.

Several other taxa including some with large radiations, i.e. the Hawaiian mints (60 species), *Chamaesyce* (27) and *Bidens* (19), have been identified as having a western North American origin as well (Table 4.1). The Hawaiian mints are found in three genera, *Phyllostegia*, *Stenogyne* and *Haplostachys*, and were previously thought to be Asian in origin. However, recent studies have shown them to be most closely related to species in the temperate North American genus *Stachys* and documented that they are the result of one colonisation event (Lindqvist & Albert, 2002; Lindqvist *et al.*, 2003). It is also likely that the 19 endemic species of *Bidens* originated from ancestors in North America, Mexico or Central America (Kimball & Crawford, 2004; Funk *et al.*, unpublished) and Hawaiian *Chamaesyce* have recently been found to be monophyletic and to be nested in a group of weedy Mexican species (Yang *et al.*, 2009).

Similarly, the six species of Hawaiian *Plantago* (Dunbar-Co *et al.*, 2008; Wagner, pers. com.), the five *Geranium* species (Pax *et al.*, 1997), and the two species of *Gunnera* (Wanntorp & Wanntorp, 2003) each form monophyletic groups based on a single introduction, most likely from North America (Table 4.1). There are also several other Hawaiian taxa related to American lineages, but these have only one known species each. The Hawaiian endemic species of *Gossypium* (DeJode & Wendel, 1992) and *Cuscuta* (Stefanovic *et al.*, 2007) and the indigenous species of *Ilex* (Cuenoud *et al.*, 2000) were found to be most closely related to North American or Meso-American taxa. A slightly different scenario has been put forward for *Rubus* whose two endemic species, *R. hawaiiensis* A. Gray and *R. macraei* A. Gray are not closely related to each other. They were found to be the result of two separate colonisations from North American ancestors (Howarth *et al.*, 1997; Alice & Campbell, 1999).

The seven species of *Silene* (Eggens *et al.*, 2007) were found to be a single radiation in Hawaii. However, the exact origin of this clade is not clear. The sister taxon is a weedy species from the Americas (*S. antirrhina* L.) but the next three clades are from the Mediterranean as well as the Middle East, Northern Africa, the Arctic and Europe. Sister to these outgroups is one from Asia reaching over into northwest North America (Eggens *et al.*, 2007). At this point it might be best to list the origin of this taxon as 'uncertain' until more North America taxa are included in the analysis.

Asia

Asia has been postulated to be the site of origin of a number of Hawaiian lineages (Table 4.1). Hawaiian *Lysimachia* (Hao *et al.*, 2004) in the subgenus *Lychimachiopsis* (A. Heller) Hand.-Mazz. were suggested to be related to Malesian taxa (Wagner *et al.*, 1999) and to be the result of two colonisation events. However, a worldwide phylogenetic study of the genus using both chloroplast and nuclear sequence data (Table 4.1) strongly support the monophyly of the 15 endemic Hawaiian species and a sister group relationship with taxa in the Asian subgenus *Palladia* (Moench) Hand.-Mazz. (Hao *et al.*, 2004). For the endemic taxa sampled only a single colonisation was supported from a Southeast Asian ancestor. However, the study did not include *L. mauritiana* Lam., an indigenous Hawaiian species also in subgenus *Palladia*, so it remains to be verified that *L. mauritiana* originated from a separate colonisation event. In addition, an Asian origin for the single Hawaiian endemic species of the genus *Rhus*, *R. sandwicensis* A. Gray, was indicated in a study of Northern Hemisphere *Rhus* species employing both chloroplast and nuclear DNA sequence data (Yi *et al.*, 2004). *Rhus sandwicensis* was found to be most closely related to *R. chinensis* Mill., distributed from Asia to Malaysia, and was estimated

to have diverged from it 13.5 + 3.0 Ma. Given the limited availability of high islands during this period, it is likely that the immediate ancestor of *R. sandwicensis* was somewhere in Asia or between Asia and Hawaii for a significant period before dispersing to the islands.

In addition to those taxa with a clearly Asian ancestry, two genera, *Cyrtandra* (Fig. 4.2) and *Labordia*, appear to have originated in a somewhat broader Asian-Pacific region. *Cyrtandra* (Cronk *et al.*, 2005) is widely distributed throughout the Pacific islands and Malesia and has *c.* 58 endemic species in the Hawaiian Islands. These species were thought to be the product of four to six independent colonisations (Wagner *et al.*, 1990, 1999). The phylogenetic study of Cronk *et al.* (2005) using nuclear DNA revealed a large Pacific clade that was sister to a species (*C. umbellifera* Merr.) from the Bataan Islands (located between Taiwan and the Philippines). Within this Pacific clade there were two smaller well-supported sister clades, a Hawaiian clade and a clade made up of the rest of the Micronesian (Guam, the Federated States of Micronesia, Kiribati, Marshall Islands and the Northern Mariana Islands) and Polynesian species (Cook Islands, Marquesas, Samoa, Society Islands and Tonga). However, the small sample size of Hawaiian and Pacific species and the sister group relationship between the two clades did not allow the identification of the location of the most recent common ancestor. The limited resolving power of the available data makes it impossible to distinguish between a single dispersal event to the Pacific with further dispersal to Hawaii or two independent dispersal events from Southeast Asia. The data do support the monophyly of the Hawaiian species sampled, and therefore indicate a single colonisation event to the islands. However, more study is needed to better resolve the relationships, as a second colonisation event could not be entirely discounted (Cronk *et al.*, 2005).

Like *Cyrtandra*, the origin of the endemic genus *Labordia* (Motley & Carr, 1998; Wen *et al.*, 2001) is not yet clear. The sister taxon in analyses to date appears to be in the Pacific, but related groups are also in Asia so it seems best at this time to include both as possible areas of origin. Finally, the origin of the Hawaiian lobelioids (Fig. 4.2d) is among the least well understood of those taxa whose ancestry may be Asian. Data indicate the possibility of an Asian-Polynesian origin, like its sister group, or in an altogether different place, Africa, where the closest outgroup is located. Only additional studies will resolve this problem. All six Hawaiian lobelioid genera (126 species) (Table 4.1) are the result of a single introduction (Givnish *et al.*, 2009).

Australia, New Zealand and the Western Pacific

The genus *Scaevola* consists of 130 species widely dispersed throughout the Pacific. In Hawaii there are 10 species, nine endemics and one indigenous pan-Pacific

species, *S. taccada* (Gaertn.) Roxb. (often referred to as *S. sericea* Vahl). Of the endemics, there are eight diploid and one tetraploid species (Wagner *et al.*, 1999). Patterson (1995), in a morphological cladistic study, postulated that all diploid Hawaiian species were the result of a single colonising event, and that the tetraploid species, *S. glabra* Hook. & Arnott, originated from a separate colonisation. The widespread *S. taccada* was found by Patterson (1995) to be the sister taxon to the Hawaiian diploid species, and New Caledonia taxa were sister to all the Hawaiian taxa. As a result it was hypothesised that there were at least two separate colonisations of the Hawaiian Islands (Patterson, 1995). Earlier Carlquist (1974) had suggested three possible colonisations, one for the diploid species, one for the tetraploid and a third for *S. taccada*. The closest relatives were previously assumed to be from nearby Pacific islands, but this was confounded by the sister group relationship of the New Caledonia species.

Howarth *et al.* (2003) used nuclear sequence data to examine the biogeography and phylogeny of *Scaevola* throughout its geographical range. The data showed a complex pattern of dispersals from Australia into the Pacific involving three different clades and six dispersal events. Three of these dispersals were to the Hawaiian Islands and each gave rise to a different lineage (Table 4.1). One of these dispersals was found to be responsible for establishment of the Hawaiian diploid clade, supporting earlier hypotheses of diploid monophyly (Patterson, 1995). However, the sister group to the diploid species was not *S. taccada*, as previously thought, but included the Cuban species, *S. wrightii* (Griseb.) M. Gómez, and the Socotran species, *S. socotraensis* St. John, along with the widespread *S. plumiere* Vahl. None of these taxa occur in Hawaii, however. *Scaevola plumiere* is morphologically similar to the Hawaiian diploid species, *S. coriacea* Nutt., and was proposed as a possible ancestor to the Hawaiian diploids (Carlquist, 1969), a finding in agreement with the data of Howarth *et al.* (2003). As a result Howarth *et al.* (2003) concluded that the original diploid colonist was likely from the Americas or Africa where *S. plumiere* is found and not from Tonga, Samoa, the Marquesas or Tahiti, all locations that are more geographically proximate to the Hawaiian Islands (Fig. 4.1) and which were earlier considered the most likely sources. The data also showed that the tetraploid species, *S. glabra*, was most closely related to two Australian species in a different section and subsection from the diploids (Howarth *et al.*, 2003). The widespread Southern Hemisphere *S. taccada* was shown to be related to taxa in Australia, New Caledonia and the South Pacific. It was established independently of other Hawaiian *Scaevola*. The three separate colonisation events responsible for establishing *Scaevola* in Hawaii are the most yet documented for any genus in the flora.

Hawaiian *Santalum* were also shown to result from more than one colonisation event. Harbaugh and Baldwin (2007) and Harbaugh (2008) investigated the

relationships among Pacific *Santalum* species using nuclear and the chloroplast DNA (Table 4.1). There are four endemic species in the Hawaiian Islands, all tetraploid (Wagner *et al.*, 1999). These have been placed in sections *Solenanthes* Tuyama and *Hawaiiensia* Skottsbo. (and sometimes sections *Polyensia* Skottsbo. and *Santalum* Skottsbo.) (Skottsberg, 1930). The two species in section *Hawaiiensia*, *S. ellipticum* Gaud. and *S. paniculatum* Hook & Am., were thought to be the result of a colonisation from Polynesia where one species, *S. insulare* Bertero ex DC., is widely distributed. The species in section *Solenanthes*, *S. freycinetianum* Gaud. and *S. halaekalae* Hillebr., were postulated to be the result of colonisation from Australia or the Austral region (Wagner *et al.*, 1990, 1999). Harbaugh and Baldwin (2007) confirmed that two separate colonisation events from Australia/Papua New Guinea, but not from Polynesia, were responsible for establishing the Hawaiian species. Within their larger study of *Santalum* they found there were at least five, putatively bird-mediated (carrying fleshy fruits), long-distance dispersal events from Australia to explain the current distribution of the 15 species found from Australia across the Pacific islands, north to the Bonin Islands off Japan and south to the Juan Fernandez Islands.

Several Hawaiian endemics that are members of widespread genera do not have specific areas of origin, although they are thought to be from Austral or Australasian/Malesian areas (Table 4.1). Among these are *Melicope/Platydesma* (Harbaugh *et al.*, 2009b), *Pittosporum* (Gemmil *et al.*, 2002), *Psychotria* (Nepokroeff *et al.*, 1999, 2003) and *Sicyos* (Sebastian *et al.*, 2009). Some of these were previously thought to be the result of multiple colonisation events as well, but have since been shown to be monophyletic and therefore the result of single colonisations.

For example, *Melicope* (Fig. 4.2e) has 47 species found across a broad range of habitats on all the high islands. It was hypothesised to be closely related to species of the Hawaiian endemic genus, *Platydesma*, the latter with only four species. It was generally thought that the Hawaiian *Melicope* arose from a single Indo-Pacific introduction (Fosberg, 1948; Hartley, 2000) and that *Platydesma* was the result of a second separate colonisation event. The molecular study of Pacific *Melicope* by Harbaugh *et al.* (2009b) using chloroplast and nuclear regions (Table 4.1) showed that *Platydesma* was nested within *Melicope*, and therefore not the result of a separate colonisation event. The ancestor of the Hawaiian species was found to be from the Austral region although, given the size and distribution of the genus (230 species widely distributed in the Southern Hemisphere from Australia, Malaysia, New Zealand, Madagascar, Southeast Asia, to the Pacific islands) and the number of species sampled, the precise source of the Hawaiian species is not clear. Similarly, *Psychotria*, estimated to have 1000–1650 species in the tropics worldwide, was thought to have originated in Australasia (Nepokroeff *et al.*, 1999, 2003). The 11 Hawaiian species were initially thought to be the result of one (Fosberg, 1962),

two or three separate colonisation events (Sohmer, 1977; Wagner *et al.*, 1999). However, Nepokroeff *et al.* (2003), using nuclear DNA sequence data (Table 4.1), showed that the Hawaiian taxa were monophyletic. As with many of the groups in Hawaii, genetic differences were low among species, suggesting rapid radiation within the islands. Nepokroeff *et al.* (2003) also identified several radiations within *Psychotria* from its Australasian origin to Africa with subsequent radiation to the neotropics and to the Pacific, including Melanesia and Hawaii. However, broader taxon sampling will be necessary to determine the origin of the Hawaii ancestor.

The precise origin of Hawaiian *Pittosporum* is also unknown due to the lack of resolution among species from New Caledonia, New Zealand, Fiji, Tonga and eastern Polynesia (Gemmil *et al.*, 2002). The nearest relatives of the 10 Hawaiian endemics were proposed to be among species in Fiji and Tonga, based on the shared presence of unisexual flowers and morphology (Haas, 1977; Wagner *et al.*, 1990; Cayzer *et al.*, 2000). The findings of Gemmil *et al.* (2002) using nuclear DNA sequence data (Table 4.1) confirmed the monophyly of the Hawaiian taxa, but the source of the original colonists remained unclear. The data indicated a close relationship between Hawaiian *Pittosporum* and two species, *P. rhytidocarpum* A. Gray from Fiji and *P. yunckeri* A. C. Smith from Tonga. The New Caledonian species, *P. gatopense* Guillaumin, was sister to the Fijian and Tongan species, although support for this relationship was not strong. The greatest diversity of *Pittosporum* is found in Australia, but a direct connection to Hawaii is lacking. In this case further work will be needed to verify whether or not a single event gave rise to the Fijian, Tongan and then to the Hawaiian species or whether perhaps the Hawaiian colonisation was separate from that giving rise to species in the other two island groups (perhaps directly from Australia or New Zealand). There are 150 species of *Pittosporum* found in Africa, Asia, Australia and New Zealand as well as the Pacific islands, suggesting high dispersibility and the likelihood of multiple introductions in the Pacific.

Single species colonisation without radiation

Although most radiations of Hawaiian endemics examined so far are the product of a single colonisation event followed by speciation, not all have this history. Some taxa have, as far as we know, failed to develop beyond the original colonisation (Table 4.1). For example, the molecular study of *Korthalsella*, a parasitic mistletoe with few definitive morphological characters, suggests that previous treatments listing multiple Hawaiian species may be in error (Molvray *et al.*, 1999). Wagner *et al.* (1990, 1999) listed four endemic and two indigenous Hawaiian species and postulated three independent introductions. However, Molvray *et al.* (1999) indicate that only one species is likely to exist in Hawaii and suggest that it may not

be endemic. They proposed that all the species but *K. cylindrica* (Tieghem) Engler should be considered as part of the widely distributed Pacific species, *K. taenioides* (Commerson ex DC.) Engler. They further suggested that additional study might show that *K. cylindrica* should also be included in *K. taenioides*. If this should prove to be the case then there would be no endemic species of *Korthalsella* in the Hawaiian Islands and its presence there is probably the result of a relatively recent colonisation event. The precise geographical origin of the genus is unknown as it has a patchy distribution, but Molvray *et al.* (1999) proposed Papuaia.

A number of other genera from a variety of different areas appear not to have speciated in the islands although they are widely distributed within the archipelago. Among these taxa with only one species each are *Rhus* (Yi *et al.*, 2004), *Hillebrandia* (Clement *et al.*, 2004) and *Broussasia* of Asian origin (Hufford *et al.*, 2001), and *Cuscuta* putatively an immigrant from western North America (Stefanovic *et al.*, 2007). Additionally, the Hawaiian endemic legume, *Kanaloa kahoowawensis* D. H. Lorence & K. R. Wood, was described from two individuals growing on the 'Ale'ale sea stack off the coast of the small island of Kaho'olawe (Lorence & Wood, 1994) and placed in the *Leucaena* group (Hughes *et al.*, 2003). The precise relationship of *Kanaloa* to *Schleinitzia*, from the Western Pacific, and to *Desmanthus*, from the Americas, is not certain so the origin of this endemic species cannot be resolved at this time.

Finally and perhaps most interestingly, is the case of the signature Hawaiian plant, *Metrosideros polymorpha* Gaud. This is the dominant tree (woody) species in the islands where it grows in multiple ecosystems ranging from bare lava flows to mesic forests and bogs. It is so variable morphologically that species identification(s) have not been resolved despite data from ecological, morphological, physiological and population studies using isozymes and RAPDs (e.g. Rock, 1917; Skottsberg, 1936; Corn, 1979; Stemmermann, 1983; Aradhya *et al.*, 1991; Cordell *et al.*, 1998; Melcher *et al.*, 2000; James *et al.*, 2004). It has been treated as a widespread endemic (Skottsberg, 1936), as five separate species (Wagner *et al.*, 1999) or as part of the widespread taxon, *M. collina* A. Gray (Rock, 1917). Wright *et al.* (2001) and Percy *et al.* (2008) studied the Hawaiian species of *Metrosideros* within the larger context of probable origin, dispersal and biogeographic affinities in the Pacific. The data showed that the origin of the clade that contains the Hawaii species is either New Zealand or the Pacific (Wright *et al.*, 2001; Percy *et al.*, 2008). Percy *et al.* (2008), using 10 non-coding chloroplast DNA regions (Table 4.1), showed that most of the 'species' were nested inside *M. polymorpha* and therefore not distinct from it. They also found that there was no correlation between genetic and morphological diversity as the same haplotype was shared by plants with differing morphologies and that those with the same morphology could have different haplotypes. The data generally supported a single colonisation event and Percy *et al.* (2008) suggested

intra-island diversification as the cause of *M. polymorpha*'s extreme morphological variability. Using microsatellites (Harbaugh *et al.*, 2009c) also supported the idea of multiple inter-island dispersals with later parallel evolution as among the major factors explaining the variability of this species. Subsequent investigations (Wagner, pers. com.) indicate that there may be from one to three species in Hawaii. Given the failure of multiple types of evidence to show consistent differences within and among islands and the lack of agreement on taxonomic status, it seems to us that this taxon will continue to be a source of controversy for the foreseeable future.

Hawaii as a source of colonists

The studies of Hawaiian and Pacific *Santalum* (Harbaugh & Baldwin, 2007; Harbaugh, 2008; Harbaugh *et al.*, 2009b), *Tetramolopium* (Lowrey *et al.*, 2001) and *Melicope* (Harbaugh *et al.*, 2009b) illustrate the importance of the previously unknown role of the Hawaiian Islands as a source of colonising species, as well as a recipient of colonists from other areas.

The phylogenies produced from nuclear and chloroplast data on Pacific *Santalum* (Harbaugh & Baldwin, 2007; Harbaugh, 2008) showed an unexpected relationship to Hawaiian taxa by two species, *S. insulare* Bert. ex DC. from the Marquesas and French Polynesia (Society Islands) and *S. boninensis* (Nakai) Tuyama from the Bonin Islands. These two tetraploid species, as well as hexaploid and octoploid varieties of *S. insulare*, were nested within the Hawaiian clade. The most parsimonious explanation of these findings (Harbaugh & Baldwin, 2007) was that these species were the products of dispersals from Hawaii. Harbaugh and Baldwin reported that this was the first time Hawaii was unequivocally shown to be the source of colonists for other Pacific radiations.

Tetramolopium has a disjunct distribution that includes, besides Hawaii and New Guinea, Mitiaro in the Cook Islands (Lowrey, 1995; Okada *et al.*, 1997; Lowrey *et al.*, 2001). The genus was shown to have an origin in New Guinea with a single colonisation of the Hawaiian Islands. The Cook Island species, *T. mitiaroense* Lowrey, R., Whitkus and W. R. Sykes, was initially considered conspecific with the Hawaiian taxon, *T. sylvae* Lowrey; however, it was found to be a distinct species based on nuclear DNA sequence (Table 4.1) and RFLP (restriction fragment length polymorphism) data (Okada *et al.*, 1997; Lowrey *et al.*, 2005). The preferred explanation, in light of the molecular data, is that the Cook Island plants were derived from those in Hawaii and that the dispersal pathway for *Tetramolopium* was New Guinea to Hawaii to the Cook Islands. Final confirmation of this pathway will require additional study, however, to rule out alternative explanations for the observed patterns.

Harbaugh *et al.* (2009b), following up with another Pacific genus, *Melicope*, found a similar pattern to that seen for *Santalum* and *Tetramolopium*. Marquesan

Melicope species were found within the Hawaiian clade at two different places in the ITS (internal transcribed spacers) phylogeny. Based on morphological and molecular data, Harbaugh *et al.* (2009b) concluded that Marquesan species were descended from one and perhaps two different colonisations from Hawaii. They further speculate that other genera will also be found to have dispersed from Hawaii to elsewhere in the Pacific (i.e. *Pritchardia* (Arecaceae), *Cheirodendron* (Araliaceae), *Phyllostegia* (Lamiaceae) and *Leptocophylla* (Epacridaceae)). Recent work by M. Knope (pers. com.) indicates that two undescribed species of *Bidens* from the Marquesas are also likely to be derived from Hawaiian species, as previously suggested by Ganders *et al.* (2000), but this remains to be confirmed.

Polyploidy and hybridisation

Polyploidisation and hybridisation have been invoked as potentially among the most important events in the establishment of taxa on distant islands and in subsequent adaptive radiation (Carr, 1998; Crawford *et al.*, 2009). This follows from the idea that polyploid colonisers would have greater genetic diversity than diploids, thus allowing for more adaptive possibilities in response to the newly encountered environments. Additionally, self-compatibility and low levels of inbreeding depression would be more likely to ensure persistence, once established. The relatively high number of polyploids among those reported for Hawaiian plants by Carr (1998) led him to conclude that a large number of Hawaiian plants originated from polyploid ancestors (palaeopolyploids). The reduced likelihood of polyploids originating from diploids on islands was discussed by Stuessy and Crawford (1998). They reasoned that this would require, first, successful establishment of both parent species, likely from different colonisation events, then hybridisation and doubling, followed by radiation, a much more unlikely set of events as compared to divergence from an original polyploid ancestor. Rapid evolution among natural and synthesised polyploids has also been demonstrated in a number of studies, making these 'excellent ancestors for rapidly diverging lineages' (Crawford *et al.*, 2009: 145). Hybridisation among species originating from both polyploid and diploid ancestors has also occurred, although this appears to be less common, or at least less well documented. Some examples of studies available are given below.

Polyploidy and hybridisation have been shown to be important in the Hawaiian silversword alliance (*Argyroxiphium*, *Dubautia*, *Wilkesia*) (Carlquist *et al.*, 2003). Crossing studies and chromosome morphology, along with allozyme and molecular data, support the derivation of the Hawaiian species from an allotetraploid ancestor ($n = 14$) that arose and diversified on the mainland before dispersing to Hawaii (Carlquist *et al.*, 2003; Carr, 2003). Natural hybridisation within and between genera (i.e. *Dubautia menziesii* (A. Gray) D. Keck \times *Argyroxiphium sandwicense* DC.),

and artificially produced hybrids between virtually any combination of taxa within the silversword alliance (Carr, 2003) indicated that hybridisation was likely, particularly given the abrupt habitat transitions and relatively frequent disruptions due to volcanic activities that are common in Hawaiian landscapes. Conflicting chloroplast and nuclear DNA phylogenies (Baldwin & Robichaux, 1995; Baldwin, 2003) also suggest that hybridisation has been important in silversword evolution (and perhaps in the entire tribe; Baldwin & Wessa, 2000). Data from floral homeotic gene sequences of the Hawaiian species and the California 'Madia' lineage also showed the allopolyploid nature of the Hawaiian taxa (Barrier *et al.*, 1999, 2001). There were two copies of homeotic genes (Table 4.1) in Hawaiian taxa, but not in mainland species, and each of these copies was most closely related to the mainland taxa (*Carlquistia muirii* (A. Gray) B. G. Baldwin and *Anisocarpus scabridus* (Eastw.) B. G. Baldwin) rather than to other Hawaiian species. Chromosome numbers of silversword taxa are $n = 14$ and $n = 13$. Molecular phylogenetic evidence showed that the $n = 13$ and $n = 14$ Hawaiian taxa were nested among those diploid Californian species in the 'Madia' alliance with chromosome numbers of $n = 6$ to $n = 9$ (Baldwin, 1996). Earlier crossing studies (Carr *et al.*, 1996) also showed that *Dubautia scabra* (DC.) D. Keck ($n = 14$) could be crossed with *Kyosia bolanderi* (A. Gray) B. G. Baldwin ($n = 6$) and *Carlquistia muirii* (A. Gray) B. G. Baldwin ($n = 8$) separately and in combination, and these crossing relationships could be extended to include *Anisocarpus scabridus* (Eastw.) B. G. Baldwin ($n = 7$). Barrier *et al.* (1999) proposed, on the basis of the close relationship of the genomes of Hawaiian and North American species, that Hawaiian taxa were descended from an extinct allopolyploid formed from among extant taxa.

Howarth and Baum (2005) examined the role of hybridisation in Hawaiian *Scaevola* using four nuclear regions (Table 4.1). Five diploid species (*S. chamissoniana* Gaudich., *S. gaudichaudiana* Cham., *S. mollis* Hook. & Arnott, *S. coriaceae* Nutt. and *S. gaudichaudii* Hook. & Arnott) showed clear monophyly when analysed separately by region and in combined analyses. However, *S. kilaueae* Degner and *S. procera* Hillebr. were placed in different parts of the individual gene trees and were not together in any of them. On the basis of genetic, morphological and ecological data it was inferred that these two diploid species were the result of homoploid hybridisation. *Scaevola kilaueae* is postulated to be a hybrid between *S. coriaceae* and *S. chamissoniana* while *S. procera* is a hybrid between *S. gaudichaudii* and *S. mollis*. The latter two species are known to hybridise when sympatric (Gillett, 1966). Howarth and Baum (2005) proposed that homoploid hybrids could be important in allowing for ecological shifts as well as adaptive radiation in *Scaevola* and perhaps in other island taxa as well. Patterson (1995) hypothesised that species of dry areas were ancestral to those of more mesic sites and that establishment was related to the ability of *Scaevola* to find suitable open habitats. *Scaevola* species are found in different habitats, but may have occurred together

at various times in the past before widespread habitat destruction extirpated connecting populations (Patterson, 1995; Howarth & Baum, 2005). *Scaevola procera* is found in a different habitat and at a different elevation from its putative parents and has a distinctly different morphology. *Scaevola kilaueae* is intermediate in morphology and genetic composition to that of its putative parents and it occurs on young lava flows on the youngest island, where the parental species are also found. New combinations generated by hybridisation could potentially increase the ability of species to adapt to new habitats.

Harbaugh (2008) also found that hybridisation and polyploidy were important in *Santalum* species. Using a nuclear gene (Table 4.1) along with flow cytometry, at least six polyploid or hybridisation events in the genus were postulated as it radiated from Australia to Malesia and across the Pacific to Hawaii. All four Hawaiian species are tetraploid (Harbaugh & Baldwin, 2007) but the data indicate that they were produced by at least two different hybridisation events. *Santalum freycinetianum* and *S. halaekalae* (section *Solenanthes*) were determined to be the result of autopolyploidy in an Australian ancestor that subsequently led to the first successful colonisation event in Hawaii (Harbaugh & Baldwin, 2007). The second colonisation event was by the lineage that gave rise to *S. ellipticum* and *S. paniculatum* (section *Hawaiiensia*). This lineage resulted from allopolyploidy following hybridisation of Australian diploid species prior to dispersal to Hawaii (Harbaugh, 2008). Disagreement between nuclear and chloroplast phylogenies (Harbaugh & Baldwin, 2007) along with the data of Harbaugh (2008) also suggested that *S. boninensis* (Nakai) Tuyama of the Bonin Islands ($n = 4$) was the result of hybridisation between Hawaiian tetraploid taxa related to *S. freycinetianum* and *S. paniculatum*. Additionally, *S. insulare* Bert. ex DC. var. *marchionense* (Skottsbo.) Skottsbo. from the Marquesas was putatively determined to be hexaploid and *S. insulare* Bert. ex DC. var. *raiateense* (J. W. Moore) Fosberg & Sachet from the Society Islands a putative octaploid, suggesting a stepwise increase in ploidy from a Hawaiian tetraploid ancestor. Harbaugh (2008) found that there were more than twice as many successful long-distance colonisation events to Pacific Islands by polyploid as diploid *Santalum* species.

Other cases of presumed hybridisation involve the Hawaiian mints (Lindqvist & Albert, 2002; Lindqvist *et al.*, 2003) and *Cyrtandra* (Cronk *et al.*, 2005) (Fig. 4.2a); experimental hybrids have also been formed between *Portulaca* species and among *Plantago* species (Carr, unpubl.) and many species in the Hawaiian flora are presumed to be polyploids as well (Wagner *et al.*, 1990, 1999).

Morphological diversity and genetic uniformity

Among endemic Hawaiian taxa, morphological and genetic diversity do not necessarily go hand in hand. For example, the genus *Bidens* (Compositae) is one of the most morphologically diverse in the Hawaiian Islands (Carlquist, 1970; Ganders

& Nagata, 1984; Helenurm & Ganders, 1985). Species vary extensively in leaf shape, growth form, inflorescence structure, head and achene morphology, the latter unique to the Hawaiian species (Carlquist, 1974; Helenurm & Ganders, 1985). The range of morphological variation is greater among the Hawaiian taxa than that found in the rest of the 200–300 species in the genus that are distributed across five continents (Ganders *et al.*, 2000). The 19 endemic Hawaiian species (and eight subspecies) also grow in a wide variety of habitats which is reflected in their morphologies. These habitats include coastal dunes, cinder cones, rainforests, montane ridges over 2000 m and bog edges. One species, *B. cosmoides* (A. Gray) Sherff, has significantly different floral morphology from the other species. It has large, pendent and nectar-rich heads and is presumed to be adapted to bird pollination. It was proposed that this species was the result of a different colonisation event from that which gave rise to the other Hawaiian species (Ganders & Nagata, 1983). They do hybridise readily, however, under artificial and natural conditions when they come into contact (Ganders & Nagata, 1984; Ganders *et al.*, 2000). Despite the great variation in morphology and habitat, Hawaiian *Bidens* are remarkably similar genetically (Ganders, 1989; Ganders *et al.*, 2000). For example, earlier data from isozymes, flavonoids and polyacetylenes showed little differentiation, supporting a single colonisation event, but failing to differentiate species (Ganders, 1989). This same low level of genetic difference was also found by Ganders *et al.* (2000) using nuclear DNA (Table 4.1). All Hawaiian species were genetically identical, confirming the monophyly of the genus in the islands, including *B. cosmoides*.

The silversword alliance is also morphologically diverse and species are found in a wide variety of habitats. There are 30 species, five in *Argyroxiphium* (Fig. 4.2c), two in *Wilkesia* and 23 in *Dubautia* that range from rosette plants, to prostrate and erect shrubs, trees, cushion plants and lianas. Species grow in a wide variety of habitats from lava and cinders, to dry cliff sides, in dry and mesic forests and bogs, and from low elevations to 3750 m with annual precipitation varying from 40 cm to 1300 cm (Carr, 1985). Molecular studies using nuclear DNA (Baldwin & Robichaux, 1995; Baldwin, 1996, 1997, 2003) showed little sequence variation among the *Argyroxiphium* species, however, and while identifying the *Dubautia/Wilkesia* sister lineage, again showed only small levels of difference within clades of *Dubautia*. This lack of variation was attributed to recent and rapid radiation (Baldwin & Sanderson, 1998) as well as to possible extinction of close relatives of *Argyroxiphium*.

The largest radiation within the Hawaiian Islands occurs within the lobeliads (*Brighamia*, *Clermontia*, *Cyanea*, *Delissia*, *Lobelia*, *Trematolobelia*; Table 4.1) (Givnish *et al.*, 1995, 2004). There are 126 species distributed among these genera, all derived from a single common ancestor (Givnish *et al.*, 2009). Taxa range from shrubs and trees to cliff-dwelling succulents, to rosette plants of high elevation

bogs and even vines. The variation in leaf morphology is notable, especially in *Clermontia* and *Cyanea*, the largest genera (Givnish *et al.*, 1995; Lammers, 1995; Wagner *et al.*, 1999). Chloroplast DNA (Table 4.1) has been used to establish relationships, including that of *Brighamia* with *Delissia* and these with *Cyanea* and *Clermontia*; however, genetic differences among taxa remain small.

Other genera that have radiated into different habitats and express morphological and ecological diversity but have relatively low genetic differentiation include *Schiedea* (now including *Alsinodendron*) (Soltis *et al.*, 1996; Sakai *et al.*, 1997; Wagner *et al.*, 2005; Harbaugh *et al.*, 2009a), the Hawaiian mints (*Haplostachys*, *Phyllostegia*, *Stenogyne*) (Lindqvist & Albert, 2002; Lindqvist *et al.*, 2003), *Tetramolopium* (Lowrey, 1995; Okada *et al.*, 1997, 2000) and *Plantago* (Dunbar-Co *et al.*, 2008).

Conclusions

Estimated dates for the time of divergence of Hawaiian lineages from their sister group have been published for 14 genera and monophyletic groups (Table 4.1). These dates reveal several different patterns of geographical origin and spread. Among those dated > 5 Ma, for instance, all appear to have been in the Hawaiian Islands c. 13–15 Ma, indicating they may have once inhabited Gardner Pinnacles in the Northwest Hawaiian Islands which formed a large high island at that time but has since eroded. *Hesperomannia*, derived from African ancestors, may be the oldest lineage in the islands with an estimated age ranging using *ndhF* from 24.0 to 17.14 ± 3.43 Ma. While a date around 14 Ma could include residence on Gardner Pinnacles, the older age estimates would mean that the ancestor was likely somewhere else between tropical Africa and the Pacific until at least 15 Ma. Age estimates for various taxa of < 5 Ma place them within the age of the current high islands (5.1–0.5 Ma). This group includes more taxa and a wider range of source areas than found for the older genera, which is not surprising. Among these are some of the best-known examples of adaptive radiation, i.e. the silverswords (30 species), mints (60 species), lobeliads (126 species) and others. Smaller radiations within this same time frame are known for *Viola* (7 species), *Geranium* (7 species), *Kokia* (4 species), and one of the arrivals of *Santalum* (4 species) (Table 4.1). The lack of detectable genetic divergence among species within genera indicates that intra- and inter-island radiations have likely been rapid as well.

The geographical sources of Hawaiian taxa vary widely and include Arctic/Boreal regions, western North America, Central America, Africa, Asia, Malesia and Australasia (Table 4.1). Among the 42 studies listed in Table 4.1, 37 have restricted areas of origin that can be estimated. These 37 groups have a total of 568 species, over half the native flora. Based on these data there are 22 groups

(60% of the lineages and 64% of the species) are derived from Asia, Australasia, Malesia or the South Pacific (a loosely used term that often includes New Zealand, Australia, Papua New Guinea and neighbouring islands). In comparison, 14 groups (38% of the lineages and 35% of the species) are estimated to be from the Americas + the Arctic; of these, 10 (27%) are proposed to be from North America (including Mexico). The remaining 2% is accounted for by the one confirmed taxon with an African origin. Correlated with the geographic origin of the lineages is the size of radiations within the islands. These radiations fall into four categories: very large (58–126 species), large (14–32 species), medium (6–11 species) and small (2–5 species). Of the very large radiations, two (*Lobeloides* and *Cyrtandra*) are Asian-Pacific in origin and one is American (Hawaiian mints). Within the large category there are seven groups, four from the Americas and three from the Asia-Pacific region. There are nine medium-size groups (six from the Asia-Pacific and three from the America-Arctic regions) and finally there are six small clades with two from the Asia-Pacific region, three from the Americas and one from Africa. There are 12 lineages that have only one taxon so they have either failed to radiate or extinction has left only one taxon from a previously larger group. These numbers indicate a much greater contribution by North American taxa to the Hawaiian flora than previously suggested (Fosberg, 1948; Wagner *et al.*, 1990; 1999). Australasian, Asian, Malesian and South Pacific groups are still in the majority. Work is under way in many additional groups and these figures are bound to change.

Adaptive radiation has been ‘explosive’ in many groups, giving rise to great morphological divergence while at the same time showing little genetic differentiation. This is likely a product of the young age and the often allopatric distribution of species on different islands (many single-island endemics) and habitat differences. As a result of close genetic similarity within monophyletic groups, hybridisation is frequent, and it is likely that hybridisation followed by polyploidy was important in their establishment and diversification. Polyploidy, whether by allo- or autopolyploidisation, also appears to have been important as more than a quarter of all endemic taxa thus far investigated (Carr, 1998) are polyploids. Intra-island as well as inter-island divergence has been important in species diversification within many genera in the islands. Diversification has also resulted in changes in habit and breeding system (e.g. *Schiedea*) which in some cases can be correlated with genetic divergence.

The original plant colonists arrived in Hawaii as a result of long-distance dispersal, largely facilitated by migratory birds, but also by wind and water. Among the taxa investigated in molecular studies, many had been suggested to be the product of more than one colonisation event. The available phylogenies, however, show monophyletic lineages resulting from a single original coloniser, in all but two cases cases, i.e. *Scaevola* and *Santalum*. The Hawaiian Islands connect floras from

the Arctic of North America south to New Zealand, and from the eastern to the western sides of the Pacific, Southeast Asia and even Africa. As the histories of more Hawaiian taxa become known it is likely that this 'laboratory of evolution' will be revealed to have a significant role in the biogeography and evolution of plant groups now found throughout the Pacific and beyond.

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