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INVITED REVIEW

Hawaiian angiosperm radiations of North American origin

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• *Background* Putative phytogeographical links between America (especially North America) and the Hawaiian Islands have figured prominently in disagreement and debate about the origin of Pacific floras and the efficacy of long-distance (oversea) plant dispersal, given the obstacles to explaining such major disjunctions by vicariance.
• *Scope* Review of past efforts, and of progress over the last 20 years, toward understanding relationships of Hawaiian angiosperms allows for a historically informed re-evaluation of the American (New World) contribution to Hawaiian diversity and evolutionary activity of American lineages in an insular setting.
• *Conclusions* Temperate and boreal North America is a much more important source of Hawaiian flora than suggested by most 20th century authorities on Pacific plant life, such as Fosberg and Skottsberg. Early views of evolution as too slow to account for divergence of highly distinctive endemics within the Hawaiian geological time frame evidently impeded biogeographical understanding, as did lack of appreciation for the importance of rare, often biotically mediated dispersal events and ecological opportunity in island ecosystems. Molecular phylogenetic evidence for North American ancestry of Hawaiian plant radiations, such as the silversword alliance, mints, sanicles, violets, schiedeas and spurges, underlines the potential of long-distance dispersal to shape floras, in accordance with hypotheses championed by Carlquist. Characteristics important to colonization of the islands, such as dispersibility by birds and ancestral hybridization or polyploidy, and ecological opportunities associated with 'sky islands' of temperate or boreal climate in the tropical Hawaiian archipelago may have been key to extensive diversification of endemic lineages of North American origin that are among the most species-rich clades of Hawaiian plants. Evident youth of flowering-plant lineages from North America is highly consistent with recent geological evidence for lack of high-elevation settings in the Hawaiian chain immediately prior to formation of the oldest, modern high-elevation island, Kaua'i.

Key words: Angiosperms, adaptive radiation, disjunctions, flora, island biogeography, long-distance dispersal, ecological opportunity, Hawaiian Islands, North America, Pacific, phytogeography, sky islands.

INTRODUCTION

Extreme isolation and endemicity of the Hawaiian flora, with 90 % of (approx. 1030) native angiosperm species found nowhere else (Wagner *et al.*, 1999, 2005*a*), have made the effort to resolve original sources of founder lineages both fascinating and complex (Fig. 1). Engler (1879–1882; Fig. 2A), in his early analysis of Hawaiian phytogeography, and Hillebrand (1888*a*; Fig. 2B), who produced the first major account of the flora of the Hawaiian Islands, concluded that long-distance dispersal of great magnitude, although unlikely, must have been required for native plants to become established in the archipelago. They both noted the association between long-term isolation of the Hawaiian Islands and the exceptional proportion of endemic Hawaiian plants, as well as the importance of birds in plant dispersal and of ecological factors in diversification of the flora. Engler (1879) reasoned that the evolutionary potential of plants dispersed to the archipelago was high because ' . . . the newly developed varieties always encountered open terrain, and they had to fight with only few competitors' (p. 130). Hillebrand (1888*a*) discussed the contribution of elevational and climatic diversity to ' . . . increase the variety of forms' (p. XV). Hillebrand (1888*a*) also appreciated that the greater age of the western

high-elevation islands, such as Kaua'i, compared with the eastern high-elevation islands, such as Hawai'i, was reflected by more single-island endemics and more extensive morphological differences between congeneric species on the older islands than on the younger islands. His questions about the relative importance of habitat diversity, evolutionary lability and paucity of founders in contributing to autochthonous development of the angiosperm flora still remain to be fully answered and demonstrate that his comprehension of island biology was well ahead of its time.

Drawing from early floristic work (e.g. Mann, 1869; Wawra, 1872–1875), Engler (1879–1882) presented a tabulation of Hawaiian vascular-plant taxa and the distributions of putative extra-Hawaiian relatives, mostly from tropical or subtropical areas, for well over one-third of the Hawaiian species and genera. Only 42 (20 %) of the indigenous Hawaiian angiosperm relationships proposed by Engler were exclusively with New World (mostly tropical) species, including all native Compositae and fleshy-fruited Campanulaceae (lobelioids). Over half of those native angiosperms proposed to have exclusively New World relatives were noted as having fleshy fruits, easily adhering seeds or fruits, or associations with wet habitats, all features favourable for dispersal by birds (see Carlquist, 1974, 1996).
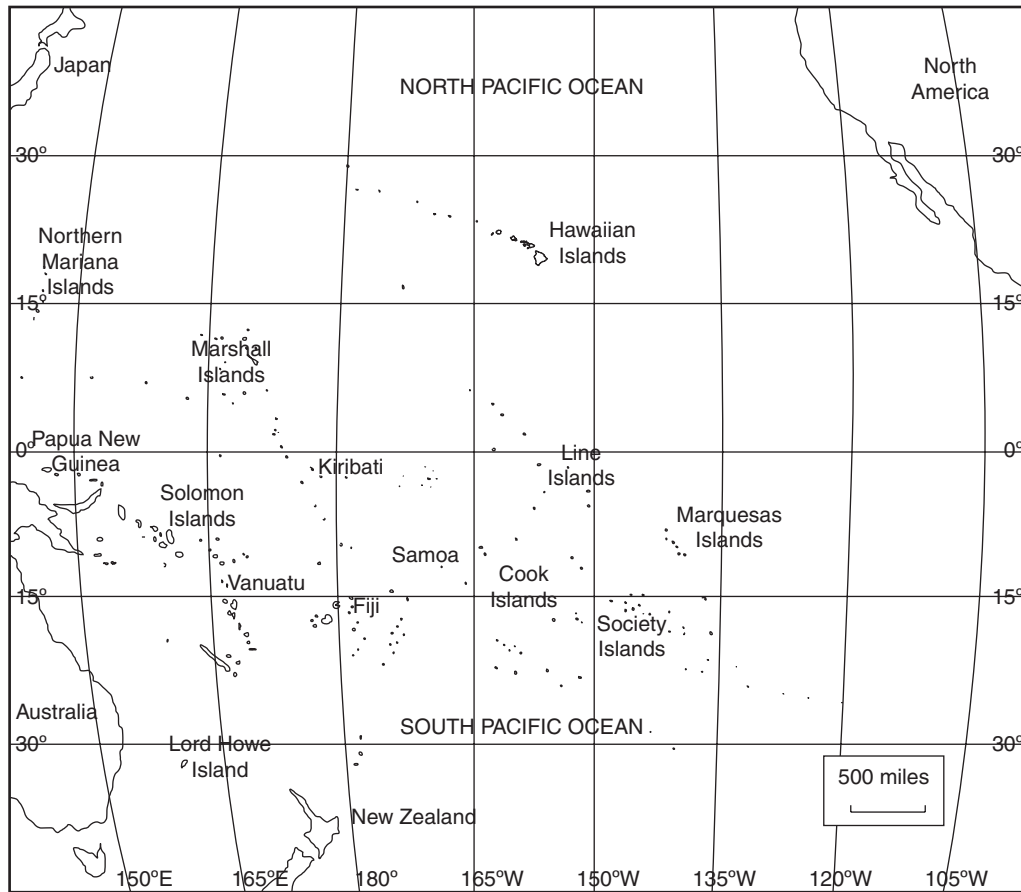
FIG. 1. Map of the Pacific Basin. The distance from southern California to the closest Hawaiian Island (Hawai'i) is approx. 3800 km to the south-west, and the distance from the Marquesas Islands (Eiao) to Hawai'i is approx. 3400 km north across the equator. Map courtesy of D. T. Harbaugh.

Although Hillebrand (1888*a*) did not provide a synthetic account of his thoughts on the original source areas for native Hawaiian plants in his flora (the introduction was incomplete at the time of his death), he did suggest elsewhere that most Hawaiian plants have Australasian affinity, excluding the majority of Hawaiian Compositae, which appeared to have closest relatives in America (Hillebrand, 1888*b*). He also recognized that the 'Hawaiian Islands (are) the only Polynesian Island group which contain a large proportion of indigenous plants with American affinities' (Hillebrand, 1888*a*, p. XXIX). By 'American', Hillebrand (1888*a*) was referring at least in part to South America, based on his comment about '…the important American element of the Andine regions which is apparent in the Hawaiian flora' (p. XIV). His reference to American sources for Hawaiian flora evidently mostly did not refer to western North America north of Mexico: '…the northwest coast of America, including California, has until quite recent times only contributed one or two inhabitants of the highest mountains, and has besides few so-called representative species' (p. XIV).

Although various hypotheses were subsequently advanced to explain the arrival of native Hawaiian plants from source areas to the west and south of the islands, the difficulty of explaining a North American element in the Hawaiian flora by means other than long-distance dispersal of intercontinental magnitude (approx. 3800 km) led to major disagreement among botanists about the extent of North American–Hawaiian phytogeographical links. Attention to that disagreement serves to illuminate the intellectual obstacle during the early 20th century posed by the widespread conception of phenotypic evolution as too slow to account for highly divergent endemics on young islands. Here we provide historical perspective on some of those conflicting ideas and review modern evidence for angiosperm dispersal across the vast (and deep) oceanic barrier between North America and the Hawaiian Islands, with special focus on Hawaiian taxa from temperate and boreal North America, and the ecological obstacles and opportunities facing such plants in a tropical archipelago.

DISPARATE EARLY IDEAS ON ORIGINS OF HAWAIIAN FLORA

Endemism and antiquity of the Hawaiian flora

Early 20th century botanists presented a diversity of views on origins of the Hawaiian flora and differed about the importance of long-distance dispersal and particular source areas – especially America – as well as the age and timing of evolution and assembly of the flora. In general, the high level of Hawaiian floral and faunal endemism and distinctiveness of the endemic taxa was viewed as evidence for greater age of the islands

FIG. 2. Scientists who proposed hypotheses on the origins of Hawaiian flora. (A) Heinrich Gustav Adolf Engler (1844–1930), (B) Wilhelm (William) B. Hillebrand (1821–1886), (C) Alfred Russel Wallace (1823–1913), (D) Forest Buffen Harkness Brown (1873–1954), (E) Douglas Houghton Campbell (1859–1953), (F) Carl Johan Fredrik Skottsberg (1880–1963), (G) David Daniels Keck (1903–1995), (H) Francis Raymond Fosberg (1908–1993), (I) Sherwin Carlquist (1930–). A, B and D–H courtesy of the Hunt Institute for Botanical Documentation, Carnegie Mellon University. C courtesy of Smithsonian Institution Libraries, from Wallace (1905).

and/or flora and fauna than is indicated by modern geological and molecular data (see Price and Clague, 2002; Clague *et al.*, 2010) and, by some, as evidence for now-untenable past land connections between the Hawaiian Islands and areas to the south (e.g. Campbell, 1918). Alfred Russel Wallace's (1881; Fig. 1C) perspective on the high level of Hawaiian

endemism in *Island Life* may have been influential: 'These facts undoubtedly indicate an immense antiquity for this group of islands, or the vicinity of some very ancient land (now submerged), from which some portion of their peculiar fauna might be derived' (p. 298).

Hypotheses of long-distance dispersal to the Hawaiian Islands

Guppy (1906) championed the idea of oversea long-distance dispersal by providing extensive evidence for dispersal ability of Hawaiian and other Pacific plants based on first-hand experimentation and detailed observations of fruit and seed characteristics. His conclusion that birds, in addition to physical forces, were an important agent of Pacific plant dispersal was corroborated and extended by subsequent studies (see Ridley, 1930; Carlquist, 1974, 1996), although Guppy's idea that high levels of floristic and avian endemism in Hawaiian forests meant that birds long ago ceased to move propagules to or from such habitats is at odds with documentation of frequent bird traffic to diverse sites in the archipelago from continental areas (see Ballard and Sytsma, 2000). Hillebrand's (1888*a*) earlier idea that the Pacific golden plover has been important in the distribution of Hawaiian plant species is still widely held (see Fosberg, 1951; Johnstone and McFarlane, 1967; Carlquist, 1974; Ballard and Sytsma, 2000; Lowrey *et al.*, 2005; Harbaugh *et al.*, 2009).

Guppy's (1906) suggestion that plant dispersal to the Hawaiian Islands occurred in distinct, successive waves, with an early and extremely ancient series of dispersals from America (during his early Tertiary 'Age of Compositae') and a much more recent (post-Pleistocene) wave from Indo-Malesia was attributed in part to Bentham (1873), who noted that the high level of endemism in Hawaiian Compositae shows '... that the ancient connexion, of whatever nature it may have been, with America ... has been so long severed as not to have left a single unmodified common form. The species are all either descendants altered by long isolation or possibly, in some instances, preserved remnants of types long since extinct elsewhere' (p. 556). Guppy also may have been influenced by Wallace's (1881) extension of Bentham's (1873) views on the antiquity and origin of the morphologically unusual, endemic lineages of Hawaiian Compositae: 'The great preponderance of American relations in the Compositae ... is very interesting and suggestive ... We may ... look upon the Compositae as representing the most ancient portion of the existing flora of the Sandwich Islands, carrying us back to a very remote period when the facilities for communication with America were greater than they are now ... (P)lants of North Temperate affinity may be nearly as old, but these may have been derived from Northern Asia by way of Japan and the extensive line of shoals which run northwestward from the Sandwich Islands ... Those which exhibit Polynesian or Australian affinities, consisting, for the most part, of less highly modified species usually of the same genera, may have had their origin at a later, though still somewhat remote, period, when large islands, indicated by the extensive shoals to the south and southwest, offered facilities for the transmission of plants from the tropical portions of the Pacific Ocean' (Wallace, 1881, pp. 303–304).

Guppy's (1906) ideas on origin and assembly of the Hawaiian flora also somewhat resemble the later speculations of Brown (1921, 1922; Fig. 2D) and Brown and Brown (1933), although not in mode of oversea dispersal or in timing of events. Brown (1922) proposed three dispersal waves for Hawaiian and South Pacific angiosperms, with the vast majority of founders arriving directly or indirectly via flotation in sea currents from the Isthmus region of Central America. He concluded that the earliest of those supposed dispersal waves included ancestors of modern endemic Hawaiian genera ('... characterized by Compositae and Lobelioideae', p. 222) and occurred during the Mesozoic, possibly as early as the Jurassic and pre-dating the known angiosperm fossil record. Although Brown (1922) acknowledged a large Indo-Malesian element in the Hawaiian flora, he believed that even those plants, which he regarded as the latest natural arrivals, probably descended ultimately from Central American ancestors that dispersed west by oceanic rafting. Ridley (1930), in considering dispersal of plants worldwide, also noted a 'distinct American element' in the Hawaiian flora, although he found it '... difficult to see how such plants as have American affinities could have crossed over 2,000 miles of sea' (p. 687).

Vanished land connections and the American 'stumbling-block'

In contrast to the ideas of Bentham, Wallace, Guppy and Brown, Campbell (1918, 1919, 1920, 1926, 1928, 1932, 1933; Fig. 2D) and Skottsberg (1925, 1939, 1941; Fig. 2F) regarded America as a relatively minor contributor to the Hawaiian flora compared with the South Pacific, Australasia and Indo-Malesia and did not believe that long-distance dispersal alone could account for the high floristic richness of the Hawaiian Islands. Bryan (1915) also concluded that '... few indeed have been the representatives of the North American flora that have been brought to the islands' (p. 191). Campbell subscribed to the Pacific snail expert Pilsbry's (1916) hypothesis of once-continuous land connections among the Hawaiian Islands and between those islands, the South Pacific, Australasia and Indo-Malesia, and Campbell suggested a southern connection with South America as well. Subsidence of the hypothetical block connecting those areas was suggested to have led to isolation of the Hawaiian volcanic peaks as islands, following occupation of those peaks by ancestors of most lineages of the modern flora. Skottsberg (1925) advanced an 'Antarctic circuit theory', based in part on evidence at that time for an ancient southern super-continent, with south-to-north overland migration from Antarctica into Polynesia and into South America to account for floristic similarities across those regions. He indicated that extending that land connection to the Hawaiian Islands, as suggested by Campbell, was '... rather daring, but it is the only manner in which to get away from transpacific bridges, if we do not believe in oversea migration' (Skottsberg, 1925, p. 34).

Campbell (1919, 1920, 1926, 1928, 1933) did believe in the possibility of oversea plant transport; he indicated that lack of North American diversity in the Hawaiian Islands was surprising in light of relatively favourable prospects for long-distance, trans-Pacific dispersal from north-west America as opposed to

over-water dispersal from areas to the south. Although Campbell (1933) did not believe that over-water dispersal could account for the high representation of South Pacific, Malesian, Australasian or even South American plants in the Hawaiian flora, he believed that the relatively few founders from the Pacific coast of North America probably were ' . . . introduced . . . since the isolation of the islands' (p. 181). Skottsberg (1925), who rejected Bryan's (1921) suggestion of a direct land connection across the deep Pacific abyss between America and the Hawaiian Islands and was highly sceptical about the efficacy of oversea dispersal, indicated that ' . . . the representatives in (the Hawaiian Islands) of American fauna and flora, even if they are few, are a stumbling-block' (p. 35).

Shattering the American–Hawaiian floristic connection?

Keck (1936*a*; Fig. 2G), in his monograph of the Hawaiian silverswords (*Argyroxiphium*, Compositae), re-evaluated the evidence for American ancestry of Hawaiian vascular plants. He concluded that Skottsberg's (1925) 'stumbling-block' of trying to account for movement of plants between America and the Hawaiian Islands could be resolved in disfavour of phytogeographical affinities between the two areas except for as few as nine 'very inconsequential' late arrivals to the islands, with closely related congeners on the American mainland.

Keck (1936*a*) was principally concerned with the origins of endemic Hawaiian genera and the persistent suggestion that some of those highly distinctive groups – especially in Compositae – might be descendants of ancestors that arrived by long-distance dispersal, which was difficult to escape as an explanation for phytogeographical ties with America, especially North America. If the endemic Hawaiian genera of putatively American origin were instead found to be more closely related to plants from outside the New World, then ' . . . it is possible to follow one's inclinations and agree with Campbell, Skottsberg, and others that the endemic element in the Hawaiian flora, at least so far as the flowering plants are concerned, is for the most part of great age, and that it may have had its beginnings on nearby land masses in the Pacific even before the present archipelago became habitable' (Keck, 1936*a*, p. 5). Like other early 20th century botanists, Keck (1936*a*) evidently viewed the high degree of endemism in the flora as indicative of greater antiquity than the islands: 'Even the flora of the youngest Hawaiian mountains is very old, with 91 percent of the species endemic. This is not easily explained by those who regard the Hawaiian islands as purely oceanic in origin and the flora as carried there from great distances across the ocean . . . ' (p. 4). He similarly noted that the species of endemic Hawaiian genera ' . . . are usually well-marked, rather static, and senile in character' (p. 5) and that ' . . . many species appear to be on the verge of extinction because of their lack of plasticity' (p. 4).

Keck's (1936*a*, *b*) focus on relationships of Hawaiian silverswords (*Argyroxiphium*; Fig. 3A) was well chosen to test an American–Hawaiian phytogeographical relationship; most botanists who had published on origins of the Hawaiian flora had pointed to *Argyroxiphium* as an example of an endemic genus of American origin (e.g. Bentham, 1873; Engler,

1879; Wallace, 1881; Hillebrand, 1888; Campbell, 1919; Brown, 1922) or at least possibly from America (Skottsberg, 1925; but see Skottsberg, 1931). Gray's (1852) taxonomic placement of *Argyroxiphium* (and the closely related *Wilkesia*) with the American tarweeds, in subtribe Madiinae, had largely held sway until Keck's (1936*a*) study, wherein he indicated that *Argyroxiphium* (including *Wilkesia*, in his classification) was most closely related to the endemic Hawaiian genus *Dubautia* (in which he included *Railliardia*) and that ' . . . the affinities of these genera are to be found to the south or southwest in the Pacific' (p. 11), with genera of tribe Senecioneae such as *Robinsonia* (Juan Fernandez Islands) or *Brachionostylum* (New Guinea), as earlier suggested by Skottsberg (1931), or *Bedfordia* (Australia) rather than with American Compositae. Keck's (1936*a*) suggestion that *Argyroxiphium*/*Wilkesia* and *Dubautia*/*Railliardia* represent a common Hawaiian group impacted two long-suggested phytogeographical links between endemic Hawaiian genera and American taxa (Gray, 1852, 1865, 1870): *Argyroxiphium*/*Wilkesia* to the mostly Californian tarweeds (Madiinae; Fig. 3B) and *Railliardia* to the mostly Californian *Raillardella sensu lato* (*s.l.*), which was then widely treated in tribe Senecioneae (following Bentham, 1873) and not yet recognized as a tarweed. Keck (1936*a*) concluded: 'By thus divorcing *Argyroxiphium* from the American genera to which it has been thought related, the most persistently proposed connection between the ancient element in the Hawaiian flora and the New World has been shattered' (p. 11).

Evolutionary inactivity of American lineages in the Hawaiian flora?

Fosberg's (1948; Fig. 2H) tabulation of the source areas for Hawaiian vascular-plant lineages was the first comprehensive assessment of extra-Hawaiian affinities of the indigenous flora since Engler's (1879) and provided a detailed perspective on the importance of American founders. Although he drew in part on Skottsberg's ideas, Fosberg (1948) recognized that the Hawaiian flora was assembled by long-distance dispersal rather than by ancient land connections to other areas, and he wryly noted: 'If we resort to land bridges or continents to account for the presence of the Hawaiian flora, then we may well have to build them in all directions' (p. 119).

Of his estimated 272 angiosperm immigrants to the Hawaiian Islands, Fosberg (1948) concluded that regions to the west and south of the archipelago, widely believed at the time to be the most important sources for Hawaiian flora, contributed the majority of founder species, as corroborated subsequently (e.g. Wright *et al.*, 2001; Lowrey *et al.*, 2001; Gemmill *et al.*, 2002; Howarth *et al.*, 2003; Nepokroeff *et al.*, 2003; Hao *et al.*, 2004; Cronk *et al.*, 2005; Costello and Motley, 2007; Harbaugh and Baldwin, 2007; Percy *et al.*, 2008; Clark *et al.*, 2009; Harbaugh *et al.*, 2009). His table of flowering-plant founders included 109 from the 'Indo-Pacific' ('Indonesia or southeastern Asia and attenuating out into the Pacific') and 45 from the 'Austral' region ('south Pacific, from Australia to Patagonia'). He also noted that temperate and tropical regions of the Americas were the source of more founder species (50) than expected, based on most contemporary views, and slightly exceeded the number of founder

F<small>IG</small>. 3. Exemplars of Hawaiian angiosperm radiations (left) and American relatives (right) in Compositae–Madiinae (top) and Umbelliferae (bottom). (A) *Argyroxiphium sandwicense* subsp. *macrocephalum*. Image by W. L. Wagner. (B) *Madia elegans*. Image by B. G. Baldwin. (C) *Sanicula mariversa*. Image courtesy of J. K. Obata. (D) *S. arctopoides*. Image by B. G. Baldwin.

species from the 'Austral' region, which was believed by some to be the most important source area for Hawaiian plant lineages (e.g. Copeland, 1948).

Fosberg (1948, 1951) reconciled the high number of Hawaiian vascular-plant founders from temperate and tropical regions of the New World (50–51 of 272 angiosperms; 16–18 of 135 pteridophytes) with the widely held view of a relatively minor American element in the Hawaiian flora by noting that most indigenous Hawaiian plant lineages from the Americas

had undergone minimal evolutionary change since arriving in the archipelago and probably represented recent arrivals, as Keck (1936*a*) also concluded. Based on Fosberg's (1948) tabulations, none of the vascular plant genera of exclusively American (and/or boreal) origin in the native Hawaiian flora had produced more than two species or infraspecific taxa per original immigrant except for *Gunnera* (Gunneraceae) and the endemic Hawaiian genera *Hesperomannia* (Compositae), *Isodendrion* (Violaceae) and *Nothocestrum* (Solanaceae).

Founders of the three endemic genera and Hawaiian *Psychotria* (Rubiaceae) are the only plants of putatively American origin that he later noted as having '...given rise to any significant number of evolutionary offshoots that still survive, and none has produced a large number. Furthermore, all these genera are among the more doubtfully American of the lot' (Fosberg, 1951, pp. 204–205). Molecular phylogenetic studies have since overturned the hypotheses of American origins for *Hesperomannia* (Kim *et al.*, 1998), *Nothocestrum* (Olmstead *et al.*, 2008) and Hawaiian *Psychotria* (Nepokroeff *et al.*, 2003), and upheld a tropical American ancestry for *Isodendrion* (Feng, 2005; Tokuoka, 2008) and Hawaiian *Gunnera* (Wanntorp *et al.*, 2002; Wanntorp and Wanntorp, 2003), which is now treated as including only two species (see Wagner *et al.*, 1990). Fosberg's (1948) suggestion of an American origin for the two species of Hawaiian raspberries (*Rubus*, Rosaceae) was confirmed by molecular phylogenetic studies, although his hypothesis of monophyly of Hawaiian *Rubus* was rejected (Howarth *et al.*, 1997; Alice and Campbell, 1999; Morden *et al.*, 2003); each of the two Hawaiian species evidently stems from distinct western North American ancestors, with *R. hawaiiensis* most closely related to the salmonberry (*R. spectabilis*) and *R. macraei* most closely related to the California blackberry (*R. ursinus*).

INVESTIGATING THE AMERICAN CONTRIBUTION TO HAWAIIAN FLOWERING PLANT DIVERSITY

Since the 1950s and especially over the last 20 years, intensive evolutionary studies have greatly improved understanding of the origins and relationships of Hawaiian angiosperms. Evidence from those efforts for ancestrally American lineages in the Hawaiian flora is detailed here.

Revisiting the silversword alliance

Carlquist's (1958*a*, *b*, 1959; Fig. 2I) comparative anatomical studies of the silverswords and relatives provided the first strong refutation of hypotheses of minimal evolution or lack of representation of American plants in the Hawaiian archipelago (e.g. Skottsberg, 1931; Keck, 1936*a*; Fosberg, 1951). Like Keck (1936*a*), Carlquist recognized that the true Hawaiian silverswords and greenswords (*Argyroxiphium*) belong to the same insular lineage as the Hawaiian na'ene'e or kupaoa group (*Dubautia*, including *Railliardia*), and not to a different tribe or subtribe of Compositae, as earlier treated (e.g. by Gray, 1870; Bentham, 1873). Unlike Keck (1936*a*), Carlquist (1957) recognized that the *iliau* (*Wilkesia*), a bizarre rosette-plant from Kaua'i, is not more closely related to the rosette-plants in *Argyroxiphium* than to the trees, shrubs, mat-plants, cushion plants and vines in *Dubautia*, and, most importantly, that the insular lineage represented by *Argyroxiphium*, *Dubautia* and *Wilkesia* (i.e. the Hawaiian silversword alliance) belongs in subtribe Madiinae, with the primarily Californian tarweeds, including *Raillardella s.l.* (Carlquist, 1958*a*, *b*, 1959). Carlquist's (1959) expansion of the tarweed subtribe Madiinae to include the Hawaiian silversword alliance and

Raillardella united the two North American–Hawaiian phytogeographical links that Keck (1936*a*) rejected (i.e. *Argyroxiphium/Wilkesia* with the tarweeds; *Dubautia/ Railliardia* with *Raillardella*). Carlquist's (1959) demonstration of a large suite of vegetative and reproductive characteristics uniting tarweeds and silverswords and his point-by-point refutation of Keck's (1936*a*) argument against a tarweed–silversword relationship provided a convincing case for a western North American origin of a major Hawaiian angiosperm radiation. In part, Keck's (1936*a*) rejection of a tarweed ancestry of the silversword alliance was based on the striking differences in habit between the mostly herbaceous tarweeds and the woody or semi-woody Hawaiian taxa. Carlquist (1959) suggested that those habital differences reflected evolution of woodiness in an insular setting in response to opportunities for year-round growth. Among the shared features of the tarweeds and silversword alliance, Carlquist (1965, 1974, 1980) noted that the sticky bracts associated with tarweed ray fruits and the pappus characteristics of tarweed disc fruits allow for ready attachment to animals, and that such external adhesion to bird feathers would have allowed for oversea transport from America to the Hawaiian Islands. Like St. John (1950), Carlquist (1959) could find no morphological support for Skottsberg's (1931) and Keck's (1936*a*) suggestions of a close relationship of the silversword alliance to genera of tribe Senecioneae from Australasia or the Juan Fernandez Islands.

Molecular phylogenetic studies confirmed Carlquist's (1958*a*, *b*, 1959) hypothesis of long-distance dispersal and subsequent adaptive radiation of tarweeds in the Hawaiian Islands by showing that the Hawaiian silversword alliance is a monophyletic group nested within the California tarweed lineage (Baldwin *et al.*, 1991). Based on chloroplast DNA (cpDNA) and nuclear rDNA trees, the Hawaiian clade is more closely related to primarily Californian genera of the 'Madia' lineage than to other major lineages of Californian Madiinae (Baldwin, 1996, 2003). Molecular evidence for evolution of woodiness in the Hawaiian setting and ecological diversification of all modern members of the silversword alliance within the last 4–6 Myr (Baldwin and Robichaux, 1995; Baldwin and Sanderson, 1998) conforms to Carlquist's hypothesis of adaptive radiation of the group and contrasts with the once-prevalent view of endemic Hawaiian Compositae genera as ancient relicts that reflect an early Tertiary or even Mesozoic age of the Hawaiian chain (e.g. Guppy, 1906; Brown, 1921, 1922). Production of vigorous Hawaiian–Californian hybrids between members of the silversword alliance and tarweeds of the 'Madia' lineage (Baldwin *et al.*, 1991; Carr *et al.*, 1996) and hybrids between members of the two diploid Californian sublineages of the 'Madia' lineage implicated in an allotetraploid ancestry of the silversword alliance (Barrier *et al.*, 1999) provided biological evidence for a level of retained genetic similiarity between tarweeds and silverswords consistent with a limited time frame for divergence from a common ancestor.

A Hawaiian offshoot of the Californian sanicles

The ecologically diverse Hawaiian sanicles (*Sanicula*, Umbelliferae; Fig. 3C) are another group judged to be of

'obscure' affinity by Fosberg (1948) that structural and molecular data have indicated are of western North American origin. Wallace (1881) noted that Hawaiian '. . . *Sanicula* (is) allied to Oregon species' (p. 302) and Hillebrand (1888) similarly indicated that the sole Hawaiian species of *Sanicula* recognized at the time, *S. sandwicensis*, '. . . comes near *S. menziesii* [= *S. crassicaulis*]. . . from California and Oregon' (p. 144). Froebe (1971) suggested that the Hawaiian species (sect. *Sandwicenses*) descended from two distinct lineages of the mostly Californian sect. *Sanicoria* (Fig. 3D), based in part on presence of a taproot in both groups. Subsequent molecular phylogenetic analyses indicated that the Hawaiian taxa constitute a monophyletic (rather than biphyletic) group that is nested within sect. *Sanicoria* (Vargas *et al.*, 1998). Three Californian or mostly Californian species share a large (24-base pair) deletion in the nuclear rDNA internal transcribed spacer 2 (ITS-2) with the Hawaiian species; all of those taxa that share the deletion and their North American sister-group have prickly fruits that adhere readily to fur or feathers and were therefore inferred to have reached the Hawaiian Islands by external attachment to a bird (Vargas *et al.*, 1998), as suggested earlier for the tarweed ancestor of the silversword alliance. Unlike silverswords, Hawaiian sanicles remain herbaceous and descended from diploid (not polyploid) continental ancestors, with diversification from a common ancestor less than 1 Mya based on an externally calibrated, rate-constant ITS tree.

Violets and boreal American plant diversification in the Hawaiian Islands

Ballard and Sytsma (2000) provided molecular evidence for a boreal, western North American origin of the Hawaiian violets (*Viola*, Violaceae; Fig. 4A), another group regarded by Fosberg (1948) to be of 'obscure' extra-Hawaiian affinity. Prevalence of woodiness and multi-flowered inflorescences among Hawaiian violets led Skottsberg (1940) to suggest that the Hawaiian members of *Viola* represent the most ancient lineage in this highly diverse, worldwide genus of mostly herbaceous, single-flowered taxa. Skottsberg (1940) and others (e.g. St. John, 1989; Wagner *et al.*, 1990) suggested a closest relationship of Hawaiian violets to Latin American woody violets of sect. *Leptidium* or sect. *Rubellium*, although St. John (1989) regarded Hawaiian violets as polyphyletic, with separate introductions accounting for woody and herbaceous taxa in the islands. Ballard and Sytsma (2000) instead found that the Hawaiian violets constitute a young clade nested among lineages of boreal, mostly North American herbaceous taxa of boggy or otherwise wet habitats, like those where some of the Hawaiian species occur. As in the silversword alliance, molecular data were decisive in demonstrating that woodiness was derived in the Hawaiian setting from an ancestrally herbaceous condition.

More specifically, Ballard and Sytsma (2000) showed that Hawaiian violets probably descended from an Arctic or far-north temperate American ancestor referable to *Viola langsdorffii s.l.* ('Alaskan violet'; Fig. 4B), which occurs from northern California to Alaska in western North America and Kamchatka in the Russian Far East to northern Japan. They found that the sampled boreal American representative of

V. langsdorffii and Hawaiian violets constituted a robust clade to the exclusion of a Japanese sample of *V. langsdorffii.* Experimental hydrolysis of seeds of *V. langsdorffii* and other violets to simulate conditions in a bird digestive tract demonstrated that violets could be avian dispersed from the American Arctic to the Hawaiian Islands without harm via internal transport. They also inferred a polyploid ancestry of Hawaiian violets based on chromosome counts consistent with hexaploidy, decaploidy and dodecaploidy of different populations of *V. langsdorffii* and with octoploidy of Hawaiian violets.

In addition to providing the first compelling evidence of a boreal origin for a diverse lineage of Hawaiian plants, Ballard and Sytsma (2000) pointed to evident niche conservatism of some Hawaiian violets to underline the importance of ecological opportunity in colonization of the Hawaiian Islands by plants from higher latitudes. They noted that lack of well-documented representation of boreal plant lineages in the Hawaiian flora ran counter to the frequent opportunities for such dispersal, given the wide diversity of Arctic- and sub-Arctic-breeding birds that migrate regularly to the islands, and suggested that transport to a suitable habitat within the tropical island setting may be a more important limitation for establishment of northern plants than crossing the oceanic expanse between the islands and boreal regions. That argument is consistent with earlier ideas expressed by Wallace (1881), Setchell (1935) and Carlquist (1974), who concluded that transport of plants to islands may be less of a limiting factor in long-distance dispersal than ecological considerations upon arrival. Ballard and Sytsma also noted that insufficient rigorous evidence about origins of other Hawaiian plants of possible northern ancestry may have resulted in underestimation of the importance of boreal lineages in the Hawaiian flora.

Hawaiian mints and American hedge nettles: another North American link to a major Hawaiian radiation

Lindqvist and Albert (2002) demonstrated that the highly diverse Hawaiian mints (approx. 59 species in *Haplostachys*, *Phyllostegia* and *Stenogyne*, Lamiaceae; Fig. 4C), previously regarded as Austral or south-east Asian in origin (e.g. Campbell, 1919; Fosberg, 1948), are phylogenetically nested within *Stachys* ('hedge nettles'; Fig. 4D) and most closely related to temperate North American members of the nearly worldwide genus. Fleshy fruits of two of the three Hawaiian mint genera (*Phyllostegia* and *Stenogyne*) were in part responsible for their earlier association with other fleshy-fruited, mostly south-east Asian members of Lamioideae (*Prasium*, *Bostrychanthera* and *Gomphostemma*) in tribe Prasieae or subfamily Prasioideae (e.g. Bentham, 1832–1836; Briquet, 1895–1897; Wunderlich, 1967), rather than with dry-fruited lamioids. Pericarp analysis led Ryding (1994) to conclude instead that fleshy fruits evolved repeatedly in Lamioideae and that the Hawaiian mints, although probably monophyletic (including the dry-fruited *Haplostachys*), are not as closely related to *Prasium* or *Gomphostemma* as earlier suggested, in accordance with the subsequent molecular data.

In addition to representing an exceptionally diverse Hawaiian lineage of vascular plants in number of recognized

FIG. 4. Exemplars of Hawaiian angiosperm radiations (left) and American relatives (right) in Violaceae (top) and Labiatae (bottom). (A) *Viola chamissoniana* subsp. *robusta.* Image courtesy of G. D. Carr. (B) *V. langsdorffii.* Image courtesy of M. Goff. (C) *Phyllostegia floribunda.* Image courtesy of J. K. Obata. (D) *Stachys chamissonis.* Image courtesy of A. Brousseau, copyright © 1995 Saint Mary's College of California.

species, Hawaiian mints have radiated across highly contrasting environmental settings, including dry shrublands and wet forests, and exhibit floral diversity associated with both insect pollination (in *Haplostachys* and *Phyllostegia*) and bird pollination (in *Stenogyne*). The presence of such diversity in pollination systems in the Hawaiian mints may reflect evolutionary lability present in their common ancestor with North

American *Stachys*; among the closest relatives of Hawaiian mints in North American *Stachys* based on the molecular trees are the insect-pollinated *S. quercetorum* and the bird-pollinated *S. chamissonis* (Lindqvist and Albert, 2002). Polyploidy, possibly of hybrid origin, was inferred by Lindqvist and Albert (2002) to have been ancestral within the American founder lineage that gave rise to Hawaiian

mints ($2n = 64, 66$) and suggested it to possibly account for the magnitude of their morphological diversification (see also Lindqvist *et al.*, 2003), as proposed earlier for the silversword alliance (Barrier *et al.*, 1999).

Hawaiian lineages of the carnation family

Schiedea. The most diverse lineage of Hawaiian Caryophyllaceae also appears to have probably descended from a North American founder, based on recent molecular results (Wagner *et al.*, 2005*b*; Harbaugh *et al.*, 2010). The endemic Hawaiian genus *Schiedea* (Fig. 5A) consists of 34 species of herbs, shrubs and vines that arguably represent the greatest diversification of reproductive traits in angiosperms of the islands, with lineages that are monomorphic and insect- or bird-pollinated (sometimes autogamous) or are dimorphic and wind-pollinated. A bird-pollinated lineage within *Schiedea* is so distinctive morphologically that it was until recently (Wagner *et al.*, 2005*b*) treated as a distinct genus, *Alsinidendron* (Fig. 5A).

Discerning relationships of *Schiedea* to other members of subfamily Alsinoideae outside the Hawaiian Islands has been complicated by extensive morphological divergence of the group from all living representatives of the subfamily. Skottsberg (1939) hesitantly suggested a boreal ancestry of *Schiedea* (including *Alsinidendron*) before concluding that the group is instead a southern ('Austral') element in the Hawaiian flora, derived ultimately from Antarctic ancestors (Skottsberg, 1941), as he concluded also for the silversword-alliance genera (see above). Fosberg (1948) treated *Schiedea* as of 'obscure' phytogeographical affinity. Extensive molecular phylogenetic sampling across Alsinoideae by Wagner *et al.* (2005*b*) and Harbaugh *et al.* (2010) led to the discovery that *Schiedea* is sister to two monotypic genera, *Honckenya* and *Wilhelmsia* (Fig. 5B), that are boreal, rather than austral, endemics. Although both boreal genera occur in Eurasia as well as North America, the founder of *Schiedea* appears most likely to have dispersed from North America, where three of the four taxa (subspecies) of *Honckenya* are restricted and where the most closely related continental relatives of *Honckenya* and *Wilhelmsia* are endemic (Harbaugh *et al.*, 2010). Based on the phylogenetic findings, woodiness in *Schiedea* appears to be secondarily derived from an herbaceous habit, which is common to *Honckenya*, *Wilhelmsia* and their closest relatives (see Carlquist, 1995). Wagner *et al.* (2005*b*) noted that successful colonization of the Hawaiian Islands by the founder of *Schiedea* was not complicated by dioecy and the associated need for dispersal of multiple individuals from the mainland; floral hermaphroditism is unequivocally estimated as ancestral in *Schiedea*, based on occurrence of that condition throughout the closest continental relatives except *Honckenya*, which appears to have independently evolved a dimorphic sexual system.

Silene. The other endemic lineage of Hawaiian Caryophyllaceae was recently resolved as the sister group to a temperate American species (Eggens *et al.*, 2007). The mostly Northern Hemisphere genus *Silene* (campions or catchflies), with approx. 650 species, is represented in the islands by seven recognized woody species that belong to two lineages of sufficiently different habit, ecology and floral morphology to have been thought to represent descendants of distinct Hawaiian founders (see Wagner *et al.*, 1990). One of these two groups contains subshrubs of often mesic habitats with white, notched petals (e.g. *S. perlmanii*; Fig. 5C); the other group comprises shrubs of dry habitats, with narrower leaves and green or cream-coloured to reddish, divided petals (e.g. *S. hawaiiensis*). Skottsberg (1941) included Hawaiian *Silene* in a group of temperate genera (including *Rubus*, *Sanicula* and *Viola*) that he regarded as being '. . . so distinct and so distant from everything else that their history here (in the Hawaiian Islands) must have been a long one' (p. 697). Fosberg (1948) regarded all members of Hawaiian *Silene* as of 'obscure' affinity. Chowdhuri (1957) classified Hawaiian members of the genus in a common section with two poorly known, putatively Japanese species, *S. japonica* and *S. tanakae*, possibly implying an East Asian origin of the Hawaiian taxa.

Based on molecular phylogenetic data from cpDNA and nuclear DNA (ITS) sequences, Eggens *et al.* (2007) found that the two morphological groups of Hawaiian *Silene* constitute a clade that is sister to *S. antirrhina* (Fig. 5D), a widespread, weedy annual of temperate North America and South America, with minimal molecular divergence between the American and Hawaiian taxa. Some uncertainty remains about the geographical affinities of Hawaiian campions because of the occurrence of *S. antirrhina* on both American continents and because of a sister-group relationship between the Hawaiian + American clade and a diverse *Silene* clade from Eurasia (specifically, the Mediterranean and Middle East), which conceivably could have been the source area for independent dispersal events to America and the Hawaiian Islands. Prevalence of herbaceousness in the continental lineages that are closely related to Hawaiian campions indicates that woodiness of the Hawaiian species probably evolved in the insular setting, as inferred for *Schiedea*, the silversword alliance and some lineages of Hawaiian mints and *Viola*.

Woody spurges from North America. The spectacular diversity of trees, shrubs and subshrubs in Hawaiian *Euphorbia* subg. *Chamaesyce* (16+ species; Fig. 6A) has been long suggested to represent an endemic lineage of Indo-Pacific origin (Degener and Croizat, 1936; Fosberg, 1948; Koutnik, 1987). Carlquist (1970, 1974, 1980) regarded the Hawaiian taxa as exemplary of adaptive radiation, based on anatomical, morphological and ecological considerations. Studies by Pearcy and colleagues (e.g. Robichaux and Pearcy, 1980; Pearcy *et al.*, 1982; Pearcy and Fransceschi, 1986) demonstrated major ecophysiological differences among the ancestrally and uniformly C_4 Hawaiian chamaesyces that correspond to the wide range of habitats occupied by different taxa, such as exposed, dry beaches and shaded, wet forests. Morden and Gregoritza (2005) noted levels of molecular variation and lineage divergence within the Hawaiian clade that are unusually high for an oceanic island group and that warrant species-level treatment for at least some of the ten endemic varieties that have been recognized recently (Koutnik, 1987, 1999).
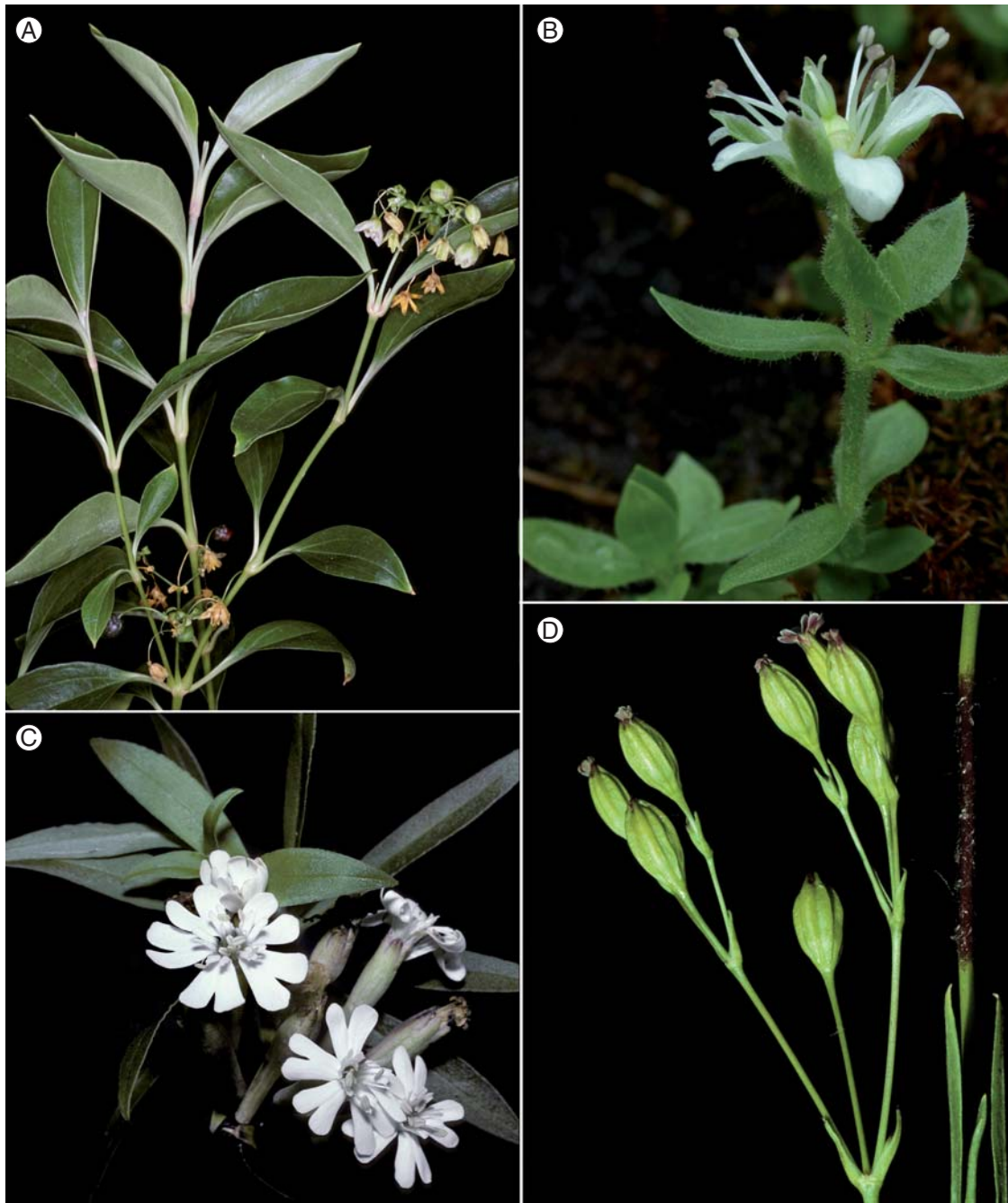
FIG. 5. Exemplars of Hawaiian angiosperm radiations (left) and American relatives (right) in Caryophyllaceae. (A) *Schiedea obovata.* Image courtesy of G. D. Carr. (B) *Wilhelmsia physodes.* Image by L. Brothers. (C) *Silene perlmanii.* Image courtesy of J. K. Obata. (D) *S. antirrhina.* Image courtesy of G. Yatskievych.

Yang *et al.* (2009) presented molecular phylogenetic evidence for a south-western North American, rather than Indo-Pacific (Fosberg, 1948), origin of the Hawaiian chamae-syces. Analysis of both cpDNA and nuclear ribosomal ITS sequences from an extensive taxonomic and geographical sampling of *Euphorbia* subg. *Chamaesyce* indicated that the sister group of the Hawaiian taxa comprises four species of Chihuahuan Desert annuals from Texas and northern Mexico such as *E. leucantha* (Fig. 6B). Monophyly of the Hawaiian

chamaesyces was established on the basis of molecular phylogenetic data in an earlier study by Raz *et al.* (1998), who contributed to Yang *et al.*'s effort (Y. Yang, University of Michigan, Ann Arbor, pers. comm.). Yang *et al.* (2009) noted that a possible hybrid origin of the Hawaiian ancestor might explain results from a low-copy nuclear gene ('deadx9' or EMB2765): one of three alleles of the sampled Hawaiian taxa was resolved as sister to the allele found in the four Chihuahuan Desert annuals; the other two alleles of

FIG. 6. Exemplars of Hawaiian angiosperm radiations (left) and American relatives (right) in Euphorbiaceae (top) and Geraniaceae (bottom). (A) *Euphorbia rockii.* Image courtesy of J. K. Obata. (B) *E. leucantha.* Image courtesy of V. Steinmann. (C) *Geranium arboreum.* Image courtesy of G. D. Carr. (D) *G. richardsonii.* Image courtesy of D. Fristrom.

the Hawaiian taxa were sister to the allele found in a fifth south-western North American herb, *Euphorbia cinerascens.* Coastal Hawaiian chamaesyces, which approach continental taxa in habit, have sticky seeds consistent with dispersal by birds from North America, with putative loss of such dispersal ability and increased woodiness in shrubs and trees of interior Hawaiian habitats (Carlquist, 1980).

Woody geraniums: another Hawaiian radiation of North American origin? The morphologically anomalous, Hawaiian members of *Geranium* (Geraniaceae), with shrubby or arboreal life-forms, undivided leaves and free stamens (Fig. 6C), were regarded to be of 'obscure' origin (Fosberg, 1948; Wagner *et al.*, 1990) until molecular data indicated that the taxa

constitute a clade of American ancestry (Pax *et al.*, 1997). Although these montane Hawaiian species can be assigned on the basis of morphology to *Geranium* sect. *Geranium*, ascertaining the source area of Hawaiian geraniums has been complicated by the great diversity (>250 species) and wide distribution of that section, as well as the highly disparate morphology of the Hawaiian taxa relative to the comparatively modest morphological variation among non-Hawaiian members of the group.

Phylogenetic analysis of cpDNA *rbc*L sequences from each of the six Hawaiian species, representatives of the three subgenera of *Geranium*, and a limited sampling of Asian, Australian and American members of sect. *Geranium* resolved a well-supported Hawaiian clade nested among montane North

American herbaceous lineages from Mexico and the western United States, i.e. *G. richardsonii* (Fig. 6D), *G. subulato-stipulatum* and *G. vulcanicola* (Pax *et al.*, 1997). The sole red- and zygomorphic-flowered, bird-pollinated species, *G. arboreum* (Fig. 6C), a tree-like Hawaiian endemic, was resolved as sister to the other, white- and actinomorphic-flowered, shrubby and subshrubby Hawaiian taxa. As noted by the authors, pinpointing the source of the Hawaiian lineage will require more extensive sampling of sect. *Geranium* and special attention to New World groups, such as alpine South American taxa sometimes treated in sect. *Andinii*, which have persistent leaf bases similar to those of the Hawaiian species. Lack of woody growth forms in *Geranium* apart from those of the Hawaiian taxa is consistent with a hypothesis of secondary woodiness evolving in the islands from an herbaceous founding lineage.

Temperate North American lineages of low diversity in the Hawaiian Islands

Engler (1879) and/or Fosberg (1948) noted some individual Hawaiian-endemic species of putative New World origin that have been confirmed as most closely related to American taxa, in addition to *Rubus macraei* and *R. hawaiiensis* (discussed above). Hawaiian purple mat, *Nama sandwicensis* (Boraginaceae *s.l.*), evidently has closest relatives among annuals of sect. *Nama* in south-western North America based on micromorphological and molecular data (see Wagner *et al.*, 1999; S. Taylor and B. Simpson, University of Texas, Austin, pers. comm.). Hawaiian dodder, *Cuscuta sandwichiana*, was placed within different clades of primarily North American taxa in cpDNA trees versus nuclear ribosomal trees of Stefanovic and Costea (2008); they concluded that the Hawaiian ancestor was of hybrid origin and probably dispersed from south-western North America, where the two putatively parental clades co-occur. *Argemone glauca* (Papaveraceae), an endemic Hawaiian prickly poppy, was suggested by Ownbey (1961) to have descended from South American species; however, an ITS-1 tree for *Argemone* indicates that the South American taxa constitute a robust clade to the exclusion of North American and Hawaiian taxa (Schwarzbach and Kadereit, 1999). The Hawaiian nettle *Hesperocnide sandwicensis* (Urticaceae) has not been studied recently, but has only one congener, *H. tenella*, which is endemic to California.

Some individual Hawaiian endemic angiosperm species or species-pairs of uncertain relationship prior to molecular studies now appear to be of American origin, as well. The Hawaiian bog orchid, *Platanthera holochila*, one of three indigenous species of Orchidaceae in the Hawaiian flora – all suggested by Fosberg (1948) to be of Indo-Pacific origin – belongs to sect. *Limnorchis* and is nested among North American taxa in ITS trees (R. K. Lauri, Rancho Santa Ana Botanic Garden, Claremont, CA, pers. comm.; see also Bateman *et al.*, 2009). Uncertainty about the relationships of two distinct groups of endemic Hawaiian sedges, *Carex alligata* + *C. kauiensis* and *C. nealae* [considered to be the Asian *C. thunbergii* by Koyama (1999)], was resolved by Dragon and Barrington (2009) in favour of separate, temperate North American origins of both lineages; they found that *C. alligata* and *C. kauaiensis* are sister to *C. obnupta* of

western North America and *C. nealae* is sister to *C. emoryi* of central–eastern North America. Another Hawaiian endemic of uncertain origin, the bunchgrass *Deschampsia nubigena*, was strongly resolved in Chiapella's (2007) ITS tree as more closely related to a sample of *D. cespitosa* from Oregon (Hsiao *et al.*, 1995; K. Jensen, US Department of Agriculture, pers. comm.) than to other samples of *D. cespitosa* from Europe and South America.

Neotropical ancestry of Hawaiian angiosperms

Some Hawaiian angiosperm lineages of neotropical origin or of uncertain life zone within the New World either appear to be from southern North America (including Central America and the Caribbean) or cannot be excluded as having North American ancestry. For example, Hawaiian *Sicyos* (Cucurbitaceae) contains three endemic sections (approx. 14 species) of monoecious climbing annuals and perennial vines that have been of obscure affinity (e.g. Fosberg, 1948); they were resolved from ITS data as a clade nested among primarily Mexican taxa (Sebastian *et al.*, 2009; P. Sebastian and S. S. Renner, University of Munich, pers. comm.). The endemic Hawaiian, shrubby genus *Isodendrion* (four species; Violaceae) has been resolved as sister to *Pombalia*, from south-western North American and Latin America; *Isodendrion* and *Pombalia* are in turn sister to Mesoamerican members of *Hybanthus* (Ballard *et al.*, 2009; H. E. Ballard, pers. comm.). Hawaiian *Gunnera* (approx. two species; Gunneraceae) was resolved as monophyletic and sister to a diverse South American clade, with the Hawaiian + South American group sister to North American *G. mexicana* (Wanntorp and Wanntorp, 2003). Although the ancestral area for the Hawaiian taxa was equivocal based on the molecular phylogeny, Wanntorp and Wanntorp (2003) entertained the hypothesis that the Hawaiian *Gunnera* clade dispersed from North America during the Tertiary, when subgenus *Panke* was widespread there, based on fossil evidence. Hawaiian-endemic *Portulaca villosa* (Portulacaceae), a putative sister-species of Hawaiian-endemic *P. sclerocarpa* (Wagner *et al.*, 1999), also has been resolved within a clade of North American (including Caribbean) and South American taxa in molecular trees (Ocampo and Columbus, 2009*a*, *b*).

Examples of a northern neotropical connection to the Hawaiian flora include well-studied, monospecific coastal lineages that may have dispersed to the islands by oceanic flotation. Hawaiian-endemic cotton, *Gossypium tomentosum* (Malvaceae), is a coastal shrub most closely related to upland cotton (*G. hirsutum*) based on multiple lines of molecular evidence (DeJoode and Wendel, 1992; Wendel *et al.*, 1995; Cronn *et al.*, 1996; Seelanan *et al.*, 1997; Small *et al.*, 1998) and was suggested by DeJoode and Wendel (1992) to represent an example of long-distance dispersal by seed- or capsule-flotation in oceanic currents from Mesoamerica, where *G. hirsutum* is native. Although *G. tomentosum* is highly unusual morphologically, it is interfertile with *G. hirsutum* and is estimated to have diverged from upland cotton since the Pleistocene (DeJoode and Wendel, 1992; Cronn *et al.*, 2002). The vine *Jacquemontia sandwicensis* (Convolvulaceae) is another coastal Hawaiian plant with closest relatives in subtropical North America. On the basis
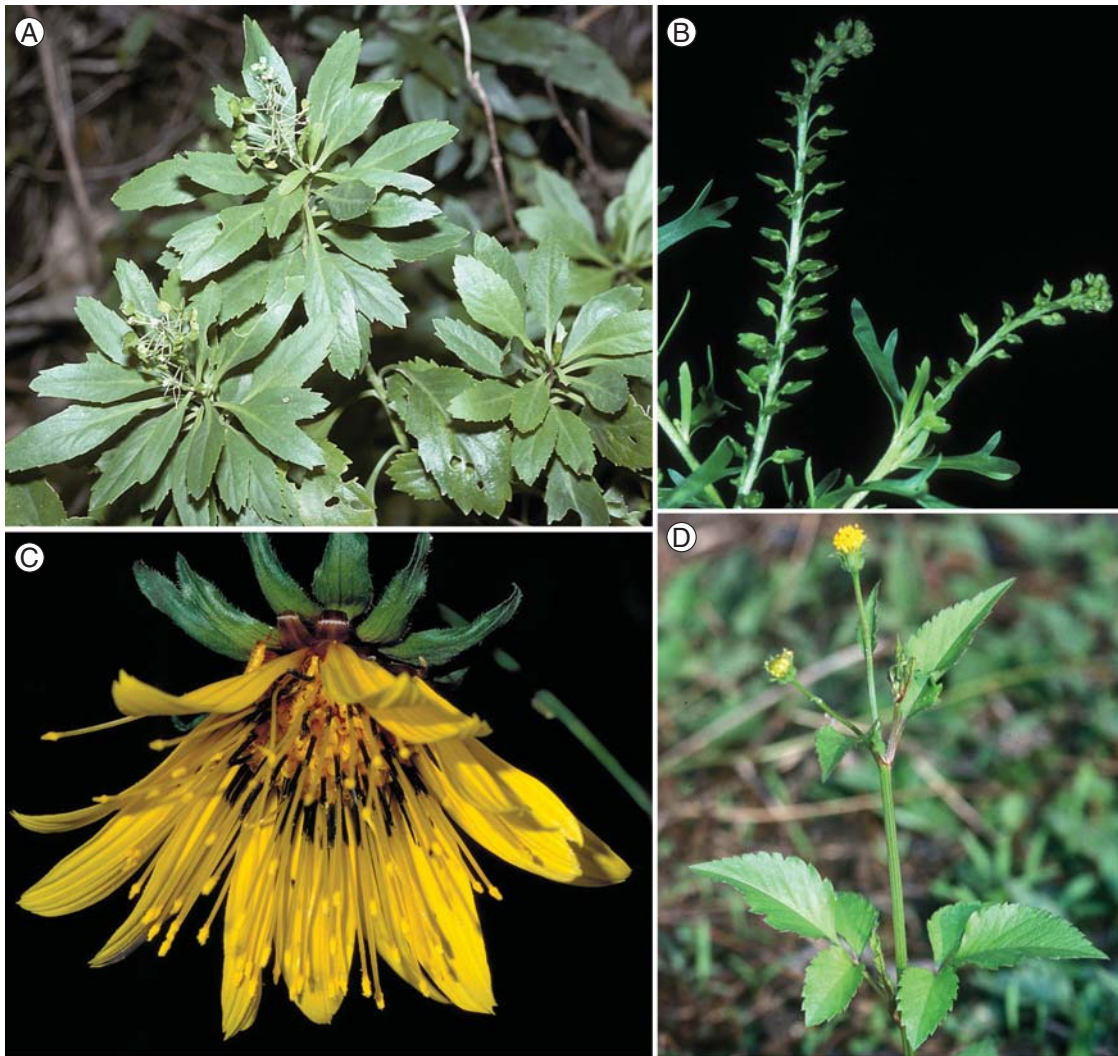
Fɪɢ. 7. Exemplars of Hawaiian angiosperm radiations (left) and American relatives (right) in Cruciferae (top) and Compositae–Coreopsideae (bottom). (A) *Lepidium arbuscula*. Image courtesy of J. K. Obata. (B) *Lepidium oblongum*. Image courtesy of J. M. DiTomaso. (C) *Bidens cosmoides*. Image courtesy of G. Diada. (D) *B. pilosa*. Image courtesy of J. M. DiTomaso.

of cpDNA and nuclear trees, Namoff *et al.* (2010) found that *J. obcordata* of the Caribbean Basin is sister to *J. sandwicensis* and that the two species are in turn sister to *J. ovalifolia* of Africa. Lack of seed buoyancy in water in *J. sandwicensis* may reflect either evolutionary loss of such ability following oceanic dispersal to the Hawaiian Islands or a history of dispersal by birds (Guppy, 1906; Ridley, 1930; Robertson, 1974; Namoff *et al.*, 2010).

Hawaiian lineages of indirect American ancestry?

Some highly diverse lineages of Hawaiian flowering plants have closest relatives in the South Pacific and cannot be excluded as having descended directly from ancestors there, although their closest continental relatives are evidently from the New World. Such Hawaiian groups may have instead originated directly from continental (New World) ancestors, either with subsequent out-of-Hawaii dispersal to the South Pacific, as resolved for various Hawaiian lineages from the

Old World (e.g. *Santalum*, Harbaugh and Baldwin, 2007; *Melicope*, Harbaugh *et al.*, 2009), or with independent dispersal to the South Pacific from the Americas. Any of the three scenarios for direct or indirect arrival in the Hawaiian Islands requires a hypothesis of long-distance dispersal of intercontinental magnitude from the New World.

Directly or indirectly, the only native crucifers in the Hawaiian Islands are evidently of temperate North American origin. A molecular phylogenetic analysis of worldwide diversity of *Lepidium* (pepperworts; Cruciferae) by Mummenhoff *et al.* (2001) indicated that the native, subshrubby or shrubby taxa of pepperworts in the islands (Fig. 7A) constitute a clade that is nested among North American lineages of mostly annual taxa, such as *L. lasiocarpum*, *L. oblongum* (Fig. 7B) and *L. virginicum*. Hawaiian pepperworts have been classified with Australian and New Zealand taxa (Thellung, 1906), although Carlquist (1967) proposed American ancestry for the Hawaiian plants, with long-distance dispersal by adhesion of the wetted, mucilaginous seeds to

birds. Based on levels of cpDNA divergence between mainland and island taxa and geographical distribution of the American species, Mummenhoff *et al.* (2001) concluded that the Hawaiian lineage probably diverged from a Californian ancestor during the Pleistocene, as suggested for Hawaiian *Sanicula* by Vargas *et al.* (1998). Based on the taxa sampled, woodiness of the Hawaiian taxa appears to be have been derived from herbaceousness in an island setting, although the authors cautioned that sampling of additional taxa and molecular markers was needed to resolve the basis of insular woodiness.

One of the five species of native Hawaiian *Lepidium* recognized by Wagner *et al.* (1999), *L. bidentatum*, occurs in low-elevation, dry, rocky sites and is widespread across islands of the Pacific; *L. bidentatum* can be inferred to represent either the ancestral phenotype of the Hawaiian clade or an example of dispersal out of Hawai'i and throughout the Pacific by a lineage that has undergone diversification in the Hawaiian Islands. Hawaiian diversification from an *L. bidentatum*-like ancestor would have involved a shift from xeric to mesic habitats, accompanied by upslope dispersal, to account for the ecological characteristics of the mesic-forest taxa, *L. orbiculare* and *L. serra*. Xeric ancestry also is consistent with ecological attributes of most of the closely related North American taxa sampled by Mummenhoff *et al.* (2001).

Hawaiian *Bidens* (Coreopsideae; Compositae), an adaptive radiation of approx. 19 species of interfertile annuals, perennial herbs and shrubs (Ganders and Nagata, 1984; Helenurm and Ganders, 1985), including the spectacular, putatively bird-pollinated *B. cosmoides* (Ganders and Nagata, 1983; Fig. 7C), has been resolved in ITS trees as most closely related to a South-east Pacific clade (Ganders *et al.*, 2000). In turn, the Hawaiian + South-east Pacific clade is nested among American members of sect. *Psilocarpaea*, with the closest sampled relatives (*B. alba* and *B. pilosa*; Fig. 7D) from southern North America, including the Caribbean (Ganders *et al.*, 2000). Fruits and pappus elements of the American relatives are barbed and readily dispersible by birds, with loss or change in dispersal ability in the Pacific clade (Carlquist, 1974). The Hawaiian taxa have been regarded as American (e.g. Engler, 1879; Hillebrand, 1888) or Austral (e.g. Fosberg, 1948) in origin and were suggested by Gillett (1972, 1973) to be ancestral to the less morphologically and ecologically diverse South-east Pacific taxa. Based on the molecular evidence for a nested phylogenetic position of the Hawaiian and South Pacific clade (sect. *Campylotheca*) among herbaceous American lineages of sect. *Psilocarpaea*, Ganders *et al.* (2000) concluded that woody and indeterminate habits evolved secondarily in the Pacific group.

Complex patterns of morphological and ecological diversity among the herbaceous and shrubby Hawaiian plantains (*Plantago*; Plantaginaceae) have been interpreted as evidence for two separate introductions from the south, one from New Zealand and one from the Juan Fernandez Islands (Rock, 1920; Fosberg, 1948; see Wagner *et al.*, 1999). Dunbar-Co *et al.* (2008) instead resolved Hawaiian *Plantago* as a monophyletic group with closest relatives in either south-temperate Polynesia (Rapa), based on cpDNA trees, or temperate North America, based on ITS trees. They also found evidence from both lines of molecular evidence for more evolutionarily distinct lineages of Hawaiian plantains than have been recently recognized taxonomically. Both allopatric and ecological diversification across the archipelago and among wet, dry and bog habitats on individual islands appear to have occurred in the Hawaiian clade. A more extensive, worldwide sampling of *Plantago* indicates a temperate North American origin for Hawaiian *Plantago*, with *P. tweedyi* resolved as the closest relative (sister-species) of the Hawaiian clade (R. Hoggard, University of Oklahoma, Norman, OK, pers. comm.).

All indigenous palms of the Hawaiian Islands (approx. 23 species) constitute a clade within the monophyletic tropical-Pacific genus *Pritchardia* (Palmae), based on nuclear and cpDNA trees (Bacon *et al.*, 2009). Molecular results also indicate that *Pritchardia* is most closely related to tropical and warm temperate New World fan palms in *Copernicia* and, probably, *Washingtonia* (Baker *et al.*, 2009; C. Bacon, pers. comm.). Although the Hawaiian fan palms may well have descended from South Pacific ancestors in *Pritchardia*, as suggested earlier (e.g. Fosberg, 1948), the genus as a whole evidently stems from a dispersal event into the Pacific from America.

Molecular data indicate that various endemic or indigenous Hawaiian lineages of widespread genera and represented by only one or two insular species also arrived directly or indirectly from the New World. *Lycium sandwicense* (Solanaceae), known from Hawaiian and South Pacific islands, is a shrub of the littoral zone that was resolved in ITS trees as most closely related to the shrubby, North American *L. carolinianum* and part of a diverse North American clade with multi-seeded, orange or red berries (Miller, 2002), implicated in long-distance dispersal by birds (Symon, 1991; Miller *et al.*, 2008). *Ilex anomala* (Aquifoliaceae), a tree or shrub of mesic to wet forests or bog habitats in the Hawaiian and South Pacific islands, was resolved in cpDNA trees as part of an otherwise New World clade including North American and South American taxa (Cuénoud *et al.*, 2000). The ancestor of *Portulaca lutea* and *P. molokiniensis* (Portulacaceae) also appears either to have dispersed directly to the Hawaiian Islands from the New World, with subsequent dispersal of *P. lutea* throughout the Pacific, or to have arrived in the South Pacific, with subsequent dispersal to the Hawaiian Islands by *P. lutea* and divergence of *P. molokiniensis* (Ocampo and Columbus, 2009*a*, *b*). Similar alternative biogeographical scenarios are evident for *Mucuna sloanei* (Leguminosae), with var. *sloanei* in South America, the South-east Pacific and the Hawaiian Islands and var. *persericea* endemic to Maui (Wilmot-Dear, 1990).

Hawaiian angiosperms of possible New World ancestry that warrant further study include the endemic genus *Lipochaeta* and relatives (Compositae) and endemic taxa of *Abutilon* (Malvaceae), *Calamagrostis* (Gramineae), *Chenopodium* (Chenopodiaceae), *Dissochondrus* (Gramineae), *Dodonaea* (Sapindaceae), *Eragrostis* (Gramineae), *Erythrina* (Leguminosae), *Ipomoea* (Convolvulaceae), *Luzula* (Juncaceae), *Myrsine* (Myrsinaceae), *Panicum* (Gramineae), *Perrottetia* (Dipentodontaceae), *Phytolacca* (Phytolaccaceae), *Poa* (Gramineae), *Ranunculus* (Ranunculaceae), *Rauvolfia* (Apocynaceae), *Rumex* (Polygonaceae), *Trisetum* (Gramineae) and *Vaccinium* (Ericaceae).
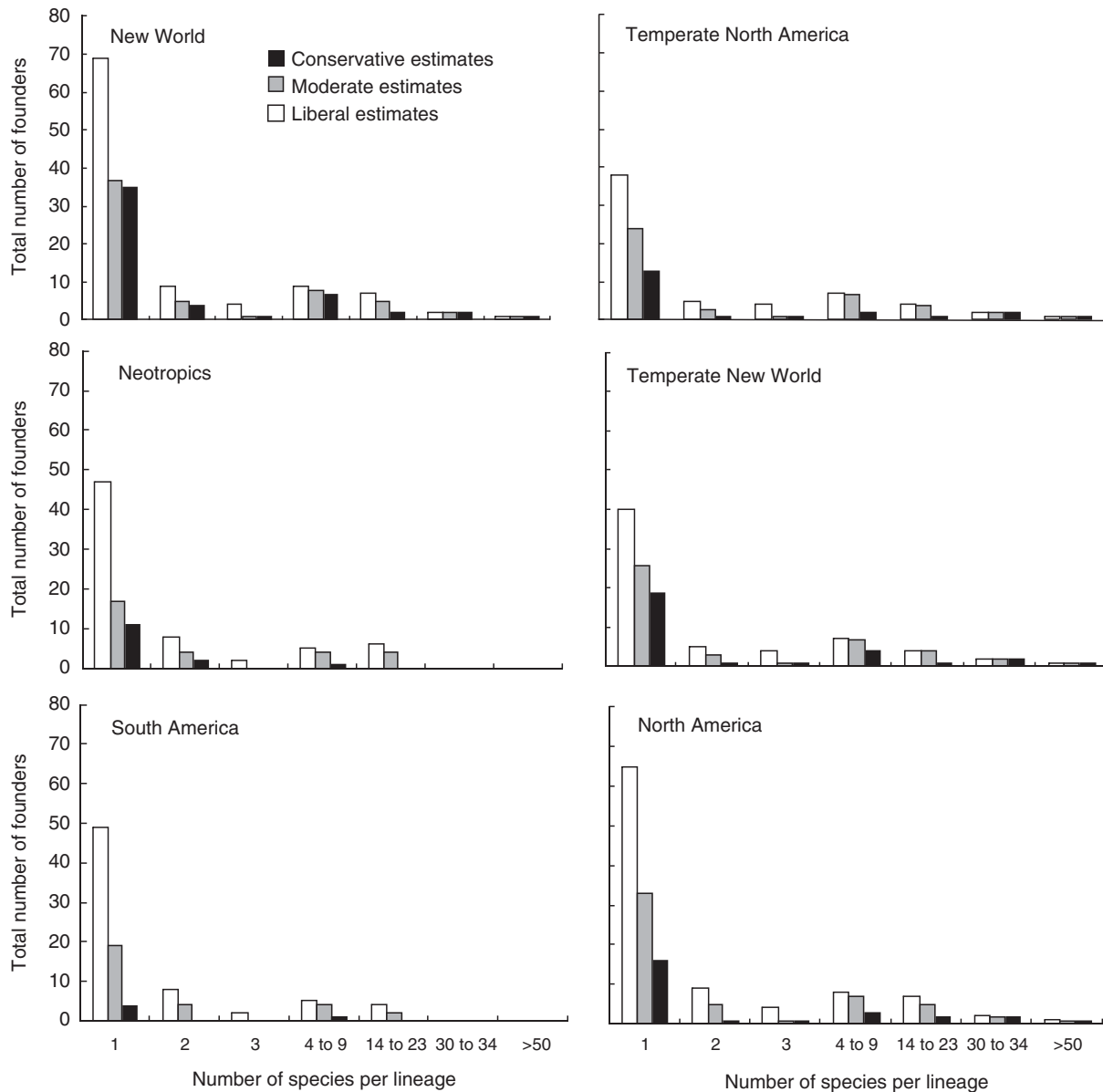
FIG. 8. Total number of Hawaiian angiosperm founders from particular source areas in the New World that gave rise to lineages with different levels of species richness. Conservative estimates = taxa confidently assigned to area based on molecular, morphological and/or distributional data; moderate estimates = conservative estimate + taxa confidently assigned to New World and either equivocally assigned to subregion or of potentially indirect dispersal to the Hawaiian Islands, via the South Pacific; liberal estimates = moderate estimate + taxa possibly originating in the New World based on available data but not verified as New World in origin, such as pantropical taxa. See Appendix 2 for taxon assignments to regions.

REASSESSMENT OF THE AMERICAN CONTRIBUTION TO THE HAWAIIAN ANGIOSPERM FLORA

Reanalysis of the overall American contribution to the Hawaiian seed-plant flora, under either conservative or liberal assignment of lineages to source areas, yields results that require a new perspective from that of Fosberg (1948, 1951), who suggested 50–51 natural New World introductions to the islands, of which only four or five, of dubious American ancestry, resulted in more than two species (of these, only *Isodendrion*, with four species, is now regarded as American in origin; see above). Although most reassessed angiosperm

founding lineages from the Americas are represented by only one endemic or indigenous Hawaiian species (Fig. 8), in keeping with such estimates for founding lineages from all Hawaiian source areas worldwide (W. Wagner and J. Price, unpubl. res.), founding lineages that gave rise to four or more endemic species include the majority of Hawaiian species of New World ancestry (Fig. 9). On a flora-wide scale, angiosperm clades of direct or indirect American origin represent at least six of 12 of the most species-rich lineages in the Hawaiian angiosperm flora (Table 1). In turn, those 12 lineages represent nearly half (approx. 47 %) of all native Hawaiian angiosperm species currently recognized.
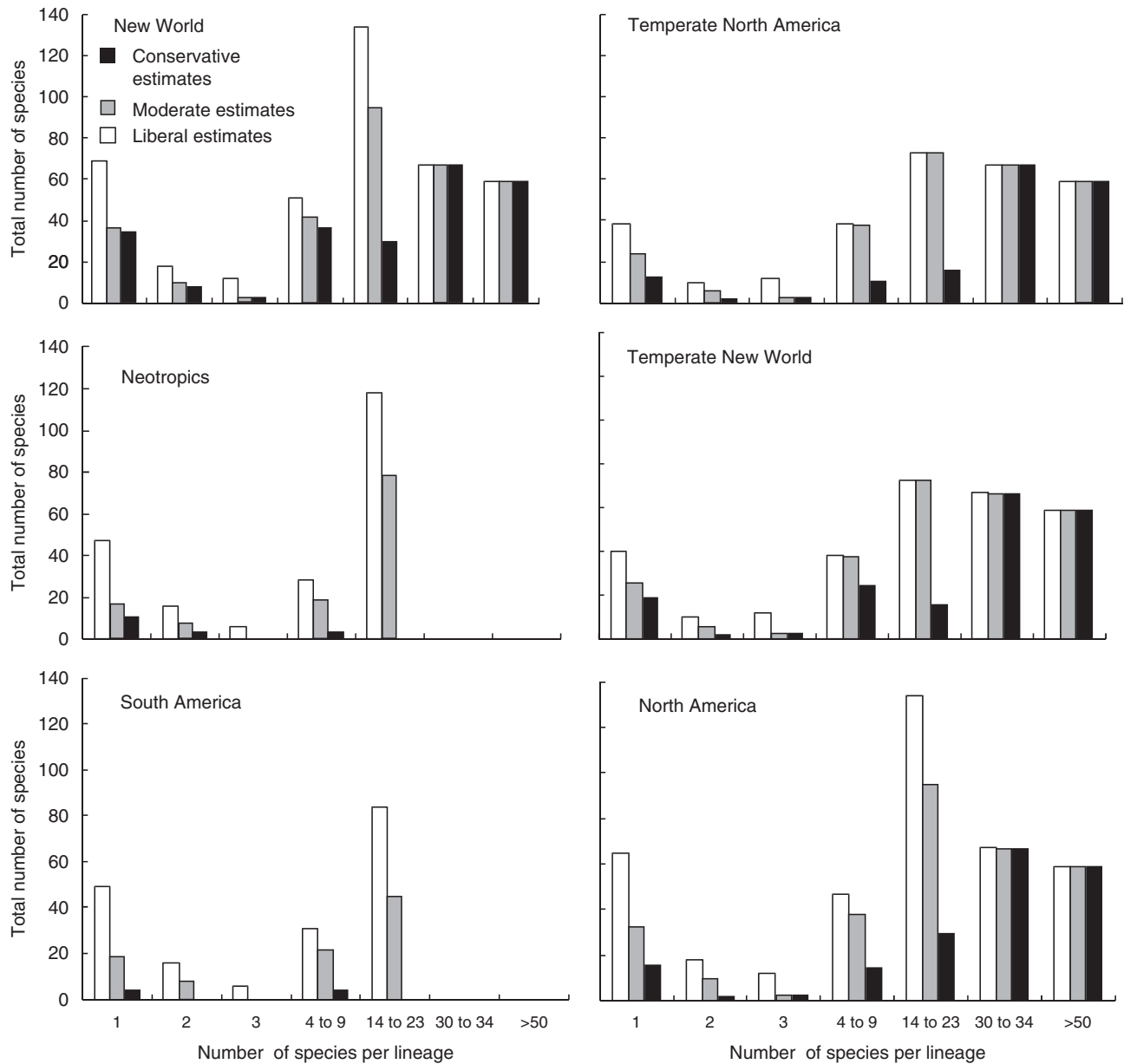
F$_{\text{IG}}$. 9. Total number of Hawaiian angiosperm species resulting from lineages of particular New World source areas with different levels of species richness: Conservative estimates, moderate estimates and liberal estimates, as indicated. See legend to Fig. 8 for method of estimation and Appendix 2 for taxon assignments to regions.

Founders from temperate North America, including desert regions, evidently spawned the majority of flowering-plant species of New World ancestry (Fig. 9), including the most species-rich clades, in contrast to earlier views that most or all New World plants in the Hawaiian flora descended from South American ancestors (e.g. Campbell, 1919; Skottsberg, 1925).

Diversification of species-rich lineages of North American origin in the Hawaiian Islands may in part reflect factors likely also to have been important to insular colonization by American plants: timing of introduction, dispersal biology, ecological opportunity, and ancestral hybridization and/or polyploidization. Where sufficient phylogenetic resolution is

available, highly diverse lineages of American origin mostly appear to date back to the oldest modern high-elevation island, Kaua'i (see above), and may represent relatively old lineages of Hawaiian angiosperms, except by comparison with the evidently much older and more diverse lobelioids (Givnish *et al.*, 2009) and the presumed relict *Hillebrandia* (Clement *et al.*, 2004). Most Hawaiian angiosperm lineages of evident American origin, and all such clades of four or more species, have seed or fruit characteristics that have been implicated in ancestral long-distance dispersal by birds or have close extra-Hawaiian relatives with such features (Carlquist, 1974; Sakai *et al.*, 1995; see Appendix 1). As discussed by Ballard and Sytsma (2000), opportunities for

TABLE 1. *Twelve most species-rich lineages of Hawaiian angiosperms*

Taxon or taxa constituting a lineage	Species number*	Source area	References
Brighamia, *Cyanea*, *Clermontia*, *Delissea*, Hawaiian *Lobelia*, *Trematolobelia* (Campanulaceae; Lobelioideae)	126	Africa, Polynesia, or southern Asia	Givnish *et al.* (2009)
Hawaiian *Cyrtandra* (Gesneriaceae)	59	South-east Asia directly or indirectly (via South Pacific islands)	Cronk *et al.* (2005), Clark *et al.* (2009)
Haplostachys, *Phyllostegia*, *Stenogyne* (Labiatae)	59	Temperate North America	Lindqvist and Albert (2002), Wood and Oppenhiemer (2008)
Melicope, *Platydesma* (Rutaceae)	52	Australia or New Guinea	Harbaugh *et al.* (2009)
Schiedea (Caryophyllaceae)	34	Temperate (boreal) North America	Wagner *et al.* (2005*b*), Harbaugh *et al.* (2010)
Argyroxiphium, *Dubautia*, *Wilkesia* (Compositae)	33	Temperate North America	Baldwin *et al.* (1991), Barrier *et al.* (1999), Baldwin and Carr (2005), Baldwin and Friar (2010)
Hawaiian *Pritchardia* (Palmae)	23	Warm temperate or tropical North America directly or indirectly (via South Pacific islands)	Bacon *et al.* (2009), Baker *et al.* (2009)
Hawaiian *Kadua* (Rubiaceae)	22	Australia, south-east Asia, or Africa directly or indirectly (via South Pacific islands)	Groeninckx *et al.* (2009), Lorence *et al.* (2010)
Hawaiian *Peperomia* (Piperaceae) endemic clade	22	Subtropical or tropical New World directly or indirectly (via South Pacific islands)	Bradley (2002), Wanke *et al.* (2006)
Lipochaeta/Melanthera (Compositae)[†]	20	Possibly of New World origin	Wagner and Robinson (2001), Chumley *et al.* (2002)
Hawaiian *Bidens* (Compositae)	19	Warm temperate or tropical North America directly or indirectly (via South Pacific)	Ganders *et al.* (2000)
Myrsine (Primulaceae)	19	Unknown (pantropical and subtropical)	see Wagner *et al.* (1999)

*From the *Flora of the Hawaiian Islands* (http://botany.si.edu/pacificislandbiodiversity/hawaiianflora/) plus cited references.

[†]Included here based on molecular evidence that the closest relatives of *Lipochaeta* ($2n = 26_{II}$), at least among sampled taxa, are Hawaiian members of *Melanthera* ($2n = 15_{II}$).

angiosperm dispersal by birds to the Hawaiian Islands appear to be ample for north temperate or boreal lineages, based on consideration of bird migration routes. As they noted, arriving in a suitable habitat in a tropical archipelago may be a more limiting factor in colonization and establishment than achieving oversea transport for bird-dispersed north temperate plants.

Once established, north temperate flowering plants (the vast majority evidently from North America; Appendix 1) would potentially have found conditions favourable for diversification in upper-elevation or dry, leeward habitats generally associated with new islands and generally less suitable for plants from tropical settings. Habitat diversity and lack of competition or interference from other plants on 'sky islands' of temperate or boreal climate in a tropical archipelago or in dry habitats in the rain shadow of major volcanoes could have allowed for ecological release, through both relaxed and redirected natural selection (see Schluter, 2000; Gillespie and Baldwin, 2009). Although inferring ancestral habitats for Hawaiian lineages often has been complicated by ecological shifts associated with adaptive radiation, climatic settings of closely related mainland clades and at least a subset of taxa in most diverse Hawaiian lineages of North American origin are consistent with initial insular colonization and diversification in situations resembling temperate or boreal habitats, e.g. in the silversword alliance, Hawaiian mints, *Geranium*, *Sanicula*, *Schiedea*, *Silene* and *Viola*. Presumed establishment

of Hawaiian *Euphorbia* subg. *Chamaesyce* in dry coastal settings (see above) is consistent with a warm-temperate, xeric (south-west North American) ancestry for that clade, as for Hawaiian *Argemone*, *Cuscuta* and *Nama*.

Price and Wagner (2004) found that dispersal by birds, especially via external adhesion, is significantly associated with species-richness in Hawaiian angiosperm clades; they proposed that intermediate levels of vagility associated with bird dispersal resulted in sufficient isolation for divergence and sufficient dispersal ability to reach new islands and habitats as opportunities for colonization arose. Hybridization and/or polyploidization shortly before dispersal to the Hawaiian Islands may also have aided establishment or evolutionary success of some American lineages, such as the silversword alliance, Hawaiian mints, *Cuscuta*, *Euphorbia* subg. *Chamaesyce* and *Viola*, by elevating genetic or genomic variation and potentially allowing for extensive recombination and expression of diverse phenotypes on which natural selection could act (Crawford and Stuessy, 1997; Carr, 1998; Barrier *et al.*, 1999; Ballard and Sytsma, 2000; Lindqvist and Albert, 2002; Stefanovic and Costea, 2008; Crawford *et al.*, 2009). Floral attributes also may have contributed to diversification of American lineages; two of the three most species-rich clades of Hawaiian angiosperms of New World origin – the mints and *Schiedea* – also are among the most diverse Hawaiian lineages in pollination biology and, in *Schiedea*, breeding system (Sakai *et al.*,

2006). The other major clade, the silversword alliance, is exceptional among Hawaiian angiosperms for sporophytic self-incompatibility in most tested taxa of the group (Carr *et al.*, 1986; S. Bainbridge and B. Baldwin, unpubl.), which may have been beneficial to adaptive evolution by facilitating retention and recombination of genetic variation within populations.

CONCLUSIONS

Species-rich lineages of temperate North American origin in the Hawaiian flora mostly appear to represent special cases of adaptive diversification in equatorial highlands, but on 'sky islands' in a tropical oceanic archipelago (high-elevation 'islands' within true islands) rather than on 'sky islands' in a tropical continental setting, where examples of adaptive radiation of ancestrally temperate plant groups are well documented (e.g. in the Andes or East African Highlands; see Carlquist, 1974; Hughes and Eastwood, 2006). Prominence of temperate North America and the New World in general as a source area for the Hawaiian angiosperm flora adds substantially to the wealth of evidence from recent phylogenetic studies for a significant impact of long-distance dispersal in shaping plant (and animal) distributions on a global scale. With the rise of molecular methods for estimating divergence times between lineages, intercontinental plant disjunctions often appear to be much too recent to be explained by simple vicariance (see Donoghue and Moore, 2003; Givnish and Renner, 2004; Sanmartín and Ronquist, 2004; de Queiroz, 2005; Moore *et al.*, 2006; Dick *et al.*, 2007; Keppel *et al.*, 2009), even within some clades presumed earlier to be of Gondwanan origin (Cook and Crisp, 2005; Won and Renner, 2006; Barker *et al.*, 2007). Vicariance explanations for origins of Hawaiian biota in particular (e.g. Van Steenis, 1963; Melville, 1981) have relied on speculative geological histories that involve time frames more ancient than can be reasonably hypothesized for the vast majority of endemic plant lineages, based on molecular phylogenetic evidence. Attempts to incorporate dispersal more explicitly within biogeographical models and methodology are important steps toward progress in understanding plant distributions on continents and islands (e.g. Funk and Wagner, 1995; Ree *et al.*, 2005; Sanmartín *et al.*, 2008), in addition to the pursuit of much more empirical work on plant relationships worldwide.

ACKNOWLEDGEMENTS

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APPENDIX 1

Native Hawaiian angiosperms of demonstrated or possible American origin

Hawaiian taxa constituting a lineage	Recognized species*	Endemic or indigenous	Family	Source area estimate for New World	Closest American relatives	References	Dispersal mode[†]
Abutilon incanum	1	i	Malvaceae	Warm temperate North America	*Abutilon incanum*	Bates (1999)	df
Abutilon eremitopetalum and *A. menziesii*	2	e	Malvaceae	Possibly New World (warm and tropical)	Unknown *Abutilon* species	Bates (1999)	df
Abutilon sandwicense	1	e	Malvaceae	Possibly New World (warm and tropical)	Unknown *Abutilon* species	Bates (1999)	df
Acaena exigua	1	e	Rosaceae	Temperate South America	*Acaena pumila*	Marticorena (2006)	bb
Argemone glauca	1	e	Papaveraceae	Warm temperate North America	Mostly SW North American *Argemone* taxa	Schwarzbach and Kadereit (1999)	bi
Argyroxiphium/ *Dubautia*/*Wilkesia* (endemic genera)	33	e	Compositae	Temperate North America	'Madia' lineage (e.g. *Anisocarpus*, *Carlquistia, Harmonia, Jensia, Madia*)	Baldwin *et al.* (1991), Baldwin (1996), Barrier *et al.* (1999), Baldwin and Carr (2005), Baldwin and Friar (2010)	bv/bb
Bacopa monnieri	1	i	Plantaginaceae	Possibly New World (pantropical, and warm temperate North America)	*Bacopa monnieri*	Wagner *et al.* (1990)	bm
Bidens	19	e	Compositae	Directly or indirectly temperate or tropical North America	New World relatives in sect. *Psilocarpaea*: *B. alba, B. pilosa* (SE Pacific *Bidens* taxa are sister to Hawaiian taxa)	Ganders *et al.* (2000)	bb
Bobea (endemic genus)	4	e	Rubiaceae	Tropical South America	*Guettarda crispiflora, G. hirsuta*	Achille *et al.* (2006)	bi
Bonamia menziesii	1	e	Convolvulaceae	Neotropics	NW South/Central American *Bonamia* species	Austin (1999)	bv/dr
Bulboschoenus maritimus subsp. *paludosus*	1	i	Cyperaceae	Temperate North America	*Bulboschoenus maritimus* subsp. *paludosus*	Koyama (1999)	bm
Caesalpinia bonduc	1	i	Leguminosae	Possibly New World (pantropical, and warm temperate North America)	*Caesalpinia boduc*	Geesink *et al.* (1999)	df
Calamagrostis expansa	1	e	Gramineae	Possibly temperate or montane tropical America	Unknown *Calamagrostis* species	O'Connor (1999)	bb
Carex alligata and *C. kauaiensis*	2	e	Cyperaceae	Temperate North America	*Carex obnupta*	Dragon and Barrington (2009)	bm/bi
Carex echinata	1	i	Cyperaceae	Temperate Northern Hemisphere	*Carex echinata*	Koyama (1999), Reznicek (2002)	bm/bi
Carex nealae	1	e	Cyperaceae	Temperate North America	*Carex emoryi*	Dragon and Barrington (2009)	bm/bi
Carex subfusca	1	i	Cyperaceae	Temperate North America	*Carex subfusca*	Koyama (1999)	bm/bi
Cassytha filiformis	1	i	Lauraceae	Possibly New World (pantropical, including subtropical N America)	*Cassytha filiformis*	van der Werff (1999)	df
Chenopodium oahuense	1	e	Chenopodiaceae	Possibly New World	Unknown *Chenopodium* species	Wagner *et al.* (1999)	bm
Cladium jamaicense	1	i	Cyperaceae	Possibly New World (warm or tropical)	*Cladium jamaicense*	Koyama (1999)	bi
Colubrina oppositifolia	1	e	Rhamnaceae	Neotropics	*Colubrina glandulosa*	Johnston (1971)	df
Cressa truxillensis	1	i	Convolvulaceae	Temperate or tropical America	North/South American populations of *Cressa truxillensis*	Austin (1999)	df

Cuscuta sandwichiana	1	e	Convolvulaceae	Warm temperate North America	'B' and 'H' clades of *Cuscuta*	Stefanovic and Costea (2008)	bi
Cyperus laevigatus	1	i	Cyperaceae	Possibly New World (warm or tropical)	*Cyperus laevigatus*	Koyama (1999)	bi/bm
Cyperus trachysanthos	1	e	Cyperaceae	Temperate or tropical America	*Cyperus elegans* and *C. oxylepis*	Koyama (1999)	bi/bm
Daucus pusillus	1	i	Umbelliferae	Temperate America	North/South American populations of *Daucus pusillus*	Constance and Affolter (1999)	bb
Deschampsia nubigena	1	e	Gramineae	Temperate North America	*Deschampsia cespitosa*	Chiapella (2007)	bb
Dichanthelium	4	e	Gramineae	Temperate or tropical America	*Dichanthelium acuminatum, D. clandestinum, D. sabulorum*	Aliscioni *et al.* (2003)	bm
Dodonaea viscosa	1	i	Sapindaceae	Possibly New World (pantropical, including warm temperate North America)	*Dodonaea viscosa*	Wagner *et al.* (1999)	df/dr
Drosera anglica	1	i	Droseraceae	Temperate Northern Hemisphere	*Drosera anglica*	Wagner *et al.* (1999), Rivadavia *et al.* (2003)	bm
Eleocharis erythropoda	1	i	Cyperaceae	Temperate North America	*Eleocharis erythropoda*	Koyama (1999)	bm
Eleocharis obtusa	1	i	Cyperaceae	Temperate North America	*Eleocharis obtusa*	Koyama (1999)	bm
Eragrostis	9	e	Gramineae	Possibly New World (warm or tropical)	Unknown *Eragrostis* species	O'Connor (1999)	bi
Erythrina sandwicensis	1	e	Leguminosae	Possibly New World (warm or tropical)	Unknown *Erythrina* species	Neill (1999)	dr/bi
Euphorbia subg. *Chamaesyce*	16	e	Euphorbiaceae	Warm temperate North America	*Euphorbia cinerascens*, other Chihuahuan Desert annuals (four species)	Yang *et al.* (2009)	bi
Fimbristylis cymosa	1	i	Cyperaceae	Possibly New World (warm or tropical)	*Fimbristylis cymosa*	Koyama (1999)	bm/bi
Fimbristylis dichotoma	1	i	Cyperaceae	Possibly New World (warm or tropical)	*Fimbristylis dichotoma*	Koyama (1999)	bm/bi
Fimbristylis hawaiiensis	1	e	Cyperaceae	Possibly New World (warm or tropical)	Possibly *Fimbristylis ferruginea*	Koyama (1999)	bm/bi
Fragaria chiloensis	1	i	Rosaceae	Temperate America	W North/S South American populations of *Fragaria chiloensis*	Wagner *et al.* (1999)	bi
Geranium	7	e	Geraniaceae	Temperate or montane tropical America	Species of *Geranium* subg. *Geranium*	Pax *et al.* (1997)	bb
Gossypium tomentosum	1	e	Malvaceae	Tropical North America	*Gossypium hirsutum*	DeJoode and Wendel (1992), Small *et al.* (1998)	dr
Gunnera	2	e	Gunneraceae	Neotropics	Central/South American *Gunnera* species; all plus Hawaiian taxa sister to *G. mexicana*	Wanntorp and Wanntorp (2003)	bi
Haplostachys/ Phyllostegia/ Stenogyne	59	e	Labiatae	Temperate North America	*Stachys*	Lindqvist & Albert (2002), Wood and Oppenheimer (2008)	bi
Heliotropium curassavicum	1	i	Boraginaceae	Possibly New World	*Heliotropium curassavicum*	Wagner *et al.* (1999)	df
Hesperocnide sandwicensis	1	e	Urticaceae	Temperate North America	*Hesperocnide tenella*	Wagner *et al.* (1999)	bb
Hibiscus furcellatus	1	i	Malvaceae	Neotropics	North/South American populations of *Hibiscus furcellatus*	Bates (1999)	dr
Ilex anomala	1	i	Aquifoliaceae	Directly or indirectly warm temperate or tropical America	All South American/most North American *Ilex* species sampled are sister to Hawaiian species (*I. anomala* also in S Pacific islands)	Cuénoud *et al.* (2000)	bi

Hawaiian taxa constituting a lineage	Recognized species*	Endemic or indigenous	Family	Source area estimate for New World	Closest American relatives	References	Dispersal mode[†]
Ipomoea imperati	1	i	Convolvulaceae	Possibly New World (pantropical, and warm temperate North America	*Ipomoea imperati*	Austin (1999)	df
Ipomoea pes-caprae subsp. *brasiliensis*	1	i	Convolvulaceae	Possibly New World (pantropical, and warm temperate North America)	*Ipomoea pes-caprae* subsp. *brasiliensis*	Austin (1999)	df
Ipomoea tuboides	1	e	Convolvulaceae	Possibly New World (warm or tropical)	Unknown *Ipomoea* species	Austin (1999)	df
Isodendrion (endemic genus)	4	e	Violaceae	Temperate or tropical North America	*Pombalia* (*Hybanthus* sensu lato)	Ballard *et al.* (2009), H. E. Ballard (pers. comm.)	bi/bm
Jacquemontia sandwicensis	1	e	Convolvulaceae	Tropical North America	*Jacquemontia obcordata*	Namoff *et al.* (2009)	dr
Kanaloa kahoolawensis	1	e	Leguminosae	Temperate or tropical America	Nested among mostly New World Mimosoideae genera (sister to *Desmanthus* and *Schleinitzia*)	Lorence and Wood (1994), Catalano *et al.* (2008)	
Lepechinia hastata	1	i	Labiatae	Tropical North America	North American (Baja California Sur, Mexico) populations of *Lepechinia hastata*	Wagner *et al.* (1999)	bv
Lepidium	5	e	Cruciferae	Directly or indirectly temperate North America	*Lepidium austrinum*, *L. lasiocarpum*, *L. oblongum*, *L. virginicum* (Hawaiian *L. bidentatum* also in S Pacific islands)	Mummenhoff *et al.* (2001)	bv
Lipochaeta (endemic genus)/ *Melanthera*	20	e	Compositae	Possibly New World (warm or tropical)	*Melanthera* species	Wagner and Robinson (2001), Chumley *et al.* (2002)	bb
Luzula hawaiiensis	1	e	Juncaceae	Possibly temperate or montane tropical America	Species of *Luzula* sect. *Luzula*	Roalson (2005)	bm
Lycium sandwicense	1	i	Solanaceae	Directly or indirectly warm temperate North American	*Lycium carolinianum* (*L. sandwicense* also in S Pacific islands)	Miller (2002)	dr
Mucuna sloanei var. *persericea* and *M. sloanei* var. *sloanei*	1	e/i	Leguminosae	Tropical South America	South American populations of *Mucuna sloanei* var. *sloanei*	Wilmot-Dear (1990)	df
Myrsine	19	e	Myrsinaceae	Possibly New World (pantropical)	Unknown *Myrsine* species	Wagner *et al.* (1999)	bi
Nama sandwicensis	1	e	Boraginaceae	Warm temperate North America	*Nama hispidum*, *N. stevensii*, *N. turneri*, *N. undulatum*	Wagner *et al.* (1999)	bb
Panicum faurieri and *P. nephelophilum*	2	e	Gramineae	Possibly New World (warm or tropical)	Species of *Panicum* subg. *Panicum*	Aliscioni *et al.* (2003)	bi/bb
Peperomia (endemic spp. except *P. remyi*)	22	e	Piperaceae	Directly or indirectly New World (warm or tropical)	Species of *Peperomia* subg. *Sphaerocarpidium* (sister to other Pacific island taxa)	Wagner *et al.* (1999), Bradley (2002), Wanke *et al.* (2006)	bv
Peperomia tetraphylla	1	i	Piperaceae	Possibly New World (pantropical)	*Peperomia tetraphylla*	Wagner *et al.* (1999), Bradley (2002), Wanke *et al.* (2006)	bv
Perrottetia sandwicensis	1	e	Dipentodontaceae	Possibly New World (warm or tropical)	Unknown *Perrottetia* species	Wagner *et al.* (1999)	bi
Phytolacca sandwicensis	1	e	Phytolaccaceae	Possibly New World (warm or tropical)	Unknown *Phytolacca* species	Wagner *et al.* (1999)	bi
Pilea peploides	1	i	Urticaceae	Tropical South America	*Pilea peploides*	Wagner *et al.* (1999)	bm
Plantago	3	e	Plantaginaceae	Temperate North America	*Plantago tweedyi*	Dunbar-Co *et al.* (2008), R. Hoggard (pers. comm.)	bv

Platanthera holochila	1	e	Orchidaceae	Temperate North America	Species of *Platanthera* sect. *Limnorchis*	R. Lauri (pers. comm.), see Bateman *et al.* (2009)	a
Poa	3	e	Gramineae	Possibly temperate or montane tropical America	Unknown *Poa* species	O'Connor (1999)	bb
Portulaca lutea and *P. molokiniensis*	2	e/i	Portulacaceae	Directly or indirectly from warm temperate or tropical America	New World *Portulaca* species (*Portulaca lutea* also in SE Pacific islands)	Ocampo and Columbus (2009*a*, *b*)	df
Portulaca sclerocarpa and *P. villosa*	2	e	Portulacaceae	Temperate or tropical America	North/South American *Portulaca* species	Ocampo and Columbus (2009*a*, *b*)	df
Potamogeton foliosus	1	i	Potamogetonaceae	Temperate or tropical North America	*Potamogeton foliosus*	Wagner *et al.* (1999)	bi
Pritchardia	23	e	Palmae	Directly or indirectly warm temperate or tropical America	New World *Copernicia* (*Pritchardia* also in S Pacific islands)	Baker *et al.* (2009)	bi/dr
Pycreus polystachyos	1	i	Cyperaceae	Possibly New World (warm or tropical)	*Pycreus polystachyos*	Koyama (1999)	bi
Ranunculus	2	e	Ranunculaceae	Possibly temperate or montane tropical America	Unknown *Ranunculus* species	Duncan (1999)	bm
Rauvolfia sandwicensis	1	e	Apocynaceae	Possibly New World (warm or tropical)	Unknown *Rauvolfia* species	Wagner *et al.* (1999)	bi
Rhynchospora rugosa subsp. *lavarum*	1	i	Cyperaceae	Neotropics	North/South American populations of *Rhynchospora rugosa* subsp. *lavarum*	Koyama (1999)	bi/bb
Rubus hawaiiensis	1	e	Rosaceae	Temperate North America	*Rubus spectabilis*	Howarth *et al.* (1997)	bi
Rubus macraei	1	e	Rosaceae	Temperate North America	*Rubus ursinus*	Morden *et al.* (2003)	bi
Rumex	3	e	Polygonaceae	Possibly New World	Unknown *Rumex* species	Wagner *et al.* (1999)	dr/bi
Ruppia maritima	1	i	Ruppiaceae	Possibly New World (pantropical, and temperate North America)	*Ruppia maritima*	Wagner *et al.* (1999)	bm
Sanicula	4	e	Umbelliferae	Temperate North America	*Sanicula arctopoides, S. arguta, S. laciniata*	Vargas *et al.* (1998)	bb
Sapindus saponaria	1	i	Sapindaceae	Possibly New World (warm or tropical)	*Sapindus saponaria*	Wagner *et al.* (1999)	bi
Schiedea (including *Alsinidendron*)	34	e	Caryophyllaceae	Temperate North America	*Honckenya, Wilhelmsia*	Wagner *et al.* (2005*b*)	bm
Schoenoplectus lacustris	1	i	Cyperaceae	Possibly New World (warm or tropical)	*Schoenoplectus lacustris*	Wagner *et al.* (1999)	bm/bi
Scleria testacea	1	i	Cyperaceae	Neotropics	North/South American populations of *Scleria testacea*	Koyama (1999)	bm
Sesuvium portulacastrum	1	i	Aizoaceae	Possibly New World (pantropical, and warm temperate North America)	*Sesuvium portulacastrum*	Wagner *et al.* (1999)	df
Sicyos	14	e	Cucurbitaceae	Temperate or tropical North America	Mostly Mexican *Sicyos* species	Sebastian *et al.* (2009), P. Sebastian and S. S. Renner (pers. comm.)	bb
Silene	7	e	Caryophyllaceae	Temperate America	*Silene antirrhina*	Eggens *et al.* (2007)	bi/bm
Sisyrinchium acre	1	e	Iridaceae	Temperate or tropical America	Possibly *S. tinctorium* (Central America)	Goldblatt and Henrich (1999)	bm
Spermolepis hawaiiensis	1	e	Umbelliferae	Temperate America	North/S South American *Spermolepis* species	Constance and Affolter (1999)	bb
Sporobolus virginicus	1	i	Gramineae	Possibly New World (pantropical, and warm temperate North America)	*Sporobolus virginicus*	O'Connor (1999)	bv

Continued

APPENDIX 1 *Continued*

Hawaiian taxa constituting a lineage	Recognized species*	Endemic or indigenous	Family	Source area estimate for New World	Closest American relatives	References	Dispersal mode[†]
Touchardia latifolia and *Urera glabra*	2	e	Urticaceae	Neotropics	Unknown *Urera* species	Wagner *et al.* (1999)	bi
Trisetum	2	e	Gramineae	Possibly temperate or montane tropical America	Unknown *Trisetum* species	O'Connor (1999)	bb
Uncinia brevicaulis	1	i	Cyperaceae	Temperate South America	S South American populations (also in Trintan de Cunha) of *Uncinia brevicaulis*	Koyama (1999)	bb
Urera kaalae	1	e	Urticaceae	Neotropics	*Urera caracasana* or relatives	Wagner *et al.* (1999)	bi
Vaccinium	3	e	Ericaceae	Temperate Northern Hemisphere	Species of *Vaccinium* sect. *Myrtillus*	Powell and Kron (2002)	bi
Vicia menziesii	1	e	Leguminosae	Temperate America	North/South American *Vicia nigricans*	Lassetter and Gunn (1979)	bi
Vigna marina	1	i	Leguminosae	Possibly New World (pantropical, including tropical West Indies, Panama)	*Vigna marina*	Geesink *et al.* (1999)	df
Viola	7	e	Violaceae	Temperate North America	*Viola langsdorffii*	Ballard and Sytsma (2000)	bi/bm
Waltheria indica	1	i	Sterculiaceae	Possibly New World (warm or tropical)	*Waltheria indica*	Wagner *et al.* (1999)	dr

*From the *Flora of the Hawaiian Islands* (http://botany.si.edu/pacificislandbiodiversity/hawaiianflora/) plus cited references.

[†]Putative mode of dispersal from the New World to the Hawaiian Islands from Sakai *et al.* (1995); a = air, bb = bird external (barbs), bi = bird internal, bm = bird external (mud), bv = bird external (viscid), df = oceanic drift–frequent, dr = oceanic drift–rare.

Assignments of native Hawaiian angiosperms to potential New World source areas under conservative (CE), moderate (ME) and liberal (LE) estimates (see Fig. 8 for methods of estimation). $+$ = assignment; $-$ = non-assignment. See Appendix 1 for details of lineages.

Hawaiian taxa constituting a lineage	New World			Neotropics			North America			Temperate North America			Temperate New World			South America		
	LE	ME	CE	LE	ME	CE	LE	ME	CE	LE	ME	CE	LE	ME	CE	LE	ME	CE
Abutilon incanum	+	+	+	−	−	−	+	+	+	+	+	+	+	+	+	−	−	−
Abutilon eremitopetalum and *A. menziesii*	+	−	−	+	−	−	+	−	−	−	−	−	−	−	−	+	−	−
Abutilon sandwicense	+	−	−	+	−	−	+	−	−	−	−	−	−	−	−	+	−	−
Acaena exigua	+	+	+	−	−	−	−	−	−	−	−	−	+	+	+	+	+	+
Argemone glauca	+	+	+	−	−	−	+	+	+	+	+	+	+	+	+	−	−	−
Argyroxiphium/Dubautia/ Wilkesia (endemic genera)	+	+	+	−	−	−	+	+	+	+	+	+	+	+	+	−	−	−
Bacopa monnieri	+	−	−	+	−	−	+	−	−	+	−	−	+	−	−	+	−	−
Bidens	+	+	−	+	+	−	+	+	−	+	+	−	+	+	−	−	−	−
Bobea (endemic genus)	+	+	+	+	+	+	−	−	−	−	−	−	−	−	−	+	+	+
Bonamia menziesii	+	+	+	+	+	+	+	+	−	−	−	−	−	−	−	+	+	−
Bulboschoenus maritimus subsp. *paludosus*	+	+	+	−	−	−	+	+	+	+	+	+	+	+	+	−	−	−
Caesalpinia bonduc	+	−	−	+	−	−	+	−	−	−	−	−	+	−	−	+	−	−
Calamagrostis expansa	+	−	−	+	−	−	+	−	−	−	−	−	+	−	−	+	−	−
Carex alligata and *C. kauaiensis*	+	+	+	−	−	−	+	+	+	+	+	+	+	+	+	−	−	−
Carex echinata	+	−	−	−	−	−	+	−	−	−	−	−	+	−	−	−	−	−
Carex nealae	+	+	+	−	−	−	+	+	+	+	+	+	+	+	+	−	−	−
Carex subfusca	+	+	+	−	−	−	+	+	+	+	+	+	+	+	+	−	−	−
Cassytha filiformis	+	−	−	+	−	−	+	−	−	−	−	−	−	−	−	+	−	−
Chenopodium oahuense	+	−	−	−	−	−	+	−	−	+	−	−	+	−	−	+	−	−
Cladium jamaicense	+	−	−	+	−	−	+	−	−	−	−	−	−	−	−	+	−	−
Colubrina oppositifolia	+	+	+	+	+	+	+	+	−	−	−	−	−	−	−	+	+	−
Cressa truxillensis	+	+	+	+	+	−	+	+	−	+	+	−	+	+	−	+	+	−
Cuscuta sandwichiana	+	+	+	−	−	−	+	+	+	+	+	+	+	+	+	−	−	−
Cyperus laevigatus	+	−	−	+	−	−	+	−	−	−	−	−	−	−	−	+	−	−
Cyperus trachysanthos	+	+	+	+	+	−	+	+	−	+	−	−	+	+	−	+	+	−
Daucus pusillus	+	+	+	+	+	−	+	+	−	+	+	−	+	+	+	+	+	−
Deschampsia nubigena	+	+	+	−	−	−	+	+	+	+	+	+	+	+	+	−	−	−
Dichanthelium	+	+	+	+	+	−	+	+	−	−	−	−	+	+	−	+	+	−
Dodonaea viscosa	+	−	−	+	−	−	+	−	−	−	−	−	+	−	−	+	−	−
Drosera anglica	+	−	−	−	−	−	+	−	−	+	−	−	+	−	−	−	−	−
Eleocharis erythropoda	+	+	+	−	−	−	+	+	+	+	+	+	+	+	+	−	−	−
Eleocharis obtusa	+	+	+	−	−	−	+	+	+	+	+	+	+	+	+	−	−	−
Eragrostis	+	−	−	+	−	−	+	−	−	−	−	−	−	−	−	+	−	−
Erythrina sandwicensis	+	−	−	+	−	−	+	−	−	−	−	−	−	−	−	+	−	−
Euphorbia subg. *Chamaesyce*	+	+	+	+	+	−	+	+	+	+	−	−	+	+	+	−	−	−
Fimbristylis cymosa	+	−	−	+	−	−	+	−	−	−	−	−	−	−	−	+	−	−
Fimbristylis dichotoma	+	−	−	+	−	−	+	−	−	−	−	−	−	−	−	+	−	−
Fimbristylis hawaiiensis	+	−	−	+	−	−	+	−	−	−	−	−	−	−	−	+	−	−
Fragaria chiloensis	+	+	+	−	−	−	+	+	−	+	+	−	+	+	+	+	+	−
Geranium	+	+	+	+	+	−	+	+	−	+	+	−	+	+	+	+	+	−
Gossypium tomentosum	+	+	+	+	+	+	+	+	+	−	−	−	−	−	−	−	−	−
Gunnera	+	+	+	+	+	+	+	−	−	−	−	−	−	−	−	+	+	+
Haplostachys/Phyllostegia/ Stenogyne	+	+	+	−	−	−	+	+	+	+	+	+	+	+	+	−	−	−
Heliotropium curassavicum	+	−	−	+	−	−	+	−	−	+	−	−	+	−	−	+	−	−
Hesperocnide sandwicensis	+	+	+	−	−	−	+	+	+	+	+	+	+	+	+	−	−	−

Continued

APPENDIX 2 *Continued*

Hawaiian taxa constituting a lineage	New World			Neotropics			North America			Temperate North America			Temperate New World			South America		
	LE	ME	CE	LE	ME	CE	LE	ME	CE	LE	ME	CE	LE	ME	CE	LE	ME	CE
Hibiscus furcellatus	+	+	+	+	+	+	+	+	−	−	−	−	−	−	−	+	+	−
Ilex anomala	+	+	−	+	+	−	+	+	−	+	+	−	+	+	−	+	+	−
Ipomoea imperati	+	−	−	+	−	−	+	−	−	+	−	−	+	−	−	+	−	−
Ipomoea pes−caprae subsp. *brasiliensis*	+	−	−	+	−	−	+	−	−	+	−	−	+	−	−	+	−	−
Ipomoea tuboides	+	−	−	+	−	−	+	−	−	−	−	−	−	−	−	+	−	−
Isodendrion (endemic genus)	+	+	+	+	+	−	+	+	+	+	+	−	+	+	−	−	−	−
Jacquemontia sandwicensis	+	+	+	+	+	+	+	+	+	−	−	−	−	−	−	−	−	−
Kanaloa kahoolawensis	+	+	+	+	+	−	+	+	−	+	+	−	+	+	−	+	+	−
Lepechinia hastata	+	+	+	+	+	+	+	+	+	−	−	−	−	−	−	+	+	−
Lepidium	+	+	−	−	−	−	+	+	−	+	+	−	+	+	−	−	−	−
Lipochaeta (endemic genus)/*Melanthera*	+	−	−	+	−	−	+	−	−	−	−	−	−	−	−	+	−	−
Luzula hawaiiensis	+	−	−	+	−	−	+	−	−	−	−	−	+	−	−	+	−	−
Lycium sandwicense	+	+	−	−	−	−	+	+	−	+	+	−	+	+	−	−	−	−
Mucuna sloanei var. *persericea* and *M. sloanei* var. *sloanei*	+	+	+	+	+	+	−	−	−	−	−	−	−	−	−	+	+	+
Myrsine	+	−	−	+	−	−	+	−	−	−	−	−	−	−	−	+	−	−
Nama sandwicensis	+	+	+	−	−	−	+	+	+	+	+	+	+	+	+	−	−	−
Panicum faurieri and *P. nephelophilum*	+	−	−	+	−	−	+	−	−	−	−	−	−	−	−	+	−	−
Peperomia (endemic spp. except *P. remyi*)	+	−	−	+	+	−	+	+	−	−	−	−	−	−	−	+	+	−
Peperomia tetraphylla	+	−	−	+	−	−	+	−	−	−	−	−	−	−	−	+	−	−
Perrottetia sandwicensis	+	−	−	+	−	−	+	−	−	−	−	−	−	−	−	+	−	−
Phytolacca sandwicensis	+	−	−	+	−	−	+	−	−	−	−	−	−	−	−	+	−	−
Pilea peploides	+	+	+	+	+	+	+	+	−	−	−	−	−	−	−	+	+	+
Plantago	+	+	+	−	−	−	+	+	+	+	+	+	+	+	+	−	−	−
Platanthera holochila	+	+	+	−	−	−	+	+	+	+	+	+	+	+	+	−	−	−
Poa	+	−	−	+	−	−	+	−	−	−	−	−	+	−	−	+	−	−
Portulaca lutea and *P. molokiniensis*	+	+	−	+	+	−	+	+	−	+	+	−	+	+	−	+	+	−
Portulaca sclerocarpa and *P. villosa*	+	+	+	+	+	−	+	+	−	+	+	−	+	+	−	+	+	−
Potamogeton foliosus	+	+	+	+	+	−	+	+	−	+	+	−	+	+	−	+	+	−
Pritchardia	+	+	−	+	+	−	+	+	−	+	+	−	+	+	−	+	+	−
Pycreus polystachyos	+	−	−	+	−	−	+	−	−	−	−	−	−	−	−	+	−	−
Ranunculus	+	−	−	−	−	−	+	−	−	+	−	−	+	−	−	+	−	−
Rauvolfia sandwicensis	+	−	−	+	−	−	+	−	−	−	−	−	−	−	−	+	−	−
Rhynchospora rugosa subsp. *lavarum*	+	+	+	+	+	+	+	+	−	−	−	−	−	−	−	+	+	−
Rubus hawaiiensis	+	+	+	−	−	−	+	+	+	+	+	+	+	+	+	−	−	−
Rubus macraei	+	+	+	−	−	−	+	+	+	+	+	+	+	+	+	−	−	−
Rumex	+	−	−	+	−	−	+	−	−	−	−	−	+	−	−	+	−	−
Ruppia maritima	+	−	−	+	−	−	+	−	−	−	−	−	−	−	−	+	−	−
Sanicula	+	+	+	−	−	−	+	+	+	+	+	+	+	+	+	−	−	−
Sapindus saponaria	+	−	−	+	−	−	+	−	−	−	−	−	+	−	−	+	−	−
Schiedea (including *Alsinidendron*)	+	+	+	−	−	−	+	+	+	+	+	+	+	+	+	−	−	−
Schoenoplectus lacustris	+	−	−	+	−	−	+	−	−	−	−	−	−	−	−	+	−	−
Scleria testacea	+	+	+	+	+	+	+	+	−	−	−	−	−	−	−	+	+	−
Sesuvium portulacastrum	+	−	−	+	−	−	+	−	−	+	−	−	+	−	−	+	−	−
Sicyos	+	+	+	+	+	−	+	+	+	−	−	−	+	+	−	+	−	−
Silene	+	+	+	−	−	−	+	+	−	+	+	+	+	+	+	+	+	+
Sisyrinchium acre	+	+	+	+	+	−	+	+	−	−	−	−	+	+	−	+	+	−
Spermolepis hawaiiensis	+	+	+	−	−	−	+	+	−	+	+	+	+	+	+	+	+	−
Sporobolus virginicus	+	−	−	+	−	−	+	−	−	+	−	−	+	−	−	+	−	−
Touchardia latifolia and *Urera glabra*	+	+	+	+	+	+	+	+	−	−	−	−	−	−	−	+	+	−

Trisetum	+	−	−	+	−	−	+	−	−	+	−	−	+	−	−	+	−	−
Uncinia brevicaulis	+	+	+	−	−	−	−	−	−	−	−	−	+	+	+	+	+	+
Urera kaalae	+	+	+	+	+	+	+	+	−	−	−	−	−	−	−	+	+	−
Vaccinium	+	−	−	−	−	−	+	−	−	+	−	−	+	−	−	−	−	−
Vicia menziesii	+	+	+	−	−	−	+	+	−	+	+	−	+	+	+	+	+	−
Vigna marina	+	−	−	+	−	−	+	−	−	−	−	−	−	−	−	+	−	−
Viola	+	+	+	−	−	−	+	+	+	+	+	+	+	+	+	−	−	−
Waltheria indica	+	−	−	+	−	−	+	−	−	−	−	−	−	−	−	+	−	−