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Adaptive radiation of island plants: evidence from *Aeonium* (Crassulaceae) of the Canary Islands

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Abstract

The presence of diverse and species-rich plant lineages on oceanic islands is most often associated with adaptive radiation. Here we discuss the possible adaptive significance of some of the most prominent traits in island plants, including woodiness, monocarpy and sexual dimorphisms. Indirect evidence that such traits have been acquired through convergent evolution on islands comes from molecular phylogenies; however, direct evidence of their selective value rarely is obtained. The importance of hybridization in the evolution of island plants is also considered as part of a more general discussion of the mechanisms governing radiations on islands. Most examples are from the Hawaiian and Canarian floras, and in particular from studies on the morphological, ecological and molecular diversification of the genus *Aeonium*, the largest plant radiation of the Canarian Islands.

Key words: Hawaiian Islands, heterophylly, hybridization, monocarpy, pollen-ovule ratios, sexual dimorphisms

Introduction

Why are some plant lineages more species-rich than others? The question arises repeatedly when studying the floras of isolated oceanic islands. Within these restricted areas, numerous plant genera contain a considerable number of endemic species. Such island radiations are of particular interest because, unlike many continental plant groups, they have radiated within a very restricted geographic area and their relatively recent, rapid radiation can be demonstrated through the geological history of the islands.

A radiation is defined as a process leading to character diversification and/or ecological diversification and eventually may lead to lineage diversification (Sanderson 1998). In this paper the focus will be on radiations leading to lineage diversification. We restrict the concept of radiation to cases in which diversification occurs at an accelerated rate, as was also done by Sanderson (1998) and Bateman (1999), though some authors avoid this more restricted view of radiation (e.g. Barrett & Graham 1997; Givinsh 1997). An adaptive radiation is defined as the diversification of a lineage into species that exploit a variety of different resource types and that differ in the morphological or physiological traits used to exploit those resources (Schluter 1996, but see Givnish 1997 for other definitions). It is generally assumed that most cases of island radiation, including the examples presented here, are adaptive in this sense.

Whether plant radiations are a more frequent phenomenon on islands and island-like habitats than on continents still needs to be investigated. It is possible, though, to list a number of deterministic and stochastic forces

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that generally promote speciation and that may be particularly prominent on oceanic islands. Determining the relative importance of these forces is a difficult task, especially since they may vary between lineages and islands. The rich diversity of habitats on many oceanic islands, created primarily by geological and climatic conditions, offers a wide array of ecological opportunities to colonizers. In addition, due to the remoteness of some islands, the number of organisms capable of colonizing from the nearest continent is limited, and competition and predation from well-established and specialized plants and animals may be low (McArthur & Wilson 1967). Under these circumstances, selection may favour characters which offer the opportunity to exploit new resources and which eliminate competition with close relatives. Sometimes the acquisition of a particular trait or traits predisposes a taxon to rapid speciation, thus giving access to a new range of resources. For example, the evolution of the spur in continental *Aquilegia* (Ranunculaceae) appears to be such a key innovation which led to rapid radiation within the genus. Other circumstances may also favour radiation: in his flush-crash-founder model Carson (1975) suggests that episodic relaxation from selection may cause disruption of old adaptive gene complexes and allow selection to operate on new genetic systems.

Random evolutionary processes are also invoked to explain island radiations (Crawford *et al.* 1987; Grant 1998a). With habitat turnover due to volcanic activity, and the opportunity for repeated cycles of inter-island dispersal and isolation, population bottlenecks, founder events and geographic separation of conspecifics may have occurred repeatedly through the evolution of island floras. These factors will promote evolution by drift; this could occur, for example, through the random fixation of different advantageous genes in separate populations experiencing similar selection pressures (Schluter 1996, and listed references).

Not all lineages on an island or archipelago are equally successful, even when they have the same ecological opportunities and are exposed to the same chance events. This may be a simple question of colonization order, or may reflect chance events which lead to extinction. Variation in the success of lineages may also be due to differences in the evolutionary potential (or genetic variability) and the phylogenetic constraints (or genetic composition) between lineages. Table 1 lists the genera in the Hawaiian and Canarian archipelagos comprising more than ten endemic species. It is apparent that genera within the Asteraceae have been particularly successful in diverging within both archipelagos, and that the family Campanulaceae has several species-rich genera in the Hawaiian archipelago. This pattern of several independent radiations within the same families suggests a phylogenetic component to island radiations. However, it may also reflect factors such as the presence within these families of a large and diverse continental species pool or advanced dispersal abilities that ensured more frequent colonizations of the islands. Soon after establishment on an island the dispersal capacity may be lost rapidly (Cody & Overton 1996).

Species richness and the presence of morphological and ecological diversity in a lineage are often taken as evidence for adaptive radiation in island plants, in particular where this is combined with low genetic differentiation (e.g. Baldwin *et al.* 1990; Okada *et al.* 1997). In such rapid, adaptive radiations, neutral characters are expected to exhibit little diversity while features related to fitness will vary considerably. Few studies, though, actually seek to identify the significant traits in these suggested adaptive radiations. In this paper, we assess this problem by discussing the possible adaptive significance of some of the most prominent traits in island plants. The importance of hybridization in the evolution of island plants is also considered as part of a more general discussion of the mechanisms governing radiations on islands. Most examples will be taken from the Hawaiian and Canarian floras and in particular from our studies on the morphological, ecological and molecular diversification of the Canarian genus *Aeonium*. Our choice of examples reflects both the geographic bias in the literature of island plant radiations and the fact that the flora of these two archipelagos has been very well recorded. Both archipelagos are of volcanic origin but differ in age and degree of remoteness. The Hawaiian Islands are situated some 4000 km off the Californian coast and comprise eight major islands varying in age from 0.5 to 7.5 Mya (MacDonald *et al.* 1983; Wagner *et al.* 1990). The seven major islands of the Canarian archipelago lie some 100 km from the African coast and range in age from 0.8 to 21 Mya (Carracedo 1978).

Table 1. Genera of vascular plants comprising more than ten endemic species in the Hawaiian and Canarian archipelagos. Data were obtained from Wagner *et al.* (1990) (Hawaiian Islands), Hansen & Sunding (1993) and Bramwell & Bramwell (1990) (Canarian Islands) supplemented with the records of newly described species of *Aeonium* (Bramwell 1982; Liu 1989; Bañares Baudet 1992, 1999; Hernández & Bañares 1996). Canarian species include those also occurring on other Macaronesian islands. The percentage of dichotomies that include vegetative, floral or fruit traits are taken from taxonomic keys to the genera as are the percentage of species producing secondary wood. The "numbers of hybrids" describe intergenic hybrids involving both endemic, indigenous and naturalized parent species.

			Dichotomies (%)				
	Endemics	Indiginous and naturalized	Vegetative	Floral	Fruit	Woody spp. (%)	Hybrids
Hawaiian Islands							
Cyrtandra (Gesneriaceae)	53	0	36	61	3	100	67
Cyanea (Campanulaceae)	52	0	25	53	6	100	3
Pelea (Rutaceae)	47	0	29	44	27	100	0
Phyllostegia (Lamiaceae)	27	0	42	58	0	37	3
Peperomia (Piperaceae)	23	3	72	25	2	0	0
Bidens (Asteraceae)	19	4	20	50	30	11	11
Chamaesyce (Euphorbiceae)	15	7	57	24	19	73	3
Clermontia (Campanulaceae)	22	0	5	92	3	100	6
Hedyotis (Rubiaceae)	20	2	43	44	13	80	3
Schiedea (Caryophyllaceae)	22	0	41	48	11	91	2
Dubautia (Asteraceae)	21	0	57	40	3	100	27
Lipochaeta (Asteraceae)	20	0	55	36	9	0	1
Myrsine (Myrsinaceae)	20	0	79	18	3	100	1
Stenogyne (Lamiaceae)	20	0	35	65	0	10	1
Labordia (Loganiaceae)	15	0	44	30	27	100	1
Lobelia (Campanulaceae)	13	1	32	65	3	95	1
Sicyos (Cucurbitaceae)	14	0	5	30	65	14	1
Coprosma (Rubiaceae)	13	0	40	44	16	100	7
Wikstroemia (Thymelaeaceae)	12	0	72	19	8	100	3
Psychotria (Rubiaceae)	11	0	44	49	7	100	4
Canary Islands							
Aeonium (Crassulaceae)	36	0	80	20	0	100	35
Echium (Boraginaceae)	24	0	50	48	2	79	4
Sideritis (Lamiaceae)	24	0	45	55	0	100	0
Argyranthemum (Asteraceae)	17	0	59	24	17	100	2
Sonchus (Asteraceae)	23	0	63	37	0	96	2
Limonium (Plumbaginaceae)	18	3	77	23	0	89	0
Micromeria (Lamiaceae)	17	0	45	55	0	100	4
Lotus (Fabaceae)	16	7	52	48	0	94	1
Senecio (Asteraceae)	16	0	62	38	0	50	0
Monanthes (Crassulaceae)	15	0	92	8	0	–	12
Cheirolophus (Asteraceae)	14	0	74	26	0	100	0
Crambe (Brassicaceae)	11	0	80	13	7	100	0
Euphorbia (Euphorbiaceae)	11	30	43	57	0	100	4

The succulent, rosette-forming species of the genus *Aeonium* (Crassulaceae) comprise the largest radiation in the Canary Islands. Thirty-six of the 42 species in the genus are endemic to the archipelago while the remainder are distributed on other Macaronesian islands (two species on Madeira and one species on the Cape Verde Islands), in Morocco (one species) and in East Africa (two species). The genus probably arose in the

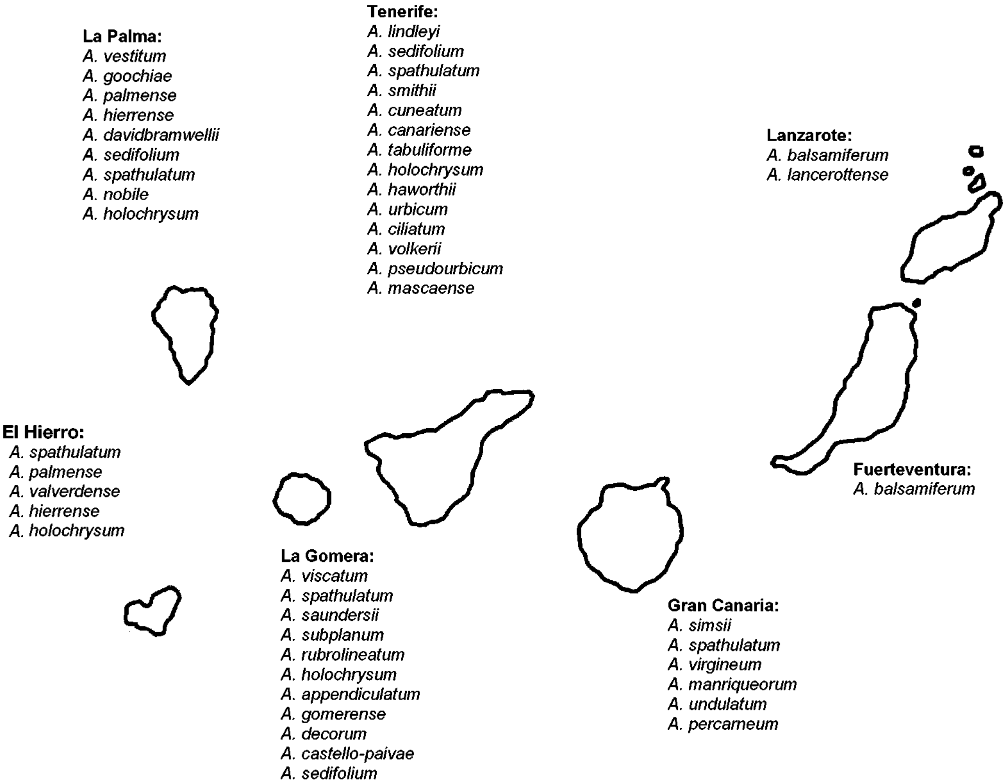

Fig. 1. The distribution of *Aeonium* spp. in the Canary Islands (Bramwell 1982; Liu 1989; Bramwell & Bramwell 1990; Bañares Baudet 1992, 1999; Hernández & Bañares 1996).

Canarian archipelago and later dispersed to Madeira, Cape Verde and Africa (Mes *et al.* 1996). All of the seven major islands of the Canarian archipelago are inhabited by members of the genus *Aeonium* (Fig. 1). Most species are single-island endemics and confined to particular habitats of an island. Various authors regard the genus as a prime example of adaptive radiation in plants due to the morphological diversity in the genus, the restricted habitat use of most species, and the wide array of habitats exploited by different species (Lems 1960; Voggenreiter 1974).

Are plant radiations in reproductive or vegetative traits?

To obtain an accurate reconstruction of character evolution within the groups requires well-resolved phylogenies, but such information is not available for these groups. However, a crude estimate of the relative amount of variation in reproductive and vegetative characters in plant groups can be obtained by counting the number of dichotomies in the taxonomic keys to these groups. This approximate method is likely to be biased towards the most obvious and apparent morphological traits of the plants. In Table 1 we present the counts of vegetative and reproductive dichotomies for the most species-rich genera (>10 endemic species per genus) in the Hawaiian and the Canarian Islands using the flora of Wagner *et al.* (1990) and Bramwell & Bramwell (1990). It appears from this analysis that many genera have approximately equal numbers of vegetative and reproductive dichotomies. In the Canary Islands, though, there is a bias towards dichotomies in vegetative characters. Genera with vegetative dichotomies are assumed to have flowers and pollinator faunas that scarcely vary among their species (Grant 1949). The pollinator faunas may also be random samples of the local pollinator community. In the Hawaiian Islands it is mainly the genera pollinated by drepanid birds (*Cyanea, Phyllostegia, Lobelia* and *Clermontia;* Sakai *et al.* 1995a) that exhibit reproductive dichotomies. This is because, following dispersal and isolation, species pollinated by only one or a few pollinator groups are more prone to differentiate in their floral structures compared to those visited by a random array of pollinators (Grant 1949). In the case of *Aeonium,* only 20% of the dichotomies in the key are floral, suggesting that this genus has a rather randomly assembled pollinator fauna. A study of *A. holochrysum* on Tenerife supports this argument. Preliminary data from two study sites show that a large part (48% and 75%) of the species observed to visit the flowering plants in the habitats (Coleoptera, Hymenoptera, Diptera and Lepidoptera) visited the flowers of *A. holochrysum* (J.M. Olesen & T.H. Jorgensen, unpubl. data).

The flowers of *Aeonium* conform to the general Crassulacean type by being radially symmetric, hypogynous, having a corolla differentiated into petals and sepals, and having two whorls of stamens and one whorl of nonfused fruits in the form of follicles. Nectariferous glands are formed at the base of each carpel. Flowers are yellow, white or reddish. Inflorescences are panicles with a variable number of branching orders. Taken as a whole, the genus appears very uniform in terms of floral shape, and this is reflected in the predominance of vegetative dichotomies in the taxonomic key (Table 1). There is, however, extensive variation in size of flowers and inflorescences, and a detailed investigation of flower morphology in 18 species revealed subtle differences between species in shape of floral organs and inflorescences (Jorgensen 2000). Correlating distances in species means of these traits to their patristic distance based on the molecular phylogeny of the genus in a partial Mantel test revealed that variation in various floral characters – size of flowers (here: petal length), pubescence of floral organs, and number of petals – has a substantial phylogenetic component (Jorgensen 2000). This provides evidence of some differentiation in reproductive traits during the early radiation of the genus despite the constraints to evolution imposed by the Crassulacean flower architecture.

Pollen and ovule production, two important components of the reproductive output of a plant, vary to some extent among species of *Aeonium*. Pollen-ovule ratios in the range of 92–313 (Table 2) might lead us to the conclusion that *Aeonium* species are facultatively autogamous (cf. Cruden 1977). Both the number of ovules per ovary and the number of pollen grains per stamen are variable among species. Other components of the reproductive output in *Aeonium* species (number of ovaries and stamens per flower, number of flowers per inflorescence) vary similarly (Table 2). For example, the monocarpic species (*A. urbicum* and *A. hierrense*) have a considerably higher flower production per inflorescence than closely related polycarpic species. Of the four components listed in Table 2 only the numbers of ovaries and stamens per flower appear to have a phylogenetic component (Jorgensen 2000). We suggest, therefore, that a part of the variation in the four components is due to present ecological conditions selecting for a fine-tuning of reproduction to specific habitat requirements by altering various components of the total reproductive output. It awaits further investigation of reproductive traits in more *Aeonium* species and, in particular, of the ecology of all members of the genus to understand fully the importance of these traits in the radiation of the genus. Other island genera without prominent differentiation in floral traits also need to be investigated.

Characters related to growth form contribute significantly to the numerous dichotomies involving vegetative traits in the taxonomic key of *Aeonium* (Bramwell & Bramwell 1990). The 42 species of *Aeonium* vary in appearances from creeping and sparsely branched, or upright, unbranched woody forms to subshrubs or tall shrubs. Leaf morphology is also an important trait in the taxonomic classification of species. The rosette leaves vary in shape, pubescence and presence of glands and ciliate margins (Bramwell & Bramwell 1990).

Molecular phylogenetic investigations imply that the evolution of the different growth forms in *Aeonium* is related to early events in the radiation of the genus (Mes & Hart 1996; Jorgensen & Frydenberg 1999). A detailed analysis of the growth forms of 22 species of *Aeonium* additionally reveals that, not only do closely related species end up with the same growth form, but they also reach their general appearance by the same form of modular growth (Jorgensen & Olesen 2000). Simple linear and logistic regression models can be developed to predict module length, branching

Table 2. Means (standard deviations) of four components of the reproductive output in 15 species of *Aeonium* and their estimated pollen-ovule ratios (P/O). Infrageneric classification is according to Mes (1995). The mean number of flowers per inflorescence was estimated from ten inflorescences per species. The numbers of ovaries per flower of a species are means of a total of 50 flowers and five flowers per inflorescence. Numbers of ovules per ovary (equal to half the number of stamens) are means of 5–16 flowers from different individuals of a species. Numbers of pollen grains per stamen are means of 5–10 stamens from different individuals of a species.

	Flowers per inflorescence (SD)	Ovaries per flower (SD)	Ovules per ovary (SD)	Pollen grains per stamen (SD)	P/O
Sect. *Canariensia*					
A. canariense	2 463 (637)	9.3 (0.6)	78 (16)	10 028 (1560)	257
A. cuneatum	2 104 (1160)	9.2 (0.5)	47 (4)	5 089 (494)	217
A. subplanum	2 136 (1150)	8.7 (0.6)	60 (10)	4 647 (943)	155
Sect. *Leuconium*					
A. davidbramwellii	1 040 (219)	8.1 (0.5)	62 (12)	5 045 (529)	163
A. decorum	104 (50)	8.0 (0.6)	74 (23)	3 384 (504)	91
A. haworthii	440 (187)	8.0 (0.9)	57 (13)	3 370 (738)	118
A. hierrense	5 503 (3057)	7.5 (0.6)	78 (14)	8 655 (1321)	222
A. percarneum	1 737 (513)	7.6 (0.5)	55 (9)	7 598 (2244)	276
A. urbicum	5 148 (1662)	8.4 (0.6)	118 (23)	11 262 (1441)	191
Sect. *Aeonium*					
A. holochrysum	920 (291)	9.2 (0.9)	52 (9)	5 266 (1838)	203
A. undulatum	2 970 (1476)	7.5 (0.7)	65 (6)	9 346 (902)	287
A. vestitum	1 092 (542)	5.5 (0.4)	47 (8)	4 923 (959)	209
A. simsii	83 (38)	6.4 (0.9)	56 (13)	7 336 (2516)	262
Sect. *Chrysocome*					
A. spathulatum	60 (24)	9.3 (0.6)	44 (7)	4 931 (1330)	224
Sect. *Petrothamnium*					
A. sedifolium	18 (5)	10.2 (0.8)	45 (10)	2 551 (1341)	113

mode and flowering probability in species of *Aeonium* based on their modular construction. When combined, the parameters of these models are species-specific and describe the growth rules of each species. Species are separated significantly at the level of phylogenetic section in a discriminant analysis based on the parameters of these growth rule models (Jorgensen & Olesen 2000). Since species with the same growth rules are confined to the same phylogenetic clade, we propose that early evolution of these growth rules has been important for further radiation in the genus.

Are radiations adaptive?

What is the relative importance of adaptive and non-adaptive evolutionary processes in the radiation of *Aeonium*? This issue can be assessed indirectly by comparing the phylogeny of a plant group with the geographic and ecological distribution of the various species. Species of *Aeonium* in the same clade and with the same growth rules often occur on different islands but in similar kinds of habitats. It is suggested that dispersal across similar habitats of different islands, followed by divergence due to isolation, is a prominent route in speciation in *Aeonium* (Jorgensen & Frydenberg 1999*)*. The same phylogenetic pattern of dispersal and diversification has been well documented in another Canarian genus, *Argyranthemum* (Francisco-Ortega *et al.* 1996b, 1997), and may also be valid for other large genera in the archipelago, e.g. *Sonchus* (Kim *et al.* 1996) and *Crambe* (Francisco-Ortega *et al.* 1996a). In other island groups, e.g. the Hawaiian silverswords alliance (Baldwin & Robinchaux 1995; Baldwin 1997*)* and *Cyanea*

(Givnish *et al.* 1995), the radiation of a lineage into new habitats within the same island appears to be more significant than divergence due to isolation after colonization of similar habitats on different islands.

A strong indication of the adaptive value of a trait is when phylogenetically separate, but ecologically similar, species converge or show parallel patterns of variation along similar ecological gradients (Endler 1986). In Canarian lizards, for example, the correlation of changes in colour pattern with environmental variation is parallel in different species on neighbouring islands, and is taken as evidence of natural selection (Brown *et al.* 1991). In *Aeonium*, similar analyses have been done for four unbranched species within the section *Leuconium.* The four species are widely distributed within both mesic and dry habitats of the four western islands. By the use of partial Mantel tests (and correcting for phylogenetic relatedness), it was revealed that traits related to plant height, leaf shape and flower morphology vary predictably with distance from continental Africa (Jorgensen 2000). The result implies that variation in these morphological traits is due to different degrees of "oceanity" and may be a result of selection. Different degrees of oceanity may reflect decreases in temperature amplitude and solar radiation with distance from the continent (Huetz de Lemps 1969). To investigate in more detail the adaptive significance of plant traits would require functional analyses or replacement experiments, such as those performed in animal radiations like Caribbean lizards (Thorpe & Malhotra 1996) or sticklebacks (Schluter 1996).

A number of distinctive traits occur repeatedly in island plants. Some of the most frequently mentioned traits in the literature of adaptive radiation on oceanic islands are the woody habit, monocarpy, developmental heterophylly and sexual dimorphism. Before concluding that these traits are particularly favourable in an island environment and facilitate adaptive radiation, it it necessary to determine their place of origin. It is reasonable to suppose that a trait, which is acquired more frequently in island lineages (and is found in different archipelagos) than in continental groups, is of selective value in the island environment and has island origin. Alternatively, a trait may be common in island floras when it has facilitated the radiation of single lineages. In the latter case, though, we will be left with the difficulty of determining whether such a trait is a key innovation or whether it is a non-adaptive trait in a lineage that has radiated due to the general availability of open, unsaturated habitats (Givnish 1998). Support for the hypothesis that a particular trait facilitates the radiation of island lineages could be obtained by comparing sister groups exhibiting the presence and absence of the trait (Guyer & Slowinski 1993; Hodges 1997). Ideally, this test should be based on a detailed knowledge of phylogenetic relationships and the timing of speciation and extinction events (Sanderson & Donoghue 1996). Such a complete knowledge appears to be lacking for island plant groups and their continental sister lineages (Baldwin 1997). The following discussion on key features thought to be involved in the adaptive radiation of island lineages are therefore not yet confirmed statistically.

Woodiness

Woodiness is a prominent trait in island endemics. In the most species-rich genera of the Canarian and Hawaiian Islands the large majority of species are woody (Table 1). But is this trait adaptive and has it facilitated diversification within islands? – Hypotheses as to why woodiness has evolved frequently in the insular condition are numerous but yet untested. It could be a non-adaptive response to a stable environment or an adaptive response to the release from seasonality (Carlquist 1974; but see Givnish 1998). If the latter is true, it could be the result of selection for increased stature improving competitive ability with other plants (Carlquist 1974; Givnish 1998) or the result of selection to increase longevity in a pollinator-scarce environment (Wallace 1878; but see Carlquist 1974). Yet another suggestion is that release from large herbivores permits delayed maturity and reproduction (Carlquist 1974).

Insular woodiness is an acquired trait in the Hawaiian silverswords, i.e. the lineage comprising *Argyroxiphium, Wilkesia* and *Dubautia* (Baldwin 1997), and in Canarian *Echium* (Böhle *et al.* 1996) and *Sonchus* (Kim *et al.* 1996). It is also likely that the North African ancestors of the monophyletic group comprising *Aeonium, Aichryson* and *Monanthes* were herbaceous (Mes *et al.* 1996), though the majority of species in these lineages are woody (Table 1). In Macaronesian Sempervivoideae there is an increase in woodiness from the most ancestral *Aichryson*, which includes annual species, to the most derived *Aeonium*, which are all woody. It is possible that woodiness was a key feature in the radiation of these lineages. The pattern is not consistent, though, as other island genera appear to have a woody continental ancestor (Givnish *et al.* 1996); many others remain to be investigated.

Monocarpy

The unbranched, monocarpic form has evolved at least four times in the genus *Aeonium* (Jorgensen & Frydenberg 1999; Jorgensen 2000), and several times in the Hawaiian *Cyanea* (Wagner *et al.* 1990; Givnish *et al.* 1995). It is also common in other plant groups of oceanic islands or island-like habitats (e.g. Canarian *Echium* and East African *Lobelia*). Factors favouring monocarpy may be of a demographic nature where ecological conditions lower the “value” of an adult compared to that of the juvenile (Stearns 1992). The disturbed and barren areas such as lava flows and abandoned fields, which are among the habitats of unbranched *Aeonium urbicum, A. appendiculatum, A. hierrense* and *A. pseudourbicum*, may be hypothesised to favour short life spans and therefore monocarpy. Alternatively, monocarpy may evolve when greater benefits of reproduction come at higher levels of reproductive effort (Schaffer & Schaffer 1977). This could apply to the pollinator-scarce environments of Wallace (1878), if pollinators prefer large inflorescences and fruit set increases relatively with inflorescence size. As with the demographic models this suggestion awaits further testing in island plants.

Herbivore defences

Traits related to herbivore defence appear repeatedly in different island lineages. The fossil record reveals the historic presence of large browsers like the ”moa-nalo” ducks and giant geese on the Hawaiian Islands (Olson & James 1991; James & Burney 1997), the flightless moas in New Zealand (Cooper *et al.* 1993), and the giant tortoises in the Canarian, Mascarene and Galápagos Islands (Dawson 1966; Arnold 1979; Hutterer *et al.* 1997). Tortoises are still present in the latter archipelago. As the only large browsers present on the islands (as deduced from the fossil record), it is apparent that these animals have exerted a strong and uniform selection pressure in contrast to that of a diverse continental herbivore fauna. The advantage of evolving anti-predator traits on these islands is obvious and may have faciliated radiations of island genera through repeated evolution in separate lineages or as a key innovation. The high incidence of developmental heterophylly (i.e. juvenile leaves different from adult leaves) in some island floras may be the result of selection for traits that deter herbivores through visual mimicry or visual divergence (Atkinson & Greenwood 1989; Givnish *et al.* 1994). Heterophylly is a widespread trait in the Mascarene Islands (Friedmann & Cadet 1976) and in New Zealand (Cockayne 1958). In the Hawaiian *Cyanea*, 17 of the 52 species are heterophyllous and the trait has evolved independently at least four times in the genus (Givnish *et al.* 1994). The trait coincides almost exclusively with the occurrence of prickles on stems and/or leaves which strongly suggests that it is an anti-herbivore defence. The original suggestion was that prickles deter herbivorous endemic snails, whereas others have argued that large avian browsers were the primary herbivores (Givnish *et al.* 1994, and references therein).

The genus *Aeonium* has no apparent morphological traits related to herbivore defence, though it remains to be investigated whether any biochemical traits are of significance in deterring herbivores.

Sexual dimorphisms

Nearly 21% of the native species in the Hawaiian flora are sexually dimorphic, the highest proportion of any flora studied (Sakai *et al.* 1995a,b). New Zealand also has a high incidence of sexual dimorphisms (Bawa 1980), while the Canaries are similar to the Galápagos in having a low number of such dimorphic species (Mcmullen 1987; Francisco-Ortega *et al.* 2000). All species of *Aeonium* appear to have sexually uniform flowers.

The selective forces suggested to favour dimorphic traits like dioecy, subdioecy, polygamodioecy and gynodioecy involve the promotion of outcrossing (Bawa 1980). Island plants may suffer from low levels of genetic diversity following colonization and establishment. The evolution of outcrossing mechanisms may therefore favour further radiation and diversification in island groups (Carlquist 1974). An alternative suggestion is that ecological factors favour dimorphism as a result of altered patterns of resource allocation and sexual selection (reviewed in Bawa 1980; Thomson & Brunet 1990). The association of sexual dimorphisms with fleshy fruits, woodiness and small, inconspicuous flowers in Hawaiian Islands and elsewhere tends to support this theory (Thomson & Brunet 1990; Sakai *et al.* 1995b).

In the Hawaiian Islands, at least 12 lineages have evolved dimorphisms upon establishment in the archipelago. These have given rise to one third of the current dimorphic species (Sakai *et al.* 1995a). Within the lineage comprising the 26 species of *Schiedea* and *Alsinidendron*, for example, dimorphisms have at least two origins, and further radiation has resulted in 10 gynodioecious, subdioecious and dioecious species (Soltis *et al.* 1996; Weller *et al.* 1998).

Hybridization

Hybridization and introgression appear to be widespread processes in flowering plants and are thought to be important in plant evolution (reviewed in Arnold 1997). Hybridization can lead to either homoploid or polyploid individuals (Stebbins 1950). The evolutionary significance of this process can be either the establishment of new stabilised taxa with morphologically intermediate or distinct characters, or the increase of the genetic diversity within species as a result of new allelic combinations and the possible breakdown of reproductive barriers following backcrosses to either parent (Abbott 1992; Arnold 1992; Rieseberg 1995).

The successful establishment of new hybrid species depends on the presence of unoccupied niches and may therefore be more likely in open, disturbed habitats (Stebbins 1950). This has been suggested as one of the main reasons that hybridization is important in evolution on islands (Gillett 1972; Carlquist 1974; Carr 1987, 1995; Smith *et al.* 1996; Grant 1998b; but see Humphries 1979 and Ganders & Nagata 1984 for opposing views). In the Canary Islands, as well as in other oceanic archipelagos, volcanic activity has repeatedly caused plant populations to become fragmented and new habitats to arise and in this way may have provided opportunities for new species of hybrid origin to establish. These opportunities may have been further enhanced by the general presence of diverse and often unsaturated habitats. Additionally, the small amount of genetic differentiation between recently radiated species within a lineage suggests a lack of genetic barriers to hybridization in many island groups (Crawford *et al.* 1987; Kim *et al.* 1996).

A survey of three continental floras and one island flora performed by Ellstrand *et al.* (1996) supplemented with a similar survey of the Canarian flora, reveals no indication that hybridization is more frequent on oceanic islands than on continents. Species of hybrid origin comprise 5–18% of the native and naturalized taxa in the continental vascular floras (excluding intraspecific taxa), while 9% of the Hawaiian taxa and 4% of the Canarian taxa appear to be derived from hybrids (Hansen & Sunding 1993; Ellstrand *et al.* 1996). Another important conclusion from the survey by Ellstrand *et al.* (1996) is that natural hybrids occur non-randomly over families and genera. This indicates that, in addition to habitat availability, phylogeny also influences the importance of hybridization in plant evolution. In the large island genera from the Canarian and Hawaiian Islands it is therefore not surprising to find great variation in the number of natural hybrids recorded (Table 1). It is apparent that species in some genera readily form hybrids, and in these groups hybridization may have had an impact on the evolution and divergence of species. The majority of contributions to the pool of natural hybrids recorded on the Canary Islands is from Crassulaceae, and from the genus *Aeonium* in particular. *Aeonium* may be extreme in its absence of internal reproductive barriers to crossing with congenerics. Natural hybrids are recorded for almost all species occurring in sympatry or parapatry with the exception of those where flowering periods do not overlap (Liu 1989; Hansen & Sunding 1993).

Whereas the occurrence of natural hybrids reflects the potential for the species of a group to hybridize, it does not necessarily reveal the actual importance of hybridization and introgression in the evolution of the group. The occasional hybrids may not become established due to low survival and reproduction. Traditional methods to investigate putative ancient hybrid species have been through morphological comparisons with suggested parent species and their artificial cross products (e.g. Gillett 1972). This is a time consuming method that relies on the existence of extant parental species. The development of numerous molecular techniques within recent years has

Table 3. Molecular studies of large genera (≥10 spp.) from the Hawaiian and Canarian archipelagos and their evidence of ancient hybridization. The total number of species in the archipelago (in brackets) are those reported by the authors, except for *Echium* which is from Bramwell & Bramwell (1990). Abbreviations: cpDNA, chloroplast DNA; nDNA, nuclear DNA; ITS, internal transcribed spacer region of the nuclear rDNA; AFLP, amplified fragment length polymorphism; RFLP, restriction fragment length polymorphism; RAPD, random amplified polymorphic DNA; (+) indicate studies where multiple populations were sampled for some species in the investigation but not for all.

Taxonomic group	Species in the study (total)	Molecular marker	Multiple populations	Ancient hybridization	Authors
Hawaiian Islands					
Tetramolopium (Asteraceae)	7 (10)	genomic DNA (RFLP)	+	+	Okada *et al.* (1997)
Schiedea, Alsinidendron (Caryophyllaceae)	20 (29)	cpDNA (RFLP), nDNA (RFLP)	(+)	–	Soltis *et al.* (1996)
Argyroxiphium, Dubautia, *Wilkesia* (Asteraceae)	24 (27)	cpDNA (cpDNA)	+	+	Baldwin *et al.* (1990)
Cyrtandra (Gesneriaceae)	16 (56)	RAPD	+	+	Smith *et al.* (1996)
Cyanea, Rollandia (Campanulaceae)	30 (63)	cpDNA (RFLP)	–	–	Givnish *et al.* (1995)
Canary Islands					
Aeonium (Crassulaceae)	33 (35)	nDNA (ITS1&2), cpDNA (RFLP)	–	+	Jorgensen & Frydenberg (1999), Mes & Hart (1996)
Echium (Boraginaceae)	19 (24)	cpDNA (*), nDNA (ITS1)	–	–	Böhle *et al.* (1996)
Sonchus (Asteraceae)	16 (23)	nDNA (ITS1&2)	(+)	–	Kim *et al.* (1996)
Argyranthemum (Asteraceae)	19 (19)	cpDNA (RFLP)	(+)	+	Francisco-Ortega *et al.* (1996b)

(* trnT_{UGU}-trnL_{UAA} spacers, trnL_{UAA} introns and trnL_{UAA}-trnF_{GAA} spacers)

created new opportunities for the identification of ancient hybridization. The most informative way is to reconstruct the molecular phylogeny of the group in question by using more than one molecular marker and preferably multiple populations. Because of incongruencies between the phylogenies based on nuclear DNA, chloroplast DNA or morphology, it has been suggested that two species of *Aeonium* are of hybrid origin. Morphological characters of *A. percarneum* and *A. lancerottense* (Liu 1989) and chloroplast restriction site data of *A. lancerottense* (not available for *A. percarneum*) (Mes & Hart 1996) suggest their close relationship to species within the section *Leuconium.* Opposing results come from sequences of nuclear ribosomal DNA (ITS regions) which group *A. percarneum* and *A. lancerottense* within the section *Aeonium* (Jorgensen & Frydenberg 1999). If we assume that the chloroplast genome is maternally inherited, these asymmetries are best explained by events of introgression solely via the transfer of pollen from a member of the section *Aeonium* to *A. percarneum* and *A. lancerottense* in the section *Leuconium.* Evolution by polyploidy appears to be of minor importance in *Aeonium* as only four species (*A. balsamiferum, A. goochiae, A. haworthii* and *A. korneliuslemsii*) are known only as tetraploids (Liu 1989; Ardévol Gonzales *et al.* 1993).

The strength of the hypothesis of hybridization depends on a number of factors. Intragenomic processes may render ancient hybridization difficult to detect on the molecular level, though the use of nuclear markers introduces the possiblity of detecting multiple variants in a plant. It is also necessary to keep in mind, when comparing the frequencies of hybridization in different genera, that differences in life histories (e.g. annuals *vs* perenials) may cause differences in the propensity for hybridization. Investigations that attempt to evaluate the importance of ancient hybridization in the radiation of large island genera are scattered and, as in *Aeonium*, often incomplete as they do not involve all species of the genus or do not include multiple populations of individual species. Table 3 lists the molecular studies performed on large genera of the Canarian and Hawaiian Islands with reports on the evidence of ancient hybridization and comments on the relevant methods. All these genera are dominated by perennials. It must be noted that many of these studies were not designed to detect ancient hybridizations. The general conclusion from Table 3 is that where sampling and/or the use of molecular markers has been extensive, evidence of ancient hybridization has usually been found, thus confirming the role of hybridization in the evolution of island genera. An exception is the genus *Echium* for which no evidence of ancient hybridization has been found.

In *Aeonium* as well as in other island genera, species often occur only as a single or as a few small populations. It is possible that events of introgression have had a large positive impact on the genetic diversity of these populations through their colonizing history (Carlquist 1974; Grant 1998a). However, in small populations, the possible negative effects must also be considered, especially when hybridization is with a more widespread species (Arnold 1992). In such cases the genotypes of the rare species can be completely absorbed by the greater gene pool of the common species and the integrity of the rare species may be destroyed. With our present knowledge, it is impossible to predict the importance of this factor in the colonization history of *Aeonium* and other island genera.

Conclusion

Our ability to interpret diversification on islands (and elsewhere) is strongly dependent on an adequate knowledge of the phylogeny of the taxon in question. Molecular data (preferably sequences from non-coding regions) are useful as they are assumed to be independent of morphological variation and avoid the problem of homoplasy (Moritz & Hillis 1996 and listed references). Several revisions of the theories and conventions concerning evolution on islands are based on molecular data. For example, the repeated confirmation of insular woodiness as a derived character state in Canarian genera (as reviewed above) leads to the rejection of the former widespread view that these species are relicts and ancestors of many modern Canarian and continental species (Meusel 1953; Lems 1960; Bramwell 1976; Sunding 1979). Similarly, detailed knowledge of phylogeny will enable us to actually test whether plant lineages on islands are more species-rich than on the continents and whether this is facilitated by the evolution of certain key features. However, there are practical problems. When traditional molecular markers are applied to island radiations we are most often left with little genetic differentiation compared to that within continental species groups (Baldwin *et al.* 1990; Sang *et al.* 1994, 1995; Givnish *et al.* 1995; Böhle *et al.* 1996; Francisco-Ortega *et al.* 1996b; Kim *et al.* 1996; Nepokroeff & Sytsma 1996; Okada *et al.* 1997). Future application of marker systems that solve relationships between closely related species is therefore needed.

Radiation and speciation in *Aeonium* have probably been facilitated by both random and non-random evolutionary processes, as well as by events of hybridization and introgression. From our current knowledge, three factors of an ecological or genetic nature have probably been particularly important in making this genus the largest radiation in the Canarian archipelago. Firstly, our molecular data suggest that dispersal of fruits and seeds may have assured the repeated colonization of different islands, leading to the evolution of new lineages after isolation. Secondly, a lack of barriers to hybridization means that natural hybrids are common, and so introgression may have contributed to formation of new taxa. Thirdly, the most prominent variable trait in the genus, growth form, is determined by simple rules of growth which are probably determined by simple genetic differences (Jorgensen & Olesen 2000). The diversification into new forms may therefore have been easily facilitated by small changes in this genetic background.

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