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The reproductive biology of island plants

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Since the review of the reproductive biology of island plants by Ehrendorfer (1979) three decades ago, there has been a veritable explosion of studies on plants of oceanic islands. Although the primary emphasis, particularly in the past two decades, has been on molecular phylogenetics of island lineages (Baldwin *et al.*, 1998; Emerson, 2002), there also has been progress in understanding their reproductive biology. However, the comment by Ehrendorfer (1979: 293) about reproductive biology of island plants still applies today: ‘This is an extensive, fascinating, and complex field of inquiry, still insufficiently covered by relevant work and factual evidence.’ And, of course, there is the exhortation by Herbert Baker from his classic paper in *Evolution* from 1967: ‘Clearly, the greatest need in this area of biology is for further field and experimental studies (by as many workers as can spare their time) on the reproductive biology of the plants which make up floras of all kinds.’

The present review uses Ehrendorfer’s (1979) chapter as a general framework for highlighting progress since that contribution. Also, Barrett (1996) presented a concise review of the reproductive biology and genetics of insular plants, and incorporated several topics (e.g. phylogenetic analyses) not featured in Ehrendorfer (1979). We will use two general approaches in discussing the evolution of the reproductive and pollination biology of island lineages as compared with their presumptive colonising ancestors. One will be to look at specific islands, and make comparisons between and among them to derive patterns. Another approach will be to discuss specific examples illustrating how plants have adapted, however perfectly or imperfectly, to the situation in the island setting. We will also consider the influence of invasive plants and pollinators on the reproductive biology and conservation of island lineages. Lastly, important areas for future studies will be considered.

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Dispersal of colonising ancestors

The attributes of a successful coloniser fall into two general categories, one concerned with dispersal to and establishment on an island, and the other with the radiation and diversification of their progeny in the insular setting. Carlquist (1981) pointed out that migration of colonisers is chiefly a matter of chance, but once they arrive selection operates on the propagules and is the determinate of whether there is successful establishment. Carlquist (1974: 12–13) suggested that chance dispersal was a lesser hurdle than establishment for colonisers. It is, of course, difficult to gather direct evidence on this issue. However, results from molecular phylogenetic studies indicate that, while in most instances the nearest continental source areas are the origins of colonising ancestors (e.g. compilation in Carine *et al.*, 2004 for Canary Islands), there are some exceptions.

Due to space constraints, extensive considerations of dispersal mechanisms and loss of dispersability in island lineages will not be considered in detail. The topics have been the subject of earlier classical reviews (Carlquist, 1966a, 1966b, 1974). Carlquist (1980) also provided an overview for Hawaii and he considered the possibilities for dispersal of Compositae in the Pacific islands (Carlquist, 1966d). These reviews, as well as the more recent one for the Robinson Crusoe (or Juan Fernández) Islands, Chile, by Bernardello *et al.* (2006), provide broad overviews of the probable geographic sources of the island ancestors, the dispersal units of the colonisers and their most likely dispersers to the islands. As with the generally held proposition for plants from other archipelagos such as Hawaii (Carlquist, 1974, 1980), Galapagos (Porter, 1976, 1983), and Bonin (Ogasawara) Islands (Ono, 1991), Bernardello *et al.* (2006) indicate that birds account for the vast majority of dispersal to the Robinson Crusoe Islands. Using a phylogenetic approach, Lowrey *et al.* (2005) investigated the fascinating distribution of the genus *Tetramolopium* in Hawaii, one of the Cook Islands and New Guinea. The data indicate an origin in New Guinea, and while not completely conclusive, the evidence favours dispersal first to Hawaii and then to the Cook Islands, rather than the other way around. Lowrey *et al.* (2005) suggested the bird, the Pacific golden plover, as the dispersal agent for the long trip (over 3000 km) from Hawaii to the Cook Islands. Likewise, Ballard and Sytsma (2000) suggested that one or more of the 50 species of birds that winter in Hawaii and breed in the Arctic likely dispersed the ancestor of the woody Hawaiian violets to the archipelago.

While it appears that birds are common dispersal agents of propagules to islands, Carlquist (1974) discussed the role of oceanic drift in dispersal to islands. Green (1999) determined the identity of disseminules (seeds and fruits) washed up on a beach on Christmas Island in the Indian Ocean. About half of the more than 60 species represented by the stranded disseminules do not grow on the island. Green (1999) discusses the possible distant sources of the seeds and fruits (he suggested

that those fruits and seeds of species growing on the island did not originate from plants on the island), and cites prevailing ocean currents and surface winds that could transport disseminules from the source areas to Christmas Island. These and other data from phylogenetic and comparative studies of island plants over the past three decades are perhaps sufficient to provide general support for Carlquist's (1974) hypothesis that dispersal is likely not the limiting process in establishment on oceanic islands.

Phylogenetic and comparative studies indicate that most colonising ancestors come from nearby source areas; however, recent studies suggest a number of instances of exceptionally long-range dispersal. Two of the more notable examples indicating distant source areas include an African origin for the Hawaiian endemic genus *Hesperomannia* (Asteraceae) (Kim *et al.*, 1998) and an Arctic origin for the ancestor of the woody violets in Hawaii (Ballard & Sytsma, 2000). In addition to Lowrey *et al.* (2005), there are other phylogenetic studies showing examples of islands not only being recipients of propagules, but sources of them as well (Harbaugh & Baldwin, 2007; Harbaugh, 2008; Harbaugh *et al.*, 2009). While loss of dispersability occurs in some island groups (Carlquist, 1974; Bernardello *et al.*, 2006), there are situations where it is clear that insular plants are capable of dispersal to other islands (Harbaugh & Baldwin, 2007; Harbaugh, 2008; Harbaugh *et al.*, 2009).

Breeding systems of colonisers

One of the most important traits of colonising ancestors of island plants is breeding system, in particular whether the invading colonisers are self-compatible (SC) or self-incompatible (SI). It has been more than half a century since Baker (1955) proposed that SC colonisers would have an advantage following long-distance dispersal because one propagule could establish a sexually reproducing population. By contrast, two or more propagules would be required to establish a sexually reproducing population with SI plants. Given that dispersal to a distant small island is not common (even if not the limiting factor in establishment, as above), multiple dispersal and establishment events would be necessary to bring in congeners with compatible breeding groups; this is in all probability especially unlikely. Stebbins (1957) was so convinced of the generality of Baker's (1955) hypothesis that he called it Baker's Law. Carlquist (1974), however, made the point that SC colonists would not provide sufficient genetic variation for the radiation and diversification of their progeny. Both Ehrendorfer (1979) and Barrett (1996) noted that available evidence supports the Baker (1955) hypothesis because the majority of endemic flowering plants that have been studied on islands are SC. Compilations subsequent to Ehrendorfer (1979) for the Galapagos (McMullen, 1987, 1990) and New

Zealand (Webb & Kelly, 1993,) and two papers published after Barrett (1996) on the Robinson Crusoe Islands (Anderson *et al.*, 2001a; Bernardello *et al.*, 2001) support their generalisations on the prevalence of SC plants on islands. While the compatibility of the current plants on an island does not confirm the state of the ancestral coloniser, there is little reason to think that initial, successful colonisers in an extant SC group were not also SC because of the aforementioned advantages that SC, and particularly self-pollinating plants, would have in establishing sexual populations. For example, Schueller (2004) demonstrated higher self-pollination in island versus mainland populations of *Nicotiana glauca*. The island populations (which are introduced) were visited as frequently as mainland populations by their hummingbird pollinators, indicating lack of selection for self-pollination in the island setting and suggesting instead that the higher selfing in the islands is due to its advantages in establishment of populations.

Although the preponderance of data indicates that most colonisers are SC, there are a number of notable exceptions to Baker's Law, particularly within Compositae, the family with the most species endemic to oceanic islands. The silversword alliance in Hawaii, one of the most spectacular radiations of island plants, has been shown to be ancestrally SI, perhaps with some leakiness, that is, some level of pseudo-self-compatibility (PSC) (Carr *et al.*, 1986; Barrier *et al.*, 1999; Baldwin, 2003). Other examples of SI or PSC colonisers include *Argyranthemum* (Francisco-Ortega *et al.*, 1997), the woody *Sonchus* alliance (S.-C. Kim, pers. com.), and *Tolpis* (Crawford *et al.*, 2008) from the Canary Islands, *Commidendrum* from St Helena (Eastwood *et al.*, 2004; A. Eastwood, pers. com.), *Dendroseris* from the Robinson Crusoe Islands (Anderson *et al.*, 2001a; Bernardello *et al.*, 2001) and *Scalesia*, which is the largest endemic genus in the Galapagos Islands (Nielsen *et al.*, 2000, 2003). As emphasised by Levin (1996) and Crawford *et al.* (2008), among others, a PSC coloniser would have the advantage of establishing a sexually reproducing population from a single propagule, and because the propagule originated from a largely outcrossing population, it would carry more genetic diversity than a seed from a highly selfing population. More information derived from careful studies of the reproductive biology and mating systems of island plants and their close relatives is needed to determine the frequency of PSC colonising ancestors of island lineages, and to document fully the level of SC versus SI in island species and their relatives.

The general syndrome for island flowers and their pollinators

Earlier surveys of island plants, particularly in Hawaii, indicated a generalised floral morphology with small, shallow, open, dull coloured 'inconspicuous' flowers (Carlquist, 1966d, 1974: 540). Subsequent studies have supported the

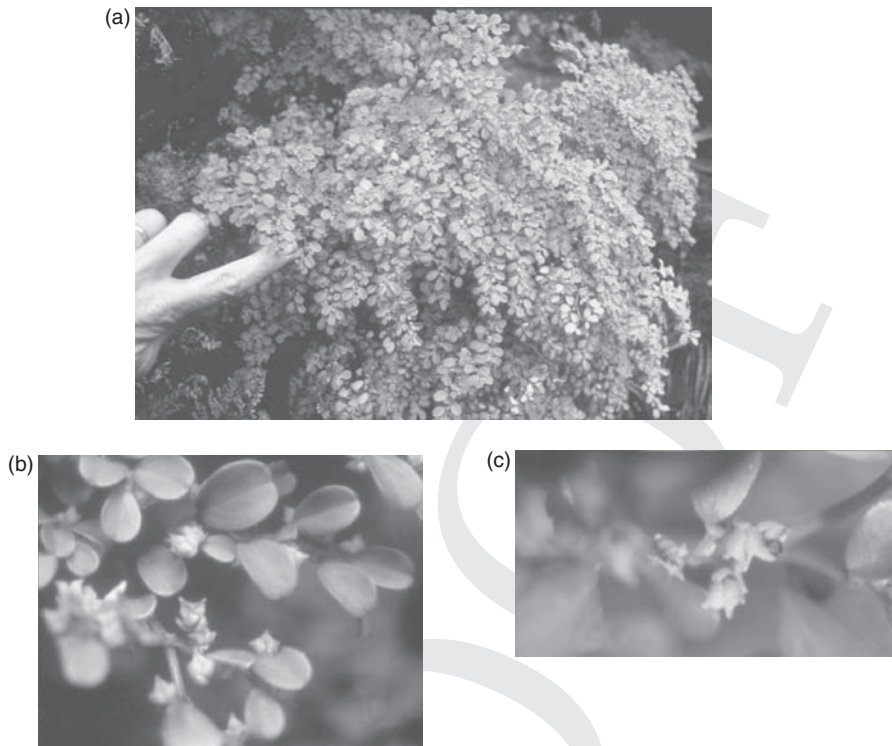


Figure 2.1 (a) *Lactoris fernandeziana* plant in field on Masatierra, Juan Fernández Islands, Chile. Photo by G. J. Anderson. (b) Branch with the small, greenish flowers of *Lactoris fernandeziana*. The three carpels are the conspicuous part of the flowers. Photos by D. J. Crawford. (c) Sepals visible at base of flowers. Scale lines: 4.0 mm in both photos. Photos by D. J. Crawford.

earlier observations for flowers of the Galapagos (McMullen, 1989, 1999: 26), the Ogasawara (Bonin) Islands (Abe, 2006), and the Robinson Crusoe Islands (Bernardello *et al.*, 2001). Bernardello *et al.* (2001) showed a very strong correlation among the features for small, inconspicuous, and green flowers (Fig. 2.1a,b,c). Another especially interesting and unusual outcome was the recognition that the floral morphology of the probable colonising ancestors and current species of the Robinson Crusoe Islands, particularly in terms of size and colour, are quite similar. This suggests that, in some cases, perhaps dependent on the age of the archipelago, the generalised floral type on islands can be related to dispersal or establishment rather than to *in situ* selection (Bernardello *et al.*, 2001), and/or that the particular system under study is relatively young in evolutionary time.

Consider next some possible reasons for the prevalence of small, open, colourless, hermaphroditic flowers in island floras. One of the major challenges faced by the colonising ancestors of island lineages is the paucity of biotic pollinators,

especially insects (Ehrendorfer, 1979; McMullen, 1987, 1990; Sakai *et al.*, 1995a; Barrett, 1996; Anderson *et al.*, 2001a; Bernardello *et al.*, 2001). The lack of pollinators on islands can also pose major limitations on successful establishment of colonists, especially those that have specialised pollination systems. Broad comparative studies, such as Anderson *et al.* (2001a), Bernardello *et al.* (2001) and Price and Wagner (2004) provide insights into possible pollinators of island colonisers as well as current pollinators of island plants. In addition to autogamy (pollination within the same flower without a pollen vector), it has been generally accepted that plants have coped with the paucity-of-pollinators problem by using either wind or generalist animal pollinators; a brief review of more recent studies will be compared to 'conventional wisdom' on the topic.

Barrett (1996) emphasised that, while there is the general perception that wind pollination is prevalent on oceanic islands, it is not clear that it is more frequent than on continental source areas. The possible advantages of wind pollination on islands include the assurance of pollination without reliance on the often-scarce biotic pollinators, atmospheric conditions on islands favouring wind over animal pollinators, and wind dispersal of pollen being more effective than animals for outcrossing (Barrett, 1996). Bernardello *et al.* (2001) contrasted the most likely pollinators of the ancestral colonisers with the current pollinators of plants of the Robinson Crusoe Islands. Pollinators are unknown for about 45% of the total flora. Bernardello *et al.* (2001) estimated that about half of the colonisers were insect pollinated and 40% wind pollinated; bird-pollinated colonisers and those with some sort of mixed pollination system were very rare. In contrast, studies on the islands suggest that the current island species are: 47% wind pollinated, 9% bird pollinated, with possibly one insect-pollinated species. One element of uncertainty in inferring the pollinators of some Robinson Crusoe species is that their flowers show certain features associated with wind pollination and other attributes suggesting biotic pollination (Bernardello *et al.*, 2001). Successful colonisers may move into new niches, and in these new environments with fewer competitors, elements of ancestral morphology may persist because of lack of selection against them. As a consequence, the recognition of wind pollination may be obscured by retention of zoophilous features, and detailed studies of pollination biology of island floras may reveal anemophily for species where morphology would not predict it.

An unusual and extreme example illustrating the impact of wind transferring pollen was identified in the species *Wahlenbergia berteroi* (Campanulaceae) from Robinson Crusoe Island (Anderson *et al.*, 2000). In other *Wahlenbergia* in the archipelago (and indeed the family as a whole; Yeo, 1993), autogamy occurs at the end of the life of a flower when the stigmatic branches recurve nearly 360° and contact pollen on the style. In *W. berteroi* the degree of stigmatic curvature is insufficient to reach the style and facilitate autogamy, yet most flowers have pollen on

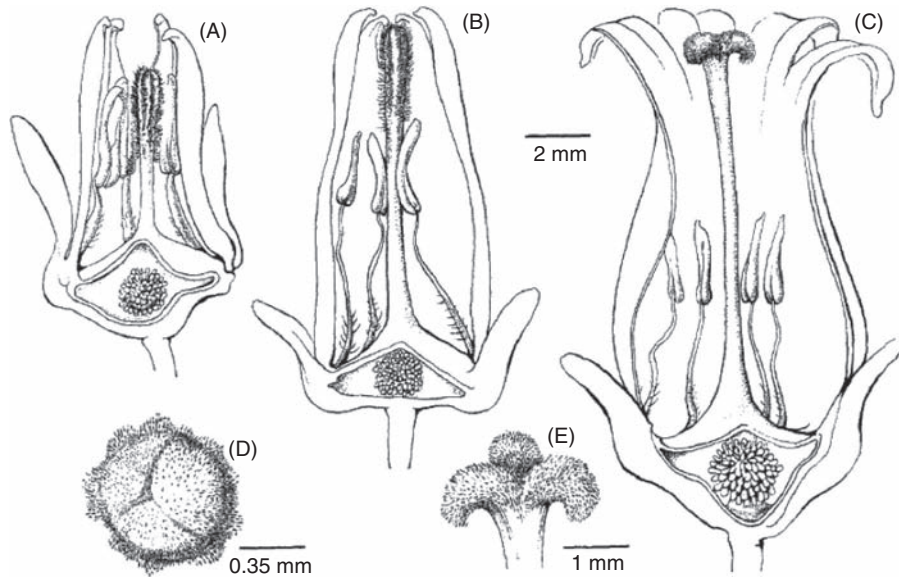


Figure 2.2 Drawings of flowers of *Whalenbergia berteroi* showing different stages of maturation. A-C, longitudinal sections of flowers; D, E, stigmatic lobes. The flowers are protandrous, and after the anthers dehisce, pollen is collected on the dense hairs on the upper part of the styles, and on the outer surface of the stigmatic lobes, which have not yet been exposed (A, D). The style elongates and carries the pollen upward near the throat of the corolla tube (B). The stigmatic lobes expand (E), the hairs on the styles retract and the anthers shrivel (C). Some pollen is deposited on the throat of the corolla at about the level of the expanded stigmatic surfaces, and self-pollination (autogamy) presumably can occur when flowers are shaken by the persistent wind, bringing the stigmatic lobes and pollen on the inner sides of the corolla in contact. See text for additional explanation. From Anderson *et al.* (2000), *Pl. Syst. Evol.* 223: 109–123. Used with permission from Springer-Verlag, Wien.

the stigmas. As anthers dehisce in bud stage (protandry), the corolla throat closely surrounds the anther cylinder and becomes coated with pollen and the stigma lobes have not expanded (Fig. 2.2 A, D). The pollen is presented by a stylar brush as the style elongates and pushes the pollen up near the open mouth of the now-open corolla, and against the inner faces of the corolla tube near its apex (Fig. 2.2 B, C). The stigma is then exposed by the reflexing of the lobes (Fig. 2.2 E). Because pollen stays viable throughout the receptive stage of the stigma, transfer from corolla to stigmata occurs when flowers are shaken by the ever present wind, thus promoting contact between the stigmata and corolla. This, and other studies on Robinson Crusoe plants, suggests that the frequency of wind pollination in the islands is slightly higher than the continental source areas but also indicates that it could, indeed, be much higher. Even by 'island standards', insect pollinators are very

scarce on the Robinson Crusoe Islands (i.e. there were no bee species reported until a very recent documentation by Engel, 2000), and there is essentially no evidence for generalist insects as effective pollinators (Anderson *et al.* 2001a; Bernardello *et al.*, 2001). If estimates of the frequency of insect pollinators of island ancestors are close to being accurate, then there has been a clear shift from insect to other means of pollination for plants native to the Robinson Crusoe Islands. While autogamy is quite rare in the species studied (Anderson *et al.*, 2001a; Bernardello *et al.*, 2001), over 40% of the Robinson Crusoe flora has not been examined, and the importance of autogamy remains an open question.

Available data for the Galapagos Islands, including morphology of flowers and airborne pollen, suggest that wind pollination, both by the colonising ancestors and the present flora of the archipelago, is rarer than in the Robinson Crusoe Islands (McMullen, 1987, 1990, 1993). However, Bernardello *et al.* (2001) caution that only 10% to 15% of the native flora of the Galapagos has been examined in detail, and suggest that flowers of some Galapagos species that otherwise do not appear to be anemophilous could in fact be wind pollinated. The endemic Galapagos carpenter bee, the only native bee (Nielsen *et al.*, 2002), is the primary insect pollinator (it has been at least observed at flowers of 79 taxa including 25 endemics) in the Galapagos (McMullen, 1987, 1990, 1993; McMullen & Close, 1993). A variety of other insects have been seen on Galapagos plants (McMullen, 1993; Philipp *et al.*, 2004), but their importance as effective transmitters of pollen versus simply random visitors is questionable. Other studies indicate that a variety of insects visit flowers of the same species, and visitors may vary by island, or the visitors may be limited and still vary by island (e.g. McMullen & Viderman, 1994). Available evidence for the Galapagos indicates that autogamy is quite common (Rick, 1966, McMullen, 2007, 2009, but additional study is needed), while generalist insect pollinators and wind pollination are relatively uncommon.

Sakai *et al.* (1995b) inferred the pollinators of the colonists of the native flora of Hawaii, and suggested that the majority were insect pollinated, with about half as many wind pollinated; much less frequent were bird pollination and self-pollination. Price and Wagner (2004) listed insects as the most frequent mode of pollination in native angiosperms, with abiotic and bird pollination equally frequent but much rarer than insects. As with any archipelago, the more ancient the initial colonisation of an archipelago the more difficult it becomes to infer with certainty the original pollinators of the ancestors of current lineages.

A wide variety of generalist insect pollinators has been observed in the relatively insect-rich Canary Islands (Forfang & Olesen, 1998; Garcia, 2000; Olesen *et al.*, 2002a; Dupont & Skov, 2004; Dupont *et al.*, 2003). Other than possible wind pollination of the Canary Island date palm (Meekijjaroenroj & Anstett, 2003), we are unaware of reports of wind pollination in the Canaries. However, despite the



Figure 2.3 Hermaphroditic flower of *Solanum vespertilio* subsp. *vespertilio* from plant on Tenerife, Canary Islands, Spain. Scale line = 4.0 cm. Photo by G. J. Anderson.

lack of known reports, members of families such as Chenopodiaceae, Cyperaceae, Myricaceae, Poaceae and Urticaceae (Bramwell & Bramwell, 2001) almost certainly are wind pollinated, and there are no doubt many other wind-pollinated plants in the archipelago. Bird pollination is apparently limited to fewer than 10 species in the Canaries (Olesen, 1985; Dupont *et al.*, 2004; Valido *et al.*, 2004), with pollination by non-specialist opportunistic nectar feeders common (Rodríguez-Rodríguez & Valido, 2008; Ollerton *et al.*, 2009). In addition to generalist pollinators, there are also instances of dedicated bee pollination, one example being the endemic *Solanum vespertilio* (Anderson *et al.*, 2006a; Prohens *et al.*, 2007; Fig. 2.3).

The Ogasawara (Bonin) Islands consist of a group of small (largest less than 25 km²) volcanic islands situated some 1000 km south of the southern tip of Japan (Abe, 2006). The oldest islands have been above sea level for several million years. The most abundant native pollinators are insects (over 70% of the species), followed by 26% of the species (mostly grasses and sedges) pollinated by wind (Abe, 2006).

A plausible explanation for this combination of features – small, dull-coloured, open, inconspicuous, hermaphroditic flowers on islands – is that they can be pollinated by the few small, generalist insects (e.g. solitary bees, flies) present, and known to visit flowers. As indicated by Carlquist (1966c), the lack of long-tongued bees and larger Hymenoptera on islands ‘disfavors many angiosperms with larger and more colorful flowers’ other than bird-pollinated species. Bernardello *et al.* (2001) suggest that the open shallow flowers may be suitable for wind pollination. In addition, autogamy could function as a pollination mechanism. While the

hypothesis of 'typical' floral morphology of island plants being related to pollination seems reasonable and available data support it, more careful field studies are needed to provide more rigorous tests of the hypothesis. The question of whether wind pollination is more frequent on islands remains open. For example, perhaps for 'young' islands with depauperate pollinator faunas like the Robinson Crusoe Islands wind pollination may be frequent but, even here, a substantial 40% of the flora is unknown in terms of field pollination studies (Bernardello *et al.*, 2001).

Sex of flowers and separation of sexes

As indicated above, there is considerable monotony among many island flowers but there has also been floral diversification in some lineages. The majority of species native or endemic to islands have hermaphroditic flowers: estimated values include over 60% for Hawaii (Wagner *et al.*, 1990), over 70% for the Robinson Crusoe Islands (Bernardello *et al.*, 2001), 75% for the Ogasawara Islands (Abe, 2006) and over 80% for the Canary Islands (Francisco-Ortega, unpubl., cited in Helfgott *et al.*, 2000) and for the Galapagos (McMullen, 1990, 1999). Among species with hermaphroditic flowers available evidence, meagre as it is, indicates that the majority are SC (e.g. Carlquist, 1974: 516–519; McMullen, 1990; Calero & Santos, 1993; Bernardello *et al.*, 2001). An important and interesting question for which there is little information is how these two floral features (hermaphroditic and SC) translate into the actual mating systems in island plants. On the one hand, autogamy would result in largely selfing populations, as appears to be the case in the Galapagos (McMullen, 1990), but on the other hand there are floral mechanisms that could promote outcrossing in SC hermaphroditic plants.

Consider some mechanisms for promoting outcrossing in SC hermaphroditic island plants. One such mechanism is dichogamy (protandry and protogyny). While dichogamy could greatly reduce autogamy, that does not necessarily mean that it promotes outcrossing because pollen could be transferred between different flowers on the same plant (geitonogamy), as appears to be the case in some plants of the Robinson Crusoe Islands (Anderson *et al.*, 2001a; Bernardello *et al.*, 2001). Barrett (2003) questioned the adaptive significance of dichogamy for promoting outcrossing because it frequently occurs in SI plants. However, in such instances, dichogamy (or herkogamy) may be beneficial because it reduces pollen 'clogging' by self pollen, in essence, interference that could reduce the occurrence or effectiveness of outcrossing. Whether this is the general situation in island plants is not known, and is in need of further study; however, the compilation found in Bernardello *et al.* (2001, table 1) shows that for species for which information is available, dichogamy and SC occur together. While the level of autogamy can be determined by bagging experiments, when a pollinating agent is required molecular markers (usually

allozymes or microsatellites) of progeny arrays provide the best estimates of the levels of selfing and outcrossing in natural populations. Unfortunately, such studies are essentially non-existent for island plants (but see discussion of *Bidens* below).

The most efficient mechanism for promoting outcrossing in hermaphroditic flowers is total SI, which precludes selfing. As indicated above, SC appears to be the common condition in island plants, but examples of SI are known, and emerging evidence indicates that the situation may not be as simple as has generally been reported or envisioned. Earlier workers such as Baker (1955, 1967), Stebbins (1957) and Carlquist (1974) envisioned the SC system as a logical feature of the establishment of plants, perhaps single plants, but at least a few individuals, on remote islands with little flora and perhaps few or likely no appropriate pollinators. Two elements of this argument will be considered. First, just conceptually, the tacit assumption in making the wholly logical proposition of SC being 'a' or 'the' reasonable system for early establishment is that the whole flora arrived at the same 'ecological' time in the sense that the islands were 'bare' or lacking other plant species, or pollinators. That certainly must be the case for early-arriving species. But, island floras are built over time, not all at once, and clearly many species arrive later in the geological evolutionary history of islands. The later arrivals may still have to deal with the issues of few propagules, and SC is advantageous. However, those later arrivals may have available a more diverse pollinator fauna than some of the early arrivals, and thus be able to have the pollen moved among their progeny at a level that was not available to the progeny of the first arrivals. Second, we will consider several examples showing that the SC system is not always clear cut. Studies by Rick (1966), McMullen (1987) and McMullen and Naranjo (1994) indicated that four of the species of *Scalesia*, the largest endemic genus in the Galapagos, are SC and do not require a vector for pollination. However, one of those species, *S. affinis*, was examined by Nielsen *et al.* (2003) and found to be partially SI and a second species, *S. divisa*, was highly SI (Nielsen *et al.*, 2000). Studies of additional island endemics such as the silversword alliance in Hawaii (Carr *et al.*, 1986) and *Tolpis* in the Canary Islands (Crawford *et al.*, 2008) show that, while apparently fundamentally SI, there can be considerable inter-populational variation in compatibility, with significant 'leakiness' in the system. In one species of *Tolpis* in the Canaries there has been total breakdown of SI, even accompanied by some floral characters associated with SC. Studies using molecular markers show that some of the 'SI' populations have mixed mating systems, with about a 1:1 mix of outcrossing and selfing (Crawford *et al.*, unpubl.).

Of course, an additional advantage of a partially SI breeding system in islands is reproductive assurance via SC when pollinators are limiting. Populations could be established from dispersal of single propagules into new areas during radiation and diversification and, because the single dispersal unit is from a highly outcrossed

population, it would presumably carry more genetic diversity than if it were from an SC population. More work is needed to elucidate the mating systems of island plants that are basically SI but display various levels of leakiness. It appears that some of the most successful insular lineages, especially in Compositae, are SI or with 'leaky' SI (Crawford *et al.*, 2009).

While hermaphroditic flowers are most common in islands, a variety of other sex expression patterns are known. The more common conditions, among others, are monoecy, andromonoecy, gynomoecy, dioecy, subdioecy and gynodioecy (e.g. Sakai *et al.*, 1995b; Helfgott *et al.*, 2000; Bernardello *et al.*, 2001). The first three, along with hermaphroditism, are sometimes designated monomorphic systems while the latter three are termed dimorphic (Lloyd, 1980; Sakai *et al.*, 1995b). One question of interest about sex expression in island plants is whether a given condition was present in the coloniser or evolved *in situ* in the island setting. Estimates for Hawaiian endemic species indicate that 11% of the colonists were dimorphic and gave rise to only dimorphic species. By contrast, nearly one-third of dimorphic species had monomorphic colonising ancestors (Sakai *et al.*, 1995b). In the Robinson Crusoe Islands, four dimorphic genera appear to have originated from dimorphic colonists whereas three genera ostensibly arose from monomorphic colonists (Bernardello *et al.*, 2001). Of all the systems, only strict dioecy (like complete SI in hermaphroditic flowers) results in obligate outcrossing, and so in a sense it is different from other forms of sex expression. An important question is how the different forms of sex expression influence mating systems in populations of island plants. Unfortunately, empirical studies of the question are largely lacking.

A study by Sun and Ganders (1988) is an example of the influences and complexities of breeding system, sex expression and dichogamy (protandry) on the mating system in Hawaiian *Bidens*. The approximately 20 endemic Hawaiian *Bidens* originated from a single introduction (Ganders *et al.*, 2000) but the extant species are diverse morphologically and ecologically (Ganders & Nagata, 1984). The clade has capitula with sterile ray florets, but there is variation in sex expression of the disk florets. Some species have hermaphroditic, SC, strongly protandrous disk florets whereas female (totally male sterile) disk florets and totally hermaphroditic disk florets occur in separate flowers on separate plants in other species (they are gynodioecious). Allozyme markers of progeny arrays and seed set without pollinators were used to estimate mating system in populations. Low seed set without pollinators indicates that protandry is effective in preventing autogamy. Gynodioecy is normally viewed as a mechanism for promoting outcrossing in SC plants, and it evolved *in situ* in Hawaiian *Bidens* (Sun & Ganders, 1986, 1988). Sun and Ganders (1986) found a positive correlation between frequencies of females and selfing rates of hermaphrodites, evidence supporting the contention that females are established

and survive in part because their outcrossed progeny are more fit than the selfed progeny of hermaphrodites. Sun and Ganders (1988) explored the components of inbreeding (autogamy, geitonogamy and biparental inbreeding) in populations with gynodioecious and hermaphroditic individuals. Autogamy can be estimated directly by seed set without pollinators, and apparent selfing estimated from allozyme markers must be due to biparental inbreeding because neither of the other two forms of inbreeding is possible with female plants. It follows then that selfing via geitonogamy can be estimated indirectly by subtracting estimates of the other two forms of inbreeding from the estimate of effective selfing in hermaphroditic flowers. In Hawaiian *Bidens*, mean effective selfing is 0.43, biparental inbreeding is 0.15 and autogamy is 0.04, which indicates that the contribution of geitonogamy to selfing is 0.24. Species of *Bidens* with capitula in compact compound capitulescences had higher levels of geitonogamy than those species with solitary capitula, which is what might be expected (Sun & Ganders, 1988). Hawaiian *Bidens* illustrates the potential complexities of mating systems in an island lineage.

The origin and evolution of dioecy has been one of the most discussed aspects of the reproductive biology of island plants. A central issue is whether dioecy was present in the colonising ancestors or the condition originated in the island setting (e.g. Baker & Cox, 1984; Sakai *et al.*, 1995b; Bernardello *et al.*, 2001). If the colonising ancestors were strictly dioecious, then obviously one propagule could not establish a sexually reproducing population. On the other hand, if the ancestors of dioecious island plants were frequently hermaphroditic, then it would be of interest to know what factor(s) are associated with the evolution of dioecy on oceanic islands. In Hawaii, the present relatively high level of dioecy appears to be the result of both dimorphic colonists and evolution from hermaphroditic colonists in the archipelago (Sakai *et al.*, 1995b). On the Robinson Crusoe Islands, four of the dioecious genera appear to have evolved from colonists that were either dioecious or manifested incipient dioecy while the largest dioecious genus, *Robinsonia*, ostensibly evolved from hermaphroditic ancestors (Bernardello *et al.*, 2001). In the Canary Islands, dioecy in the *Bencomia* alliance (Rosaceae) has apparently arisen twice within the archipelago, either from monoecious or gynomonocious ancestors (Helfgott *et al.*, 2000) and the functionally dioecious *Withania aristata* (Solanaceae) (Fig. 2.4) reputedly originated from an SC colonist (Anderson *et al.*, 2006b). Thus, accumulating data indicate that dioecy on islands does not have one simple explanation; dioecious taxa have originated both from dimorphic colonists and the autochthonous evolution of dioecy in the island setting.

For those lineages originating from dimorphic colonists, it is instructive to examine such features as the probable dispersal unit of their colonising ancestors and possible 'leakiness' in dioecy because either (or both) could facilitate the establishment of sexual populations from a single colonising event. One dispersal

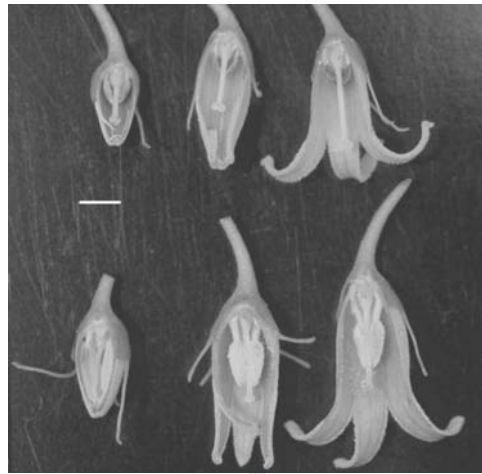


Figure 2.4 Female (top row) and male (bottom row) flowers of *Withania aristata* on Tenerife, Canary Islands, Spain. Scale line = 3.0 cm. Photo by G. Bernardello.

event could be effective in establishing a sexual, dioecious population if the dispersal unit were a fleshy fruit and a bird (the most common dispersal agents, see above) ingested a single multi-seeded fruit or several single-seeded fruits. Sakai *et al.* (1995a) found an association between fleshy fruits and dimorphism for genera in Hawaii. The fleshy fruits were presumably dispersed via bird ingestion. In the Robinson Crusoe Islands, three of the four dioecious genera that presumably originated from dimorphic colonists have fleshy fruits, and likely were ingested and dispersed by birds (Bernardello *et al.*, 2001, 2006). Over 70% of the endemic or native dioecious species in the Canary Islands have fleshy fruits (Bramwell & Bramwell, 2001), and a similar or higher value characterises the Azores (Schäfer, 2005). Lastly, over half of the dioecious natives or endemics in the Galapagos have fleshy fruits (McMullen, 1999).

Consider, next, 'leaky' dioecy (rare occurrence of functionally hermaphroditic flowers in a population) in island colonists as a means of facilitating establishment after long-distance dispersal. If the species is SC, then seed could be produced on the rare hermaphroditic flowers even though a coloniser is largely dioecious. This topic was reviewed by Baker and Cox (1984). Anderson *et al.* (2006b) report the rare occurrence of fruits on male plants of the Canary Island endemic *Withania aristata*, and cite additional examples of the phenomenon from the more recent literature. The frequency of leaky dioecy and its significance in the establishment of dioecious colonists in oceanic archipelagos are largely unknown.

The stage has now been reached, or perhaps was reached much earlier, when there is little point in discussing the relative frequency with which insular dioecious plants originated from dioecious colonisers versus the autochthonous origin

of dioecy in the island setting. It is now evident that both can occur, and detailed phylogenetic-evolutionary-ecological studies of individual island lineages are needed to provide additional insight into the origin and evolution of dioecy. One of the most extensive series of studies of the phylogeny, evolution and ecology of breeding systems (particularly dimorphic ones) in an island lineage is on the genus *Schiedea*, a monophyletic group of some 35 species that originated from a hermaphroditic colonising ancestor (e.g. Sakai *et al.*, 1997, 2006; Culley *et al.*, 1999, 2006; Weller & Sakai, 1991; Weller *et al.*, 1998, 2005). A phylogeny for the lineage (Wagner *et al.*, 2005) indicates that dimorphic breeding systems originated twice and autogamy evolved three times. Dimorphic species usually occur in dry windy habitats and are pollinated by wind whereas autogamous species are generally found in more moist areas (Sakai *et al.*, 2006). The hypothesis is that with shifts to drier, more open habitats there were higher selfing rates due to pollinator loss, resulting in high inbreeding depression. The high inbreeding depression provided selection pressure for a dimorphic breeding system, and the open dry habitat would facilitate wind pollination in areas where biotic pollinators are lacking (Sakai *et al.*, 2006). In contrast, autogamy may have evolved in the small populations of very wet areas, and the small, pendent flowers would be 'sheltered' from heavy precipitation. Similar comprehensive studies on other island lineages and other archipelagos would be most helpful in achieving a deeper understanding of the evolution of complex breeding systems and the factors that may shape them.

Conservation of island plants: reproductive biology and the impact of invasive plants and pollinators

It almost goes without saying that reproductive biology is among the most important aspects of the conservation of island plants. Any study of reproductive biology should include its conservation implications (Holsinger, 1991; Anderson, 1995; Anderson *et al.*, 2001a, 2001b; Bernardello *et al.*, 1999, 2001, 2004; Dupont & Skov, 2004; Abe, 2006). Conservation issues may be particularly complex when both plants and pollinators are involved (Inoue, 1993; Kearns *et al.*, 1998). Important factors in formulating conservation strategies include breeding and mating systems, and cross-compatibility and interfertility among congeneric species. Lastly, the influence of invasive species, both plants and pollinators, may have an impact on the reproductive biology of island plants (Anderson *et al.*, 2001b; Dupont *et al.*, 2003; Abe, 2006). In many instances, it is the rarity of island species that makes reproductive biology of such critical concern in conservation; Weller (1994) reviewed some of the important relationships between rarity and reproductive biology, and many of the issues he raised are relevant to island plants. Basically, the challenge for a rare plant on an island (or anywhere) is finding a compatible mate of

the same species, with the fitness of their resulting progeny sufficient for survival and reproduction. Conservation strategies are aimed at increasing the likelihood of this happening, considered in the context of what is known about the reproductive biology of the species.

A case study from the Robinson Crusoe Islands illustrates some of the conservation implications of reproductive biology mentioned above. Bernardello *et al.* (2004) studied *Sophora fernandeziana* (Leguminosae), which has been classified as endangered because of the small size and number of extant populations (Ricci, 2006). The results of Bernardello *et al.* (2004) were not totally conclusive, but indicate strongly that the species exhibits ovarian SI, which is known for other legumes. If indeed the species is SI, then the lack of compatible mates in the very small populations, and especially if individual plants become isolated, would be a serious impediment to seed set. Genetic (allozyme) diversity in the species is quite low, even by island standards (Crawford *et al.*, 2001). The pollinators of the plant are two species of hummingbird, one endemic and the other native, and they obtain nectar from *S. fernandeziana*. When it is blooming there are few other species from which the birds can get nectar (Bernardello *et al.*, 2004). This system is an example of a mutualism where a decline in either the plant or the pollinator would have a negative effect on the other. Another possible negative factor for *Sophora* on the Robinson Crusoe Islands is invasive plant species such as *Rubus ulmifolius* (Rosaceae), which can outcompete native species (Stuessy *et al.*, 1998; Greimler *et al.*, 2002). In addition, if an invasive species could provide nectar for the hummingbirds at the same time that *S. fernandeziana* is blooming and the invasive also occurs in greater density, which is a certainty, then *Sophora* would suffer from lower bird visitation and pollination. The low seed set observed by Bernardello *et al.* (2004) in a natural population of *S. fernandeziana* is a clear indication that one or more of the factors mentioned above, and possibly others, act in concert to reduce greatly the production of viable seeds.

The impact of invasive plants and pollinators on endemic and native plants and animals in insular biotas is receiving particular attention by island biologists. Efforts to understand the role of invasives in the reproductive biology of island plants and their pollinators are particularly important because the more frequent travel to many islands by tourists and other visitors will increase the introduction of alien elements into insular biotas. *A priori* predictions or broad generalisations about the impact of invasives may not be warranted for many individual situations. Rather, detailed observations, especially over time, are needed to elucidate the effects of invasive species on individual endemics, both plant and pollinator, or the impact on the dynamics of plant-pollinator networks (Kearns & Inouye, 1997; Kearns *et al.*, 1998; Cox & Elqvist, 2000; Olesen *et al.*, 2002b; Dupont *et al.*, 2003; Abe, 2006).

The impact of introduction of pollinators could be positive or negative, or perhaps both, in particular situations. For example, the impacts of the presence (or at least documented occurrence) of bees, possibly a new species (Engel, 2000), on Robinson Crusoe Island during the past 30 years are not yet apparent (Anderson *et al.*, 2001b). The bees are found almost exclusively around the single village, and have not yet been detected on native-endemic plants in native habitats (Anderson *et al.*, 2001a, 2001b; Bernardello *et al.*, 2001). Given the essentially total lack of bee pollinators on Robinson Crusoe, it is conceivable that the bees could be effective pollinators of some endemic largely (by necessity) wind pollinated species that retain features such as colourful corollas and nectar rewards from their presumed biotically-pollinated ancestors (Anderson *et al.*, 2001a, 2001b; Bernardello *et al.*, 2001). On the negative side, if the bees were to take nectar from species pollinated by the one native and one endemic hummingbird species, then the hummingbirds could suffer from loss of their limited food sources. Or, if the bees prefer the often more abundant floral rewards of the invasives, they may indirectly facilitate the spread of the invasives at a cost to the natives.

In the Bonin Islands there are observations suggesting that introduced honeybees are displacing endemic visitors to plants (Abe, 2006). For example, on the two main islands of the archipelago, honeybees visited about 60% of the observed plant species. By contrast, on smaller satellite islands lacking honeybees, endemic small bees were the most frequent visitors to the majority (about 65%) of the native species. It is clear that the honeybees, and other introduced pollinators such as wasps and butterflies, could have a major impact on pollinator networks in the Bonin Islands, and on the native bee fauna. More recently, Abe *et al.* (2008) have shown that an invasive lizard is a threat to native pollinators on the Bonin Islands.

Dupont *et al.* (2003) studied the network (interactions among different plants and animals) of plants and their flower visitors in the subalpine high desert on Tenerife in the Canary Islands. This habitat has a short growing season, and the plants and animals are nearly all endemic or native to the Canaries. One exception is the introduced honeybee, which is very abundant in the subalpine zone. Dupont *et al.* (2003) state that they cannot at present assess the impact, if any, of the honeybees on the interactions among native plants and animals. However, because the honeybees visit more than half of the plant species, and they are very efficient at collecting resources from the plants, there is the potential for the bees to outcompete native visitors.

Dupont and Skov (2004) studied bee visitors to members (20 endemic and one introduced species) of the plant genus *Echium*, one of the largest and most diverse radiations in the Canary Islands (Bramwell & Bramwell, 2001). They found that the only good predictor of the richness (number of species) of bees visiting species of *Echium* was the distribution range of the plant species. That is, more widely distributed plant species were visited by more bee species. A species introduced

into the Canary Islands, *Echium plantagineum*, has spread over several islands; it occurs with endemic congeners, is more widespread than any of the endemic species and attracts the same suite of bee visitors as the endemic species. In fact, the introduced species attracted a higher number of bee species than any of the endemics. One of the conservation concerns is whether the introduced plant species will compete with the endemic taxa for pollinators and, since most species of *Echium* are obligately outcrossing, seed set could be reduced in the endemic taxa. Another potential conservation implication of the introduced plant species is its hybridisation with the less abundant endemic species; the results would vary depending on the fertility and vigour of the hybrids (Levin *et al.*, 1996; Francisco-Ortega *et al.*, 2000). For example, if hybrids are vigorous and fertile, then the rarer endemics could be assimilated by the alien species.

It is evident from the above discussion of specific examples that an accurate assessment or prediction of the impact of invasives, whether plant or animal, in any given situation, requires basic information on many aspects of the reproductive biology of both native and endemic plants.

Future studies

Regardless of the area of biological research, it is always fashionable, and probably valid, to say that what is needed in the future is more of the same kinds of studies that have already been done, as the quote in the opening paragraph from H. G. Baker advocated. In addition, we suggest that more basic, meticulous studies of the reproductive biology of island plants such as breeding systems, pollinators and mating systems (Neal & Anderson, 2005) are needed. This is true because very few species have been critically examined, and in more than a few cases such studies have shown that the situation is more complex or subtle than it appears from casual observation. Several examples include: flowers appearing to be hermaphroditic may be functionally dioecious; the role of biotic pollinators versus wind in the pollination of 'typical' (small, shallow, colourless) island flowers; and the significance of 'leaky' SI and 'leaky' dioecy in colonisation and the subsequent diversification of island lineages. Superficial observations of island plants may lead to interpretations of reproductive biology that are heavily influenced by results from continental species. While island plants are often viewed, and correctly so, as wonderful bizarre organisms in general habit and vegetative features, it is evident that in some instances evolution to the island habitat has involved very subtle or cryptic changes in reproductive biology. Additional studies may call into question, or at least reveal many additional exceptions to, some of the more popular generalisations about reproductive biology of island plants.

It would also be desirable to have more highly integrated studies in which more traditional investigations are combined with additional approaches. For example,

molecular markers (e.g. allozymes, microsatellites, etc.) could be employed to estimate outcrossing rates; data from field observations of pollinators, floral morphology (separation of sexes) and breeding system studies would provide insight into the factors yielding the observed mating system.

As indicated in the introduction, molecular phylogenetic studies of island plants have flourished over the past 20 years, but with the notable exceptions of several investigations cited earlier, there have been relatively few attempts to examine reproductive biology within a phylogenetic context. This applies both to the colonising ancestors of insular lineages as well as within the lineages themselves.

In closing, it is appropriate to place future research on islands within a global perspective. Islands are scattered throughout the oceans of the world, and are under the political jurisdiction of many different countries. These geographical and political factors create challenges to those wishing to do research on oceanic islands, including the logistics of getting to the islands and of obtaining access to facilities and personnel for research in the islands. Acquiring the necessary permissions to work in an archipelago can be a daunting task. Studies of plant reproductive biology of island plants may be especially challenging because of the time, effort and local assistance required for locating, observing and manipulating plants in natural populations. In this regard, there is a need for a research coordination network in which basic information on the logistics of getting to and working on islands is available.

Another challenge for those working on oceanic islands is being aware of similar projects or efforts occurring in different archipelagos around the world so that information on methodology, etc., could be shared. Island researchers often work in geographic isolation, and local researchers in smaller archipelagos may not have easy access to current developments in theory and practices related to ecological, evolutionary and conservation issues of common concern. As discussed earlier, information on reproductive biology is critical for formulating conservation strategies. Thus, the sharing of basic information and observations, some of which have not and perhaps never will be published, on breeding systems, pollinators and mating systems of both native and invasive species on a global scale is an especially important component of any plan to conserve the vulnerable plant treasures often teetering on the brink of extinction on small specks of lava in the vast oceans of the world. Clearly, it is past time for those interested in preserving these treasures to develop a vehicle for sharing information and coordinating efforts in this important enterprise.

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