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The Reproductive Biology and Genetics of Island Plants [and Discussion]

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The reproductive biology and genetics of island plants

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SUMMARY

Island and mainland populations of plants often differ in their reproductive biology and genetics. The differences become more pronounced the further islands are from mainland sources. Altered pollination conditions have influenced the floral biology and mating systems of island plants in distinct ways. Insufficient pollination has favoured selection of floral traits promoting selfing. In contrast, inferior pollinator service resulting in selfing and inbreeding depression appears to be a factor involved in the evolution of sexual dimorphisms. Stochastic forces play a major role in governing patterns of genetic variation. Island populations are usually more differentiated and contain less diversity than comparable mainland samples. Many general issues in evolutionary biology can be addressed by studies of reproduction and genetics in island plants.

1. INTRODUCTION

Islands have long held a fascination for biologists and those interested in natural history. The distinctive biotas of oceanic islands were of considerable significance to Darwin and Wallace in developing their ideas on evolution and the recognition that islands act as 'evolutionary laboratories' has stimulated considerable modern work on the systematics, genetics and ecology of island groups. This research has provided some of the clearest evidence for the mechanisms responsible for evolutionary diversification and has contributed significantly to the development of ecological and evolutionary theory. Why do islands provide such a rich source of biological novelty for evolutionary enquiry? The answer to this question is not always obvious although their unsaturated habitats, non-equilibrial communities, unique biotas and isolation from recurrent gene flow have all been implicated as playing a role in directing evolutionary responses distinct from those observed in related continental taxa. In addition, stochastic forces involving founder events and genetic drift have also been frequently invoked to account for the unusual patterns of variation that occur in many island groups.

Most work on island plants this century has been systematic or biogeographic in focus addressing issues concerned with endemism, adaptive radiation, and the phylogenetic history of island taxa (Carlquist 1974; Bramwell 1979; Wagner & Funk 1995). Despite their capacity for long-distance dispersal, comparative investigations of the ecology and genetics of continental and island plant populations are few compared to the sizable literature for many animal groups (reviewed in Frankham 1996). Studies of this type are important for assessing whether the genetic systems of island populations are distinct from those on the mainland and for testing theories concerned with the population genetic consequences of long-distance migration and the role of genetic bottlenecks in evolution (Carson & Templeton 1984; Barton 1989). The paucity of such comparisons may be because following establishment many plant groups, particularly those on oceanic islands, diversify rapidly in morphology and ecology as a result of adaptive radiation (e.g. Carr *et al.* 1989; Ganders 1989). It is therefore often difficult to determine ancestral relationships and explicit continent – island comparisons are usually not possible. Archipelagos that are less isolated and closer to the mainland can sometimes offer more rewarding model systems for intraspecific studies on the microevolutionary processes associated with island colonization.

Successful colonization and establishment on islands for any group of organisms will be influenced by their life histories and reproductive systems. The predominantly hermaphrodite condition of most plant species combined with self-compatibility has been proposed as an advantage in enabling establishment following long-distance dispersal (Baker 1955). The requirement for specialized animal pollinators by some species may, in contrast, be an impediment to island establishment if particular pollinators are absent. Species with floral syndromes capable of being serviced by a range of pollinators may be more likely to succeed on some islands. These issues raise the question of how much the distinctive nature of some island floras reflects selection of particular traits during establishment or whether characteristics of island plants have evolved autochthonously due to special ecological circumstances on islands.

In this paper I review the growing literature concerned with the reproductive biology and genetics of island plants. Several questions often raised when considering the evolutionary biology of island groups are addressed. Are the pollination biology and mating systems of island plants different from the mainland and if so why? What role have stochastic forces played in the reproductive biology and genetics of island plants? Do island populations of plants contain less genetic diversity than those from the mainland? Islands vary enormously in size, geographical isolation, topography, climate and ecology and are therefore by no means a homogeneous group. As a result equivocal results for the above questions may sometimes be obtained. Despite this caveat I hope this review, by pointing out gaps in our knowledge, will draw attention to future work that needs to be undertaken on the reproduction and genetics of island plants.

2. POLLINATION BIOLOGY OF ISLAND PLANTS

Islands usually support fewer animal species than occur on comparable mainland areas (MacArthur & Wilson 1967). Pollinator faunas on islands are often depauperate with important groups of pollinators either absent or poorly represented. In the Hawaiian islands, for example, only 15% of known families of insects are represented with only six native species of hawkmoths, two species of butterflies, and no bumble bees (Howarth & Mull 1992). Small moths and flies are disproportionately represented as pollinators. Among the Galápagos Islands few insects are reported as pollinators and only one species of pollinating bee occurs (*Xylocopa darwinii*, McMullen 1987). Long-tongued bees and hawkmoths are entirely absent from New Zealand and no genuine case of a plant adapted to butterfly pollination has been reported (Lloyd 1985). Instead, flies are the predominant pollinators with beetles, wasps and small moths also playing some role. Such groups usually forage promiscuously visiting a broad range of taxa, thus reducing opportunities for specialized plant – pollinator interactions to evolve. The disproportionate representation of small insects on oceanic islands probably reflects their superior migratory abilities.

The pollination biology of mainland and island populations of individual species has seldom been compared. The limited data that are available indicate that patterns of pollinator visitation usually differ. Spears (1987) found significant differences in pollinator diversity and visitation rates between island and mainland populations of *Centrosema virginianum* and *Opuntia stricta* on the west coast of Florida. Differences in the quantity and quality of pollinators visiting flowers of the two species were shown to influence components of female and male reproductive success. Similarly, Inoue *et al.* (1996) found reduced pollinator diversity and visitation rates between mainland and island populations of *Campanula* taxa with declines in both with distance of the island from the Japanese mainland. Differences in the diversity and rates of floral visitation by hummingbird species between Trinidad and Tobago, two islands which differ in size and distance from the mainland, have also been shown to have important reproductive consequences to conspecific taxa occurring on them (Feinsinger *et al.* 1982).

(*a*) *Floral biology*

What evidence is there that the floral biology of island plants differs significantly from mainland sources as a result of altered pollination conditions? Several authors have drawn attention to the low representation of brightly coloured, tubular, zygomorphic flowers on oceanic islands and instead a high frequency of small, white or green non-showy flowers with simple bowl-shaped corollas (Carlquist 1974). Nowhere is this contrast more evident than in the floras of Australia and New Zealand (Webb & Kelly 1993). Many Australian species possess showy complex flowers while those in New Zealand are commonly dull, white and unspecialized. These differences are often maintained within genera that occur in both areas and are probably associated with the relative importance of promiscuous flies and other generalist flower visitors for pollination in the two regions. The contributions of allochthonous versus autochthonous origins in accounting for the small, unspecialized flowers of island floras such as New Zealand is not known. Lloyd (1985) developed a simple method to estimate the relative importance of these two processes based on the character states present in related taxa in the presumed source region. Modern methods of phylogenetic reconstruction offer an alternative and more sophisticated approach for inferring the origins of reproductive traits.

Microevolutionary investigations of taxa with island and mainland populations provide opportunities to determine whether the reproductive consequences of altered pollination conditions have resulted in evolutionary responses. Inoue *et al.* (1996) found that variation in flower size among mainland and island populations of *Campanula* taxa was associated with different pollinators visiting populations. A significant positive relation was observed between the mean flower width of populations and the mean body size of pollinators. In mainland and offshore island populations, which have larger flowers, the predominant pollinators were bumblebees and megachilid bees. In contrast, in islands further from the mainland where populations possess smaller flowers, halictid bees were the main pollinators. Experimental studies on the preferences of these bees demonstrated that pollen-collecting halictids were indifferent to flower size whereas nectar-feeding megachilids and bumblebees preferred flowers of larger size. These results are consistent with the hypothesis that pollinator-mediated selection maintains variation in flowers size among mainland and island populations of *Campanula*.

(*b*) *Wind pollination*

The apparently high incidence of wind pollination on some oceanic islands has prompted several authors to propose adaptive hypotheses on the benefits of wind pollination on islands (Carlquist 1974; Ehrendorfer 1979). These involve the following ideas: (i) wind-pollinated taxa are favoured over animal-pollinated taxa during island establishment because of their independence from pollinators; (ii) strong winds and inclement weather conditions on some islands favour wind pollination over animal pollination; and (iii) wind pollination is more effective than animal pollination in promoting pollen dispersal and the associated benefits of outcrossing. Before adaptive hypotheses are tested it is important to determine whether wind pollination is indeed more frequent on islands compared to mainland source areas. This is by no means clear. On the Galápagos Islands, for example, several authors have commented on the paucity of wind-pollinated taxa (McMullen 1987). Moreover, because wind pollination on islands is often associated with life-history features such as woodiness and dioecy (Lloyd 1985; Sakai *et al.* 1995*a*), it is important that these potentially confounding factors are assessed using comparative approaches. However, where the autochthonous evolution of wind pollination from animal pollination has occurred (e.g. *Schiedea*, Weller *et al.* 1995), excellent opportunities for investigating the selective forces responsible for this shift in pollination system are provided. Studies on this topic are of general significance as the change from animal to wind pollination is one of the most important evolutionary trends in flowering plants, yet little is known about the microevolutionary processes that are responsible.

3. EVOLUTION OF MATING SYSTEMS

Studies of reproduction in island plants have been dominated by two central questions in mating-system biology: the evolutionary forces responsible for different amounts of self- versus cross-fertilization in populations; and the selection of combined versus separate sexes. Several island groups have been used as experimental systems for addressing these problems.

(*a*) *Evolution of self-fertilization*

Baker's Rule (1955) proposes that self-compatible rather than self-incompatible plants will be favoured in establishment following long-distance dispersal to islands. This is because a single self-compatible immigrant is sufficient to initiate a sexually reproducing colony. Surveys of the compatibility status of island plants are rudimentary, but what data do exist strongly support the prediction that self-incompatible species are disadvantaged during island colonization and establishment. The floras of New Zealand (Webb & Kelly 1993), Hawaii (Carr *et al.* 1986) and the Galápagos (McMullen 1987) are deficient in taxa possessing homomorphic or hetermorphic incompatibility compared to continental areas. The predominance of self-compatible plants on the Galápagos Islands probably results from the scant insect fauna and availability of extensive pioneer habitats. These ecological factors are known to favour the evolution of self-compatibility.

Insufficient pollination caused by a paucity of pollinators favours floral traits that promote increased levels of selfing in self-compatible island colonists. Several comparative studies of mainland and island taxa have documented reductions in flower size and the loss of floral adaptations that promote cross-pollination associated with island colonization (e.g. Barrett 1985; Barrett & Shore 1987; Inoue *et al.* 1996). In the Mediterranean the 14 *Nigella* species in Greece and Turkey are largely outcrossing but on Aegean Islands the two endemic species have small flowers and are predominantly selfing (Strid 1969). A revealing contrast involves the distribution of the outcrossing *N. degenii* and selfing *N. doerfleri* among the Kikladhian Islands. Whereas the outcrossing species is confined to large and more topographically complex mesic islands, the selfer occurs on these islands and a series of much smaller, low and more arid islands. This pattern would be expected if repeated cycles of colonization and extinction on smaller islands favoured selfing immigrants because of their ability to establish colonies without the requirements of insect pollinators.

In the Caribbean similar biogeographical patterns involving island size and the distribution of selfing and outcrossing forms are evident in *Turnera ulmifolia*, a complex of perennial weeds composed of self-incompatible distylous and self-compatible homostylous forms (Barrett & Shore 1987). In this group island colonization favours selfing homostylous forms, however, on larger islands such as Jamaica selection to increase outcrossing through herkogamy in homostyled colonists may explain the complex patterns of floral variation that occur. The open bowl-shaped flowers of *Turnera* are relatively unspecialized and levels of pollinator visitation on Jamaica are sufficient to enable moderate levels of outcrossing to occur (Belaoussoff & Shore 1995).

In the self-compatible, tristylous, annual aquatic *Eichhornia paniculata*, a particularly striking biogeographical pattern of mating-system variation is evident between continental and island populations (Barrett *et al.* 1989; Barrett & Husband 1990*a*). In N. E. Brazil, the centre of the range for the species, most populations are tristylous, serviced by long-tongued anthophorid bees and outcrossing. In contrast, in Jamaica pollinator visitation to *E. paniculata* is extremely low and selfing is high. Unlike *Turnera*, the flowers of *E. paniculata* are tubular, zygomorphic and for effective cross-pollination require long-tongued pollinators. Two floral morphs of *E. paniculata* occur in Jamaica with very different frequencies. The dominant morph is a self-pollinating, mid-styled variant, while the other morph occurs sporadically in approximately one third of the island's populations and is an unmodified long-styled morph. The morphs differ dramatically in mating patterns and fertility owing to their differences in floral morphology. The close proximity of sexual organs in the mid-styled variant promotes high selfing and assures abundant seed set. In the long-styled morph, anthers and stigmas are widely separated promoting high outcrossing but preventing autonomous self-pollination. Because in Jamaica levels of pollinator visitation to *E. paniculata* are so low this morph is unable to found colonies, as indicated by the absence of populations fixed for this form, and in dimorphic populations it suffers severe reductions in fertility compared with the mid-styled variant. If these fitness asymmetries persist the long-styled morph should become extinct on Jamaica. However, because this phenotype is governed by recessive alleles (see below) selective elimination could be quite protracted.

If selfing is adaptive under Jamaican conditions, why have mating-system modifier genes not spread in the long-styled morph? Studies on the inheritance of the stamen modifications that cause autonomous

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selfing in mid-styled variants indicate that a small number of recessive genes are responsible (Fenster & Barrett 1994). These modifiers have no phenotypic effects when transferred into long-styled plants, presumably because they are morph-limited in expression. Does this imply that genetic constraints prevent the long-styled morph from evolving a selfing habit? The recent discovery of small disjunct populations of *E. paniculata* in Nicaragua and Mexico composed exclusively of an autogamous variant of the long-styled morph suggest otherwise. Preliminary studies on the inheritance of this phenotype indicate that the floral modifications responsible for selfing are polygenically controlled (S. C. H. Barrett, unpublished data).

The contrasting patterns of floral variation in *E. paniculata* may be explained by founder events and the alternative genetic pathways to selfing that occur in the long- and mid-styled morphs. Allozyme studies (Husband & Barrett 1991) indicate that populations on Jamaica are descended from two separate colonization events with at least one involving a mid-styled plant heterozygous at the *M* locus governing mid- (*Mm* or *MM*) versus long-styles (*mm*). In contrast, in Central America the mid-styled morph is missing implying that migration only involved the long-styled morph. Because of homozygosity at the *M* locus, the mid-styled phenotype cannot arise through segregation from long-styled plants. The contrasting morph structure of populations in the two regions is likely to mean that the selection dynamics of selfing genes will be quite different. Selection for selfing in Jamaica by a small number of favourable recessive modifiers has probably occurred much more rapidly than in Central America where polygenic variation is responsible. It is possible that because of these different modes of inheritance, the likelihood of selfing evolving in the long-styled morph is conditional on whether the mid-styled morph is present or absent from populations.

An important issue for understanding the evolution of mating systems in Jamaican populations of *E. paniculata* concerns their genetic load. Theoretical models predict that inbreeding depression should evolve with the mating system, with selfing populations maintaining significantly less inbreeding depression than outcrossing populations due to selective purging of deleterious recessives in inbred populations (Charlesworth & Charlesworth 1987). Experimental work on populations of *E. paniculata* with known rates of selfing support these predictions (Barrett & Charlesworth 1991). Studies on six predominantly inbreeding populations sampled in Jamaica have failed to detect inbreeding depression for both vegetative and reproductive traits when grown in the glasshouse and compared under both competitive and non-competitive conditions (figure 1; P. Toppings & S. C. H. Barrett, unpublished data). These results are in contrast to several recent studies that have found moderate to high levels of inbreeding depression in selfing species (see Lande *et al.* 1995).

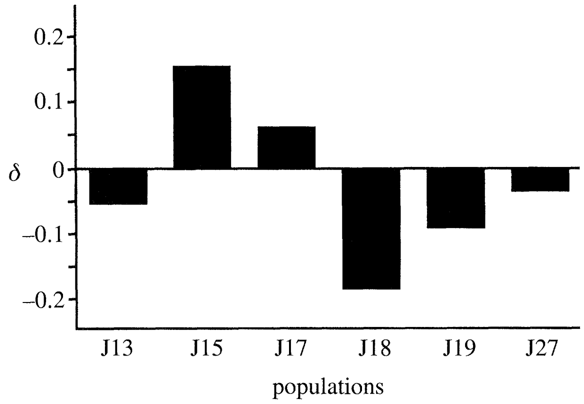

Figure 1. The occurrence of weak or no inbreeding depression (δ) in six predominantly selfing populations of *Eichhornia paniculata* from Jamaica. Estimates were based on multiplicative measures of parental seed set following self and outcrossing*percentage germination of seed*flower production of selfed and outcrossed offspring. All comparisons were made in the glasshouse and involved 6–10 families per population and 6–10 offspring per pollination treatment grown under non-competitive conditions.

The failure to detect significant inbreeding depression in Jamaican populations of *E. paniculata* may be because comparisons were made under glasshouse rather than field conditions. Although an attempt at ecological realism was made by using competitive treatments, more intense inbreeding depression is usually found when fitness comparisons are made under natural conditions (see Barrett & Kohn 1991). Genetic bottlenecks during island colonization resulting in severe reductions in genetic load might also account for the observed results. However, several recent studies of partially selfing taxa occurring on islands have demonstrated significant inbreeding depression (Sakai *et al.* 1989; Belaoussoff & Shore 1995; Schultz & Ganders 1996). Presumably bottlenecks have also occurred during their evolutionary history. Another possibility is that the genome-wide mutation rate for deleterious genes is lower in *E. paniculata* than in other species examined to date, perhaps owing to reduction in the mutation rate associated with evolution of predominant selfing (Kondrashov 1995 and personal communication). Information on the genetic architecture of inbreeding depression and the factors controlling genomic mutation rates for lethal and deleterious genes is required to interpret patterns of inbreeding depression in plant species (Lande *et al.* 1994). For island taxa knowledge of their colonization history, residency period on islands and the types of selection they are exposed to will also be important.

(*b*) *Evolution of outcrossing*

Whereas the advantages of self-fertilization for island colonization are apparent, a dominant theme in island plant reproductive biology concerns the selection of 'outcrossing mechanisms' after establishment on islands (Carlquist 1974; Ehrendorfer 1979; Thomson & Barrett 1981). 'Escape from homozygosity' is often seen as an essential prerequisite for subsequent radiation and diversification in island groups. Wind pollination, various diclinous sexual systems (e.g. dioecy, gynodioecy), and floral traits such as herkogamy and dichogamy have all been interpreted as different means of achieving outcrossing in island plants. It has even been proposed that the occurrence of weak isolating mechanisms in many island groups promotes evolutionary flexibility by providing high levels of heterozygosity through hybridization (Rattenbury 1962; Carlquist 1974).

There are several issues that need to be addressed in interpreting the adaptive significance of outcrossing, not the least of which is that group rather than individual selection is implied in the case of the supposed benefits of hybridization in island plants. First, some controversy surrounds the particular advantages of the genetic consequences of this pattern of mating. Biotic selection imposed by pest, parasite and disease pressures may play an important role in maintaining outcrossing (Levin 1975). Paradoxically, however, many islands appear to have reduced diversity and biotic interactions may be more relaxed in comparison with the mainland. The ecological benefits of genetic variation therefore need to be critically assessed for island taxa. Second, alternative perspectives on the adaptive significance of reproductive traits that emphasize selective factors such as fitness gain through male function and pollen – stigma interference need to be considered before assuming that their primary function is to promote outcrossing (Barrett & Harder 1996). Finally, before assuming that the special ecological conditions on islands have resulted in the selection of 'outcrossing mechanisms' it is of importance, as discussed earlier, to determine the place of origin of reproductive traits and whether island immigrants were likely to have possessed them on arrival. This particular issue has been of considerable importance in interpreting the factors responsible for the high incidence of sexual dimorphism in the floras of the Hawaiian Islands and New Zealand.

Recent biogeographical analyses of the Hawaiian flora by Sakai *et al.* (1995*a*, *b*) have provided new insights into the origins of sexual dimorphism and the conditions favouring the evolution of dioecy. By using a lineage-by-lineage analysis of the entire flora these authors obtained the following results.

1. Of the 971 native species, 14.7% are dioecious and 20.7% are sexually dimorphic, proportions that are the highest of any flora studied.
2. Of the 291 inferred colonists, 10% were dimorphic with 55.2% of all current dimorphic species arising from these lineages.
3. Autochthonous evolution of dimorphism from monomorphism occurred in at least 12 lineages giving rise to approximately one third of the current dimorphic species.
4. Sexual dimorphism is significantly associated with woodiness and small green flowers and among dioecious woody species wind pollination is disproportionately represented.
5. Among colonists sexual dimorphism is associated with fleshy fruits at the generic level.

These results clearly show that the high incidence of dioecy in the Hawaiian islands results from a variety of factors. While broad generalities await explicit phylogenetic analyses of individual groups, it is clear that dioecy has not acted as a constraint to island colonization as Baker's Rule originally implied. In some lineages bird dispersal via multiseeded fleshy fruits and unspecialized requirements for pollination probably favoured establishment of sexually dimorphic taxa on islands (see Lloyd (1985) for similar arguments for New Zealand). In other groups, sexual dimorphism has arisen autochthonously through the spread of unisexual individuals in hermaphrodite populations. These latter cases have provided model systems for investigations of the outcrossing-advantage hypothesis.

Of the 27 taxa of *Bidens* endemic to the Hawaiian Islands, 13 are gynodioecious (separate hermaphrodite and female plants), a condition unknown in the 200 species occurring elsewhere. Schultz & Ganders (1996) studied the evolution and maintenance of gynodioecy in *Bidens sandvicensis* by attempting to find the source(s) of female advantage. With nuclear control of male sterility and where outcrossing advantage is the only source of female superiority then the product of the selfing rate and inbreeding depression must exceed 0.5 (Charlesworth & Charlesworth 1978). However, the occurrence of intense inbreeding depression and high selfing is controversial, in part, because high selfing should purge deleterious recessive alleles thus eliminating inbreeding depression. In gynodioecious *B. sandvicensis*, selfing rates of hermaphrodites exceeded 0.57 and inbreeding depression measured in the field averaged 0.94, among the highest documented values for an angiosperm species. Since the product of the selfing rate and inbreeding depression is greater than 0.5 the conditions required for the maintenance of a stable polymorphism are met. Similar results involving extremely high inbreeding depression and partial selfing have also been found in *Schiedea* (Caryophyllaceae), an endemic Hawaiian genus with both sexually monomorphic and dimorphic taxa (Sakai *et al.* 1989). In both genera there is therefore evidence supporting the outcrossing-advantage hypothesis for the evolution of sexual dimorphisms in island plants. Further work is required, however, to determine the ecological and genetic factors that enable stable coexistence of severe inbreeding depression and high selfing. Inferior pollinator service has been implicated as a factor causing increased selfing in both groups.

4. GENETICS OF ISLAND POPULATIONS

Because migration to islands is inevitably associated with periods of small population size, especially during the establishment phase, stochastic forces involving founder events and genetic drift have been recognized as playing a dominant role in determining patterns of genetic variation in animal groups colonizing islands (e.g. Giddings *et al.* 1989; Brakefield 1990). What evidence exists that stochasticity has influenced the patterns and amount of genetic diversity in island versus mainland populations of plants?

(*a*) *Stochastic processes*

Island isolation and opportunities for gene flow from source populations are of prime importance in assessing the likelihood of stochastic influences. For most plant

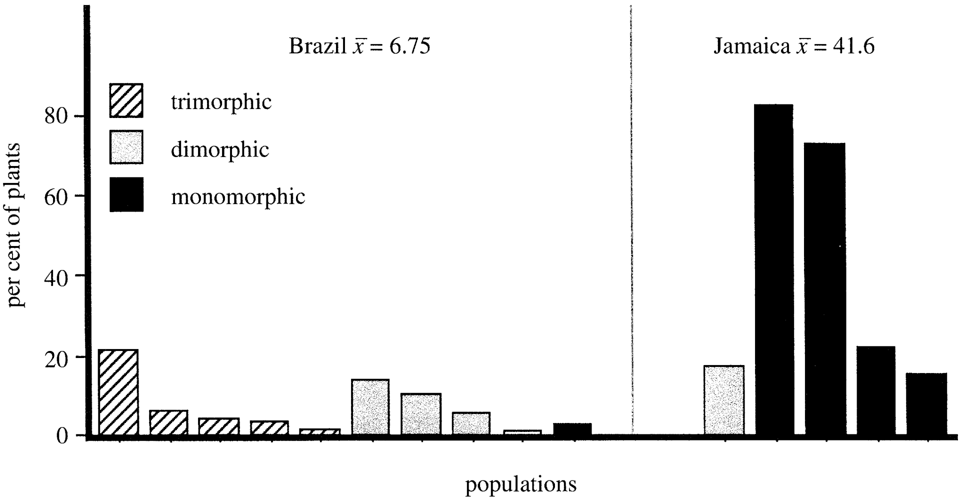

Figure 2. Differences in developmental instability of flowers between 10 continental (N.E. Brazil) and five island (Jamaica) populations of *Eichhornia paniculata*. All flowers open on a single inflorescence in 25 plants per population were scored for abnormal tepal development. Populations from Jamaica are highly selfing, those from Brazil vary from outcrossing (trimorphic) to those with mixed mating systems (dimorphic and monomorphic).

groups on remote oceanic islands extreme genetic bottlenecks must have been involved in their evolutionary history. However, the occurrence of such events and their evolutionary significance is poorly understood. Molecular studies provide opportunities for detecting historical bottlenecks, but as yet these approaches have not been applied to questions concerned with island colonization.

What empirical evidence is there that contemporary variation patterns in island plant populations have been influenced by genetic drift? Apparently non-adaptive differentiation of several morphological traits in Aegean island populations of taxa in *Erysimum* section Cheiranthus was interpreted by Snogerup (1967) as resulting from drift operating in populations of these rare cliff plants. Only 107 populations were found and estimates of population size indicated that *ca*. 10% of populations contained only 1–2 plants and more than 50% had 50 or less individuals. The occurrence of non-adaptive and in some cases even maladaptive traits in island plants is most easily explained by the random fixation of recessive genes exposed through inbreeding in small populations. High levels of developmental instability in *E. paniculata* flowers from island compared to mainland populations also appear to have arisen in this manner (figure 2; Richards & Barrett 1992). Some of the striking morphological differentiation that characterizes island taxa displaying 'adaptive' radiation may result from stochastic processes operating during founder events and periods of small population size.

Founder events and genetic drift have been invoked to explain the absence of the short-styled morph from Jamaican populations of *E. paniculata* (Barrett *et al.* 1989). Stochastic theory indicates that this morph is more vulnerable to loss following bottlenecks due to a constraint imposed by the genetic system governing the inheritance of the tristylous polymorphism (Barrett 1993). Stochastic forces have also played an important role in reducing genetic variation at allozyme loci compared to those on the mainland (Glover & Barrett 1987) and in structuring the patterns of genetic diversity within and among island populations (Husband & Barrett 1991). Allele frequencies at polymorphic loci are highly asymmetrical in most Jamaican populations with a relatively small number of different multilocus genotypes dominating. This pattern involving high levels of gametic disequilibrium is expected for neutral loci if populations are founded by a small number of genotypes and restricted gene flow and inbreeding act to preserve particular allelic combinations.

(*b*) *Genetic variation in island populations*

Theoretical work on population structure has used the continent – island and island models as paradigms for understanding how interactions between gene flow, effective population size and genetic drift influence patterns of genetic variation. Under most scenarios theory predicts that island populations should be less variable and more genetically differentiated relative to source populations. Few studies of plant populations have, however, explicitly tested models of population structure and only a small number of comparisons of genetic diversity in island and mainland plant populations of the same species is available. What data do exist generally indicate that island populations contain less variation than those from mainland areas (figure 3; and reviewed in Barrett & Husband 1990*b*; Frankham 1996). Where exceptions do occur these arise either because the species involved has little or no allozyme diversity in either area (Ledig & Conkle 1983; Mosseler *et al.* 1991), the islands sampled were not isolated from the mainland (Gauthier *et al.* 1992) or known historical factors are involved (Tsumura & Ohba 1993).

Interpretation of the factors causing particular patterns of allozyme variation on islands can be complicated because colonization is often confounded with evolutionary modifications to the genetic system

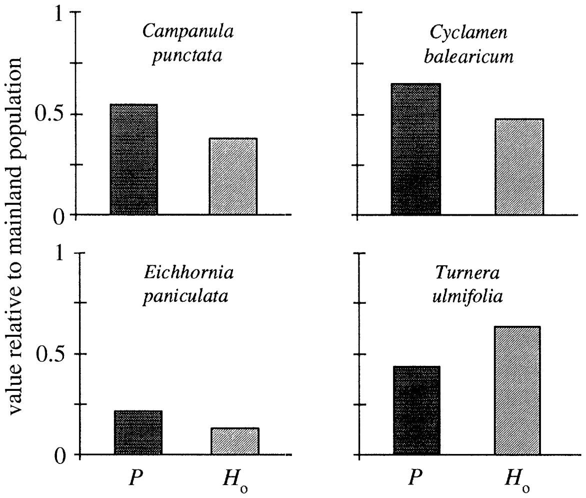

Figure 3. Reduced genetic variation at allozyme loci in island versus mainland populations of four plant species. Values for the percentage of loci polymorphic (*P*) and observed heterozygosity (H_o) for each species are calculated as the percentage reduction from mainland populations. Sources: *Eichhornia* & *Turnera*, see Barrett & Husband (1991), *Campanula* & *Cyclamen*, see Inoue & Kawahara (1990) and Affre *et al.* (1996), respectively.

(e.g. diploidy to polyploidy in *Turnera*, outcrossing to selfing in *Campanula* and *Eichhornia*). These changes directly affect patterns of genetic variation and can also influence interactions with stochastic factors. For example, a loss of neutral genetic variation is expected in selfing organisms due to reductions in effective population size, hitch-hiking and background selection (Charlesworth *et al.* 1993). While bottlenecks also reduce variation it is unclear whether these various processes can be distinguished by their genetic consequences. Geographical surveys of allozyme variation are insufficient for disentangling the individual and combined effects of these factors on genetic diversity. These problems are exacerbated because no detailed theoretical treatment is available for the influence of bottlenecks on variability in partially selfing populations, although Jarne (1995) has recently made a start on this problem.

Restricted gene flow, inbreeding and genetic drift will strongly influence the extent of diffentiation among populations. Not unexpectedly island plant populations often exhibit a higher degree of genetic differentiation both among populations on a single island (*Eichhornia*) and among populations on different islands (*Campanula*) in comparison with corresponding mainland samples. However exceptions to this pattern occur, as in the Mediterranean endemic *Cyclamen balearicum*. Affre *et al.* (1996) found population differentiation at allozyme loci to be significantly higher among mainland populations in southern France than among those occurring on the Balearic Islands off the north coast of Spain. They suggested that glaciation and habitat fragmentation due to human land use patterns resulted in greater reductions in effective population size and more isolation in southern France than on the Balearic Islands, where populations are large and found over a wider range of ecological conditions. This interpretation should remind us of the increasing number of 'terrestrial habitat islands' that are being formed because of ecosystem modifications through agriculture, forestry and urbanization. Studies of true island populations may assist in predicting the genetic consequences of such anthropogenic changes.

5. CONCLUSIONS

A recurring theme throughout this review is that many general problems in evolutionary biology can be addressed through investigations of the reproductive biology and genetics of island plants. The adaptive benefits of selfing and outcrossing, selection of combined versus separate sexes, the role of stochastic processes in evolution, and models of population structure can each be investigated by exploiting island plant taxa as model systems. Also, genera displaying adaptive radiation frequently exhibit weak isolating mechanisms and can provide unsurpassed opportunities to investigate the genetic basis of adaptation and of the speciation process itself. Unfortunately, island populations are more vulnerable to extinction than those in continental regions and many endemic plant taxa, including several discussed above, are rare or threatened. It would be regrettable if this rich biological heritage was lost and with it opportunities for increased understanding of evolutionary processes.

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Discussion

B. Emerson (*University of East Anglia*, *Norwich*, *U.K.*). Given that the New Zealand flora is comparatively colourless in relation to the Australian flora, and that this is due to a lack of specialization to attract pollinators, what might be the reason for the colourful flora of the Sub-Antarctic Islands, which does not conform to this theory.

S. C. H. Barrett. This problem has intrigued New Zealand botanists for some time but we still do not have a satisfactory answer. On the Sub-Antarctic Islands and Chatham Island at least ten genera with showy-flowered species are known with close relatives in New Zealand that have dull inconspicuous flowers. As the climatic conditions on these islands are unfavourable for most pollinators and the pollinator faunas are even more depauperate than New Zealand, the pattern is certainly puzzling. Both non-adaptive and adaptive hypotheses have been proposed and were reviewed by David Lloyd (*N.Z. Jl Bot.* **23**, 707–722 (1985)).

J. Mallet (*Galton Laboratory*, *University College London*, *U.K.*). A selectionist skeptic might argue that the loss of short-styled morphs in *Eichhornia* is an adaptation to allow selfing (in mid-styled) rather than an effect of genetic drift. Does Professor Barrett have good evidence for genetic drift?

S. C. H. Barrett. It is hard to imagine that natural selection could lead to the loss of the short-styled morph to, as you say. 'allow selfing'. In any case, I think that the evidence for genetic drift is quite convincing. First, the patterns of morph-frequency variation in natural populations are those predicted by theoretical models of the influence of drift operating in finite populations. Because of the mode of inheritance of tristyly, the short-styled morph is more likely to be lost from small populations than the other two morphs. This is exactly what we have observed in large-scale surveys of *E. paniculata* and tristylous species such as *Lythrum salicaria*. Moreover, *in E. paniculata* genetic estimates of effective population size (N_e) indicate that N_e is often well below that required to maintain the polymorphisms. Evidence for the role of drift in the destabilization of tristyly is reviewed by Barrett (*Oxf. Surv. Evol. Biol.* **9**, 283–326 (1993)).