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**The reproductive biology of island plants:
the Juan Fernández and Canary Islands
(Facilitated by the work of Arnaldo Santos Guerra)**

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RESUMEN: El conocimiento de la biología reproductiva es fundamental para entender la colonización exitosa y la posterior evolución de las plantas en archipiélagos oceánicos, para establecer programas de conservación eficaces para la biota de islas y para comprender la evolución de las plantas en general. Esta revisión se centra en la biología reproductiva de plantas de las Islas Canarias a través de una comparación con la de las Islas chilenas Juan Fernández (Islas Robinson Crusoe). Nos centramos en los sistemas reproductivos (i.e., compatibilidad, capacidad de autopolinización) y la polinización. El sistema de reproducción de los progenitores de los linajes de islas se infieren para evaluar la interpretación usual: que los colonizadores exitosos son autocompatibles, i.e., siguen la ‘Ley de Baker’ vs. la alternativa de un sistema de cruzamiento mixto (autoincompatibilidad “permeada”). Se revisan brevemente los mecanismos que promueven polinización cruzada en especies hermafroditas autocompatibles. Se evalúa si las formas florales actuales reflejan características de polinización de los antepasados colonizadores o si representan selección in situ en las islas. El limitado rango de polinizadores disponibles para los nuevos colonizadores de islas, especialmente de archipiélagos más jóvenes, obliga a adaptaciones a nuevos síndromes que no siempre son reflejados en la morfología floral o en néctar. A pesar del amplio interés en las plantas de islas, hay pocos estudios completos sobre sistemas de cruzamiento o biología de la polinización. Así, generalizaciones sobre sistemas de islas pueden dar lugar a malentendidos: como Baker exhortó hace casi medio siglo, más estudios de biología reproductiva de plantas de islas son

necesarios. Por otra parte, programas de conservación no serán eficaces sin conocimiento de la biología reproductiva de las plantas nativas de islas.

Palabras clave: biología reproductiva, Islas Canarias, Islas Juan Fernández, Santos-Guerra

ABSTRACT: Knowledge of reproductive biology is fundamental to understanding successful colonization and subsequent evolution of island plants, to founding effective conservation programs for island biota, and for the insights provided from island studies to understanding the evolution of plants in general. We focus on the reproductive biology of plants of the Canary Islands via a comparison with that of plants from the Chilean Juan Fernández (Robinson Crusoe Islands). We focus on breeding systems (i.e., compatibility, ability to self pollinate) and pollination. The breeding system of the progenitors of island lineages are inferred to assess the usual interpretation: i.e., that successful colonists are self compatible, i.e., following ‘Baker’s Law’ vs. the alternative of a mixed breeding system (‘leaky’ self incompatibility). We briefly review the mechanisms promoting outcrossing in self compatible hermaphroditic species. We assess whether current floral forms reflect pollination features of the colonizing ancestors or whether they represent selection on islands *in situ*. The limited range of pollinators available to new island colonists especially of younger archipelagoes, forces adaptation to new syndromes that are not always reflected in their floral morphology or nectar. Despite the broad interest in island plants, there are few comprehensive studies of either breeding systems or pollination biology. Thus, generalizations about island systems can lead to misunderstandings: as Baker exhorted nearly a half century ago, more studies of island plant reproductive biology are needed. Furthermore, conservation programs will not be effective without a knowledge of reproductive biology of island natives.

Key words: reproductive biology, Canary Islands, Juan Fernández Islands, Santos-Guerra

INTRODUCTION

Endemic insular floras constitute about 25% of the species of vascular plants occurring on about 5% of the Earth’s land surface (Kreft *et al.*, 2008); and between 5-10% of those endemic species are highly threatened (Caujapé-Castells *et al.*, 2010). We recognize that many factors impact the origin and evolution of island plants; in the present review we focus on reproductive biology. Island natives are excellent subjects for studying the evolution of reproductive systems. Especially interesting and informative is how colonizing ancestors adapt to the insular setting, and meet such challenges as the loss of biotic pollinators and compatible mates. Reproductive biology is critical in the establishment and diversification of sexually reproducing insular lineages, making knowledge of reproductive biology critical in developing effective conservation strategies.

This paper provides a general overview of the reproductive biology of island plants, and focuses on studies needed to address questions about their evolution. We will emphasize the Canary Islands flora, but will make some comparisons with the reproductive biology of native plants of the Juan Fernández Islands. We hope these comparisons will produce hypotheses to consider for islands in general. Our use of reproductive biology will include pollination biology, breeding systems (features promoting selfing or outcrossing), and mating system (level of selfing and outcrossing) (Neal & Anderson, 2005).

COMPARISONS OF JUAN FERNÁNDEZ AND CANARY ISLANDS

The Canary Islands are an auspicious archipelago for comparisons. Most important are the excellent studies by a wide range of researchers that have yielded a strong foundation. Also, the flora and fauna are relatively diverse and, together with the geology of the islands, are fairly well documented. The Juan Fernández were selected for primary comparisons because we have engaged in extensive evolutionary and ecological studies of the plants for more than two decades.

Location, age and size

The Juan Fernández is a simple insular system of two major islands at 33° S latitude 670 km W of Santiago, Chile: Masatierra (4 million yrs old [myr] and Masafuera 1-2 myr, and 150 km further W), each about 50 km² in area. The present land area of Masatierra is about 10% its original size (Sanders *et al.*, 1987). The highest point is now 950 m but originally was about 3,000 m. The more distant island, Masafuera, bears coastal cliffs of close to 1000 m (and about 400m more to the highest point), it is much more rugged, and also infested with feral goats. Masafuera is not inhabited by permanent human populations. There has been no volcanic activity or massive land slides since the origin of the archipelago. In addition, there are no known submerged stepping stones between these two islands or connecting this archipelago with the continent, a fact important to setting the date for colonization and interpreting the evolution of the constituent flora. The situation is different for the Canary Islands: the seven islands are 75 times larger in area, are 10 times closer to a continent, are 4-5 times older, and have been subjected to volcanic activity (the most recent terrestrial volcanic eruption occurred in 1971 in La Palma) and massive landslides (Carracedo & Day, 2002). Although the Juan Fernández are younger, they may be declining, without any active volcanic eruptions and are actually shrinking.

Floras

The two islands of the Juan Fernández have a flora of about 155 native species, about 65% endemic. The major source areas are South America (followed by Pantropics, Australia, New Zealand; Bernardello *et al.*, 2006). The largest lineage (i.e., the endemic genus *Dendroseris*: Asteraceae) has only 11 species. About 55 colonizations probably account for the endemic flora. The Canary Islands have a much larger native flora with ca. 600 endemics, which is 45% of the native flora. Major source areas are the Mediterranean Basin

and Africa. The endemics may have originated from 156 colonizations (A. Santos 1998, unpubl.). It is interesting that only 17 introductions have generated 270 endemic species. In contrast to Juan Fernández, 14 lineages in the Canary Islands have 10 or more species.

Pollination

The pollination of the Juan Fernández is dramatically simple, with wind (nearly 50% of the flora) and hummingbirds playing major roles; there are no native bees (one newly introduced-Anderson *et al.*, 2001b), wasps, flies, butterflies or moths that are regular flower visitors (Bernardello *et al.*, 2001; Anderson, *et al.*, 2001a). The only native biotic pollinators are two hummingbirds, one endemic (i.e., *Sephanoides fernandensis*). The hummingbirds are obviously flower specialists, and visit 14 species (~8% of the flora; 14% of the endemics). There are very few reports of wind pollination in the Canary Islands, but studies of endemics from several wind-pollinated families are lacking. The pattern in the Canary Islands is more typical of other island systems (Hawaii, Galápagos, Bonin) where insect-pollinated colonists remained as insect-pollinated in the archipelago as well (Garcia, 2000; Olesen *et al.*, 2002; Dupont & Skov 2004; reviewed by Crawford *et al.*, 2011), given that appropriate classes of insect pollinators exist on the archipelagos. There have been some shifts to wind, a phenomenon meriting more detailed study.

Hummingbirds on the Juan Fernández have not had to compete with other biotic pollinators for plants. This contrasts with the Canary Islands (and most other archipelagos), where, although a similar number of plants (11) are visited by bird species (six of them), this number constitutes a proportionately small part of the entire flora (> 2% of endemics, > 1% of flora). Importantly, the birds on the Canaries are all passerines (Ollerton *et al.*, 2009), i.e., not nectar-feeding specialists (notably, not from the African Sun Bird flower-specialists - Nectariniidae), and, reciprocally, most of the bird-pollinated plants are not exclusively ornithophilous. Valido *et al.* (2004) conclude that most bird-flower syndromes on the Canary Islands came to the islands already developed – the ‘relict condition’ – and that Macaronesian ornithophilous species sometimes represent survival in their island ‘refugia’ when ancestral forms went extinct in continental areas. González and Furtés (2011) arrive at similar conclusions. The majority (60-70%) of Juan Fernández ornithophilous plants also seem to have been derived from bird-pollinated colonists (Bernardello *et al.*, 2001). The higher proportion of ornithophily on the Juan Fernández probably represents exploitation of an open niche for hummingbirds; they did not have to compete with the full panoply of insect pollinators (see below).

Pollination by the other biotic groups typical of continental floras is much more common on the Canary than on the Juan Fernández Islands. For instance, it is estimated that the 125 Canary Islands bee species visit many plants, exemplified by the at least 88 Canary Islands endemics pollinated by the ubiquitous endemic *Bombus* (Olesen *et al.*, 2002). These authors also show that plants in three different floristic zones range from moderate specialists to generalists. Even so, the Canary Islands pollinator fauna is much less rich than the continent.

Immigrants to islands are few, highly selected/ filtered by distance, dispersal capabilities, and adaptations for establishment. Furthermore, their survival depends on dealing with what is available on the islands. This is manifest in two very different ways. First, the

immigrants that arrive early in the history of an archipelago, where habitats may be wide open with little or no biotic competition for niches, likely encounter little or no competition (Silvertown, 2004; Silvertown *et al.*, 2005). As a result, there are impressive morphological / functional radiations in some groups that evolve relatively free of the constraints that intra-continental diaspores encounter (Carlquist, 1965, 1974). There is the caveat, however, that one of the ways in which near-source archipelagos like the Canary Islands may be somewhat different is the much more likely constant source of immigrants from the nearby continent. The perhaps-regular later arriving immigrants encounter “full” niches (similar ideas proposed in Silvertown, 2004; Silvertown *et al.*, 2005), more like intra-continental diaspores. These immigrants have to deal with what is there, there is no analog of the ‘universe of possibilities’ that the early immigrants encountered. Thus, care must be taken in island generalizations given that the ecological/evolutionary pressures may be very different for species arriving on a relatively newly formed island vs. those arriving much later.

BAKER’S LAW, COLONIZING ANCESTORS AND ISLAND RADIATIONS

Colonizing ancestors

Baker’s “Law” (he preferred “generalization”) posits that self compatible colonizers, especially autogamous ones, would be most effective in establishing sexually reproducing populations following long distance dispersal because, unlike self incompatible plants, no pollen vector may be needed and only a single disseminule is required. Baker’s Law has been widely accepted despite concerns about whether the low diversity carried by a single propagule from a selfing source population would preclude the development of a diverse island lineage, concerns expressed even at the time Baker was promoting his ideas in the 1950s and 60s (Carlquist, 1974, chaps. 1, 13). There appear to be conflicting optimal characters for establishment on the one hand, and on diversification and radiation on the other. This is one of the basic questions in the reproductive biology of island plants, and has several important implications for understanding the origin and evolution of insular lineages. One of the continuing problems with applying Baker’s Law and testing the ideas is the lack of comprehensive data on the compatibility of island plants. There are some generalizations from a few carefully studied species: there are few comprehensive studies, because it takes a great deal of time in the field to determine self compatibility. We have good data for the Juan Fernández where, like the Galápagos (McMullen, 2009; Chamorro *et al.*, 2012), a number of species have been surveyed, and 70 to 80% (>90% for Galápagos natives) of the species are self compatible (Anderson & Bernardello, in press). There are few comprehensive data for most other archipelagoes; such data are needed for comparisons that generate testable hypotheses on plant evolution. It has been our intention to summarize work on the Canary Islands to facilitate these comparisons.

There are several mechanisms by which plants may escape from this seeming conundrum. In the Juan Fernández, the 80% of self compatible species are not highly autogamous and many require a vector to move pollen from anther to stigma. Thus, the ancestral source populations likely were not highly homozygous, as would be true for highly selfing popu-

lations. The same is true for the remote Hawaiian Islands, where there is little evidence for autogamous ancestors (Price & Wagner, 2004). Thus, knowing the mating systems of the colonizing ancestors of self compatible island lineages is important.

Examples are slowly accumulating of the feasibility of establishing sexually reproducing populations from a single self incompatible diaspore. The source population would be outcrossing and highly heterozygous. Preliminary data indicate that over 40% of the 27 lineages examined from the Canary Islands originated from self incompatible ancestors. Detailed studies from the genus *Tolpis* indicate that “obligately” self incompatible species in fact exhibit various levels of selfed seed (Crawford *et al.*, 2008). There is some evidence (Francisco-Ortega *et al.* 1997) that the large Canary Islands radiation, *Argyranthemum*, is pseudo-self-compatible (PSC, i.e. has ‘leaky’ self incompatibility). PSC occurs in the largest lineage (*Scalesia*, Nielsen *et al.*, 2000, 2003) in the Galápagos and in a large radiation (silversword alliance, Carr *et al.*, 1986; Barrier *et al.*, 1999; Baldwin, 2003) in Hawaii; both likely evolved from PSC ancestors. Five of the six largest radiations in the Canary Islands have self incompatible members, and likely originated from self incompatible or PSC ancestors (Anderson *et al.* unpubl.). The breeding systems of these and other lineages, and their continental ancestors should be examined in detail to ascertain the potential role of PSC in the establishment and radiation of island plants. How general is PSC as a way of establishing genetically diverse populations from a single disseminule?

The cryptic dioecy we found on the Juan Fernández (*Pernettya*; Anderson *et al.*, 2000), and Canary Islands (*Withania*; Anderson *et al.*, 2006b), and leaky dioecy in *Solanum conocarpum* and *S. polygamum* from the Virgin Islands (see Anderson *et al.*, 2010 and more below) of course might have arisen similarly. That is, the dioecy might be autochthonous. Or, perhaps the first diaspores to arrive are from an already established dioecious condition, but those first colonists exhibit some ‘leakiness’ in the dioecious system. New observations on greenhouse populations of *S. polygamum* show that an hermaphroditic flower, that is self compatible, can be produced, very rarely, on otherwise only staminate-flowered plants (i.e., males; Anderson, ms. in prep.). Both the rare hermaphrodite and the self compatibility are notable. The former because it is so unexpected (at one in several hundred flowers at the minimum), and self compatibility simply because it is normally not possible to determine compatibility in a dioecious species. Thus, this exceptional response offers direct evidence (vs. inferences from cladograms) in the debate over dioecy as an evolutionary (e.g., to promote outcrossing) or ecological response (Anderson & Symon, 1989).

Mating systems in island populations: how little we know

Regardless of the diversity brought to an island by colonizers, establishment in new niches and outcrossing are probably important in the initial diversification and radiation of a lineage. The two most effective mechanisms for promoting outcrossing are complete separation of the sexes on different plants (dioecy) and obligate self incompatibility in hermaphroditic plants. Dioecy is rare in flowering plants (6%; Renner & Ricklefs 1995) and is likewise infrequent on Canary Islands (perhaps as high as 6% when cryptic and temporally functional dioecy are considered; Pérez de Paz *et al.*, 2011), though more frequent in other archipelagos such as Hawaii (15%; Sakai *et al.*, 1995) and Bonin Islands (13%; Abe, 2006). On the Juan Fernández it is about 9% (Bernardello *et al.*, 2001). Other mechanisms

promoting outcrossing in self compatible species of Juan Fernández include monoecy (9%) and herkogamy, with about 30% of species protandrous and 7% protogynous; meager published data suggest similar mechanisms in the Canary Islands (Francisco-Ortega *et al.*, 2000). Thus, although self incompatibility *per se* has not been important in promoting outcrossing in the Juan Fernández and its frequency in the Canary Islands is largely unknown, there are other ways of promoting outcrossing in self compatible species. Data for continental ancestors are needed to infer whether factors promoting outcrossing were brought to an island or evolved *in situ*; data from Juan Fernández and Hawaii indicate that both have occurred (Anderson *et al.*, 2001a; Bernardello *et al.*, 2001; Sakai *et al.*, 1995).

Despite observations on factors promoting selfing and outcrossing, there is very little information on how these factors actually shape mating systems in natural populations of insular endemics. Recent studies of highly self incompatible *Tolpis* in the Canary Islands revealed a mixed mating system in several populations (Crawford *et al.*, 2010). These unexpected results illustrate the possible pitfalls of inferring the mating system from the breeding system data. Similarly, studies of the mating system in Hawaiian *Bidens*, a large radiation of self compatible plants, revealed that protandry and gynodioecy function to produce mixed mating (Sun & Ganders, 1988). On islands one cannot necessarily judge the pollination of a flower from its morphology (Bernardello *et al.*, 2001), nor the mating system from the breeding system.

While outcrossing may be an important factor in the diversification of island lineages, the conditions under which higher selfing, including autogamy, would be favored must be considered. Two commonly cited advantages of autogamy are lack of pollinators and/or lack of compatible mates. There are few extensive studies of mating system variation in island lineages; a notable exception is *Schiedea* in Hawaii (Sakai *et al.*, 2006). From self compatible hermaphroditic ancestors, autogamy evolved three times in small populations in wet areas; dioecy originated twice in dry, open areas with no biotic pollinators (but wind pollination occurs). In *Tolpis* in the Canary Islands, increased selfing could occur by higher levels of PSC; preliminary results indicate higher selfed seed and lower allozyme diversity in populations from the El Golfo region of El Hierro (Crawford *et al.*, unpubl.); more studies are needed to confirm whether, there may be correlations between the occurrence of selfed seed and areas of disturbance. True self compatibility has evolved within *Tolpis* in the Canary Islands: *T. coronopifolia* exhibits floral features typical of selfers (selfing syndrome, Ornduff 1969) and is highly autogamous (Crawford *et al.*, 2008). The genetics or adaptive significance of this mating system have not yet been elucidated. Analyses of synthetic F₂ hybrids between a self compatible *T. coronopifolia* and a self incompatible plant from another species of Canarian *Tolpis* show that self incompatibility is controlled by a single major dominant locus with modifiers, and that morphological characters co-segregate with the S locus (Soto-Trjo *et al.*, 2013). Thus, evolution of true self compatibility and the associated morphological characters could be rapid. The breakdown of self incompatibility occurs in *Dendroseris* in Juan Fernández, but the selfing syndrome has not evolved, with retention of outcrossing features (Anderson *et al.*, 2001).

Studies of comparative breeding-mating systems within lineages in the Canary Islands are needed. Examination of one to several species within lineages may not detect evolutionarily important variation. The Canary Islands are an ideal system because of diversity of habi-

tats, opportunities for colonization of new islands and new open areas on individual islands. Some larger survey studies are underway (Pérez de Paz, 2011; Anderson *et al.* unpubl.).

REPRODUCTIVE BIOLOGY AND CONSERVATION OF ISLAND PLANTS

Successful sexual reproduction is critical to the survival and evolution of island lineages, and thus any conservation effort without knowledge of reproductive biology is in danger of failure. Any study of reproductive biology has conservation implications, and this is especially true for species present as a few small island populations. Some important issues linking reproductive biology and conservation include the following.

For a self incompatibility system to be functional and successful, there should be conservation of S alleles in self incompatible species from very small island populations. This is important for both *in situ* and *ex situ* conservation efforts to assure compatible matings.

For dioecious species, the conservation plan has to take account of the mix of sexes and behavior of pollinators toward them. Dioecy leads to skewed sex ratios in smaller populations (Ellstrand & Elam, 1993; Percy & Cronk 1997), reducing effective population size, possibly to only one gender in a species. Leaky dioecy could be a mechanism for generating seeds. There is a good example of this in the newly discovered cryptic dioecy (and ‘leaky dioecy’) of the critically endangered (> 200 pls. in wild) *Solanum conocarpum* and the known dioecious *S. polygamum* from the Virgin Islands (Anderson *et al.* 2010; and Anderson *et al.*, in prep.)

Highly selfing species may have high inter-population differentiation, knowledge of which is critical for effective sampling in conservation planning (Hamrick & Godt, 1989; Nybom & Bartish, 2000; Coates & Byrne, 2005).

Loss of pollinators outright, or the competitive loss of pollinators to invasives, and/or the reduction of island plant populations to levels insufficient to sustain pollinators have significant implications for effective conservation (e.g., Bond, 1994; Biesmeijer *et al.*, 2006; Memmott *et al.*, 2007).

Pollination ‘networks’ may be disrupted or destroyed by invasive pollinators or invasive plants (Kevan, 1970; Olesen *et al.*, 2009; Trøjelsgaard & Olesen, 2011).

Understanding the mating system and pollen flow, i.e., genetic assimilation via hybridization, is critical: e.g., hybridization between natives, and between natives and invasives by virtue of habitat alteration can dramatically alter the genetic structure of island natives, with the potential assimilation or exclusion of the native species (Levin *et al.*, 1996; González-Pérez *et al.*, 2004; Daehler & Carino, 2005).

FUTURE STUDIES

Some topics regarding the reproductive biology of island plants were described above and elsewhere (Crawford *et al.*, 2011). Here we outline some areas for future research.

1. Reproductive biology research *sensu lato* must include both in-depth and multifaceted studies within lineages to elucidate subtle variation in effective pollination — *not* just records of floral visitation— and breeding and mating systems.

2. Generation of accurate general principles requires comparative studies of similarities and differences among lineages within the same and among different archipelagos.

3. Comprehensive comparative studies require research teams within an archipelago and coordination of efforts among archipelagos. To quote H. G. Baker (1967) “Clearly, the greatest need in this area of biology is for further field and experimental studies (by as many workers as can spare the time) on the reproductive biology of plants which make up floras of all kinds——”.

4. Molecular data are needed to place evolution of reproductive biology within a phylogenetic-biogeographical context. Molecular markers allow estimation of mating systems in populations. The potential rewards are great in yielding an understanding of the complicated biological world we are privileged to study.

5. Once the mating system has been estimated for populations-species, a next step is to elucidate the factors shaping the mating system. With very few exceptions, the roles of reproductive assurance versus inbreeding depression in selecting toward selfing versus outcrossing has not been examined in island lineages. These too are time-consuming, labor-intensive studies, but they provide insights into mating system evolution and the adaptation of plants to the diverse and dynamic habitats occurring over short spatial scales on oceanic islands.

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