



REVIEW ARTICLE

Interpretation of patterns of genetic variation in endemic plant species of oceanic islands

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Oceanic islands offer special opportunities for understanding the patterns and processes of evolution. The availability of molecular markers in recent decades has enhanced these opportunities, facilitating the use of population genetics to reveal divergence and speciation in island systems. A common pattern seen in taxa on oceanic islands is a decreased level of genetic variation within and among populations, and the founder effect has often been invoked to explain this observation. Founder effects have a major impact on immigrant populations, but, over millions of years, the original genetic signature will normally be erased as a result of mutation, recombination, drift and selection. Therefore, the types and degrees of genetic modifications that occur must often be caused by other factors, which should be considered when explaining the patterns of genetic variation. The age of the island is extremely important because oceanic islands subside on their submarine plates over time. Erosion caused by wind, rain and wave action combine to grind down soft volcanic substrates. These geomorphological events can have a dramatic impact on population number and size, and hence levels of genetic diversity. The mode of speciation is also of significance. With anagenesis, genetic variation accumulates through time, whereas, with cladogenesis, the gene pool splits into populations of adaptively radiating species. Breeding systems, population sizes and generation times are also important, as is hybridization between closely related taxa. Human disturbance has affected plant population number and size through the harvesting of forests and the introduction of invasive plants and animals. Therefore, the explanation of the observed levels of genetic variation in species of oceanic islands requires the consideration of many interconnected physical, biological and anthropomorphic factors. © 2013 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2014, **174**, 276–288.

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INTRODUCTION

Oceanic islands offer many opportunities for understanding the patterns and processes of organic evolution, and they provide dramatic settings for testing

the hypotheses of evolution and biogeography (Emerson, 2002). Many studies in the 20th century have focused on large adaptive complexes of species, such as the lobelioids (Givnish *et al.*, 2009) and silverswords (Carlquist, Baldwin & Carr, 2003) in Hawaii, *Aeonium* Webb & Berthel. (Mort *et al.*, 2002) in the Canary Islands and *Scalesia* Arn. (Eliasson, 1974) in the Galapagos Islands. Through these studies have come numerous insights regarding the patterns and processes of evolution in the island

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setting (Whittaker & Fernández-Palacios, 2007; Bramwell & Caujapé-Castells, 2011).

The advent of molecular markers has resulted in an improved ability to track evolution in islands through a better understanding of genetic variation within and among populations and added phylogenetic perspectives (Crawford *et al.*, 2001; Emerson, 2002; Sanmartín, Van der Mark & Ronquist, 2008; Ronquist & Sanmartín, 2011). Molecular markers studied in island plants, and in plants in general, consist almost exclusively of markers deemed to be neutral or near-neutral (Lewontin, 1991; McKay & Latta, 2002; Leinonen *et al.*, 2008). These include isozyme loci (Hamrick, 1989; Hamrick & Godt, 1989) and various polymerase chain reaction (PCR)-based markers (Nybom, 2004; Guichoux *et al.*, 2011). As a result, the present discussion of genetic diversity is restricted almost exclusively to presumably neutral or near-neutral loci. The advantage of neutral markers, in addition to their relative ease of study, is their utility in providing estimates of random processes, such as genetic drift. However, it is not known how accurately the relatively small number of loci sampled is representative of genome-wide diversity (Kirk & Freeland, 2011). In certain island lineages, such as *Tetramolopium* Nees in Hawaii, there has been extensive diversification and speciation (Lowrey, 1986), with little diversity detected at putatively neutral isozyme loci (Lowrey & Crawford, 1985). This pattern indicates that isozyme diversity is not an accurate indicator of genomic diversity for phenotypic and ecological features important in insular radiations. The continued advances in next-generation sequencing (NGS) will elucidate the genome-wide diversity (Carstens, Lemmon & Lemmon, 2012; Grover, Salmon & Wendel, 2012) and eventually allow the identification of the genetic basis of adaptive traits that facilitate radiation and diversification in island lineages. Only then will it be possible to gain refined insights into the impact of founder events and other stochastic processes on the adaptive potential of island lineages.

One of the major results of molecular population genetics studies in islands has been that populations of endemic species often show reduced levels of variation in comparison with continental populations (deJooode & Wendel, 1992; Frankham, 1997), a situation frequently attributed to the founder effect (Frankham, 1997; Whittaker & Fernández-Palacios, 2007; Templeton, 2008). It has recently been stressed, however, that it is nearly impossible to see genetic signatures of original founder effects in any *endemic* species on oceanic islands (Stuessy, Takayama & López Sepúlveda, 2012). Many, if not most, island endemic species have been in existence on their respective islands for millions of years (Heaney, 2007) and, by the time speciation has taken place, little

trace of the original genetic founding event can be seen. Furthermore, although many studies have shown low levels of genetic variation within and among populations, fewer actual comparisons have been made with progenitors or sister species in continental (or source) regions. Some population-based investigations have also shown similar or even higher levels of genetic variation in widespread island taxa in comparison with continental relatives (i.e. Francisco-Ortega *et al.*, 2000; Su, Ting & Deng, 2010), as a result of many inter-related factors (Chiang *et al.*, 2006; García-Verdugo *et al.*, 2013).

Although initial founder effects clearly play a role in setting a genetic context in which speciation in islands can occur (Carson & Templeton, 1984), there are numerous other factors that are more important in regulating genetic levels within populations of endemic island species over time. Factors that have been recognized for populations in continental areas, such as population sizes, rates of mutation, breeding systems, hybridization and phylogenetic position (Hamrick & Godt, 1996, 1997), also help to explain genetic variation for island plants. Also important are changes in the physical island environment, especially subsidence and erosion. Impacts on endemic species from human activities must not be neglected, especially as they affect population number and size.

Modes of speciation also play a role in influencing the levels of genetic variation within island populations. In an island with low habitat heterogeneity, the original population may enlarge and spread over the island, eventually accumulating morphological and genetic change that is taxonomically and biologically regarded as a new species. This transformational process of speciation has been called anagenesis (Stuessy *et al.*, 2006). On ecologically heterogeneous islands, however, speciation by cladogenesis (splitting) frequently occurs, resulting in genetically closely related species which may be quite different from each other morphologically. The amount of genetic variation within and among populations of each cladogenetically originating species may be much less than that in anagenetically derived species (Stuessy, 2007).

Therefore, the challenge of attempting to explain levels of genetic variation in populations of oceanic islands requires an understanding of many physical, evolutionary, biological and anthropomorphic factors. Simply assuming that low levels are caused by a founder effect is no longer satisfactory. The purposes of this article are to: (1) review the different factors that influence the levels of genetic diversity in endemic species of oceanic islands; (2) provide examples of how patterns can best be interpreted in specific cases; and (3) offer a general perspective for the interpretation of patterns of genetic variation in endemic species.

FACTORS INFLUENCING LEVELS OF GENETIC VARIATION IN ENDEMIC SPECIES

Many factors influence the development of genetic variation within and among populations of introduced, native and endemic island plants. The principal factors deal with the physical dimensions of the islands, biological characteristics of the species (including mutation rates), modes of speciation, hybridization and human disturbance.

Our focus in this review is on endemic species, but, obviously, these same factors may also regulate such genetic variation in introduced and native plants. For these species, however, a conspicuous founder effect during the establishment of the initial population(s) should still be observable.

PHYSICAL DIMENSIONS

Oceanic islands differ in age, size, elevation, substrate and ecology. Islands that are larger and have greater habitat heterogeneity offer greater opportunities for speciation via adaptive radiation than do smaller islands of lower elevation and reduced ecological diversity (Stuessy *et al.*, 2006; Givnish, 2010). The distance of an island from a major source area can also play a role in influencing the level of genetic variation found in island populations. The closer an island is to a source area, the higher the probability that more than one immigration event might have taken place (MacArthur & Wilson, 1967), hence increasing the initial genetic diversity. The presence of neighbouring islands in complex archipelagos can also be significant.

Important concepts with regard to the physical dimensions of oceanic islands are that: (1) they do not have long life spans; and (2) they change through time. A new island being formed from a hotspot under the ocean floor may subside, erode and completely submerge after 6 Myr (Stuessy *et al.*, 1998a; Stuessy, 2007). Some oceanic islands are older, i.e. Fuerteventura in the Canary Islands at *c.* 20 Myr (Whittaker & Fernández-Palacios, 2007). With the loss of surface area also comes a reduction in elevation and a loss of ecological zones. This has a marked impact on the populations on the island, eventually resulting in the extinction of all taxa when the island disappears under the ocean.

Floristic ontogenies also develop in these geomorphological changes to the islands. The initial stage of floristic development is immigration and establishment, followed by the development of specific and genetic diversity, eventual loss of diversity and, finally, extinction of the flora (Stuessy, 2007; Whittaker, Triantis & Ladle, 2008). Therefore, the interpretation of levels of genetic diversity in endemic

species must be performed in the context of island ontogeny and corresponding vegetational modifications. Ignoring such ontogenetic effects can lead to dubious conclusions with regard to the modes of speciation (i.e. Savolainen *et al.*, 2006; for comments, see Stuessy, 2006) and on the existence (or not) of presumptive founder effects (Stuessy *et al.*, 2012).

Another feature of importance on oceanic islands is catastrophes. Secondary volcanic events, usually occurring within the first million years or less, can devastate large areas through eruptions of ash and lava, accompanied by gas and mudflows. Hurricanes (or typhoons) can damage vegetation in certain sectors, particularly by snapping stems or blowing down trees. Earthquakes can also cause landslides and damming of ravines, and tsunamis, associated with submarine earthquakes, can have an impact on coastal vegetation. Not all major disturbances are negative, however, as they may create evolutionary opportunities by increasing reproductive isolation or promoting interspecific hybridization.

Pleistocene glaciation also played a major role in influencing the population number and size on islands. The most conspicuous impact has been to lower the sea level by *c.* 100 m (Donn, Farrand & Ewing, 1962). In some cases, islands that had previously been isolated by the sea have been physically joined, as is the case with the present Molokai, Lanai, Maui and Kahoolawe in the Hawaiian Islands (Ziegler, 2002), thus facilitating gene flow among populations, including possibilities for interspecific hybridization. For single isolated islands, however, the impact would have been confined to a lowered, but then later restored, coastline. On an extremely high elevation island, such as Hawaii or Tenerife, Pleistocene cooling would have resulted in the lowering of vegetation zones by several hundred metres.

BIOLOGICAL CHARACTERISTICS

Other factors that influence levels of genetic variation in island populations are the biological characteristics of the colonizing organisms. Obviously important are adaptations for general survival, particularly physiological attributes, allowing populations to become established in the new island environment. Noteworthy features are dispersal abilities, mating systems and generation times. The levels of genetic variation encountered will also depend on the actual sizes and numbers of populations that develop, with larger and more numerous populations tending to accumulate more variation than smaller ones (Frankham, 1996; Crawford *et al.*, 2001).

Some species on oceanic islands have (or originally had) morphological features suited to long-distance dispersal, such as barbs on fruits or fleshy edible

fruits, but these features become negative adaptations for remaining on the islands and are sometimes lost (Carlquist, 1966a, b; Cody & Overton, 1996). These features, by themselves, do not impact directly on genetic variation in the founding population, but are often well developed in successful families (i.e. Asteraceae) in which taxa have great dispersal capacity combined with selfing and/or short generation times. That is, efficient dispersal is a part of the successful colonizing syndrome (Carlquist, 1974). These species, on arrival on a new island, are especially pre-adapted for the development of large populations that harbour conspicuous genetic variation (Crawford *et al.*, 2009). If the colonizers are exceptional dispersers, it becomes more probable that two or more introductions will occur, resulting in broader dispersal within the island and hence contributing to the levels of genetic variation. The number of outcrossed seeds within fruits being dispersed can also play a significant role. Polyploid colonizers, particularly neopolyploids, also have an advantage because of the expression of many duplicate loci (Crawford & Stuessy, 1997; Crawford *et al.*, 2009).

Breeding systems also regulate the levels of genetic variation in populations of oceanic islands. Herbert Baker (1955, 1967) suggested that the most successful immigrants should initially be selfers, because only one colonizer is needed to set seed and develop a new population. Many studies have tested this hypothesis over the past 30 years, often referred to as 'Baker's rule', and, in general, it seems to hold, with some exceptions (Crawford *et al.*, 2009), although thorough studies of island lineages are rare (for positive steps in this direction, see Bernardello *et al.*, 2001 for the Juan Fernández Islands, and Chamorro *et al.*, 2012 for the Galapagos Islands). In addition, recently developed theory casts some doubt on the general pattern of the association of dispersal and selfing, and suggests rather that adaptation favours a dispersal-outcrossing syndrome when both parameters are free to evolve (Cheptou & Massol, 2009; Massol & Cheptou, 2011; Cheptou, 2012). All other factors being equal, a population that evolves towards outcrossing will be better suited for the accumulation of higher levels of genetic variation, and a tendency towards dioecy (often via monoecy, gynodioecy, etc.) has also been well documented in oceanic island floras (Carlquist, 1974; Baker & Cox, 1984; Sakai *et al.*, 1995).

The generation time of immigrants to oceanic islands is also a factor that will regulate the development of genetic variation within populations by influencing the rates of recombination. In general, few successful island immigrants are large trees. Most groups, especially those that have radiated extensively and adaptively, such as the silverswords

or Campanulaceae in Hawaii, were derived from herbaceous colonizers, some of which acquired woody tissue during evolution and now occupy shrubby or tree niches on the islands. Large endemic tree species exist on some oceanic islands, such as *Drimys confertifolia* Phil. (Winteraceae) on the Juan Fernández Islands, but this is not common.

The size of a founding population and the number of generations in which the population remains in a bottleneck have a strong effect on genetic diversity (Templeton, 2006). Loss of diversity will be greater in smaller populations, and loss will continue through the generations in which the populations remain small. Drift will be inversely related to the effective population size ($1/2N_e$) (Frankham, Ballou & Briscoe, 2010: chapter 8), and the loss of heterozygosity will continue exponentially through the generations whilst the population sizes remain small.

MODES OF SPECIATION

Another important factor that needs to be carefully evaluated in interpreting genetic variation in endemic species is the mode of speciation. Some types of speciation are extremely rare in island systems, particularly neopolyploidy, involving either allopolyploidy or autopolyploidy. These mechanisms have rarely been documented for oceanic islands, although island lineages often exist at ancient polyploid levels (Stuessy & Crawford, 1998; Crawford *et al.*, 2009). Aneuploidy and dysploidy, involving gain or loss of single chromosomes, are likewise quite rare on isolated islands (Carr, 1998; Stuessy & Crawford, 1998). Perhaps the most conspicuous examples of such an evolutionary mode are in an endemic lineage of *Dubautia* Gaudich. (Asteraceae) in Hawaii, which changed from a base number of $x = 14$ to $x = 13$ (Carr, 1998, 2003a), and the remarkable increasing and decreasing dysploid series in *Sideritis* L. (Lamiaceae) of Macaronesia (Barber *et al.*, 2000). Such chromosomal alterations, however, are not common in islands.

The greatest impact on the levels of genetic variation within and among populations of endemic species derives from cladogenesis or anagenesis. These are two principal modes of speciation that yield species endemic to an island or archipelago (Stuessy, 2007). Cladogenesis occurs when populations divide spatially, and each portion changes morphologically and genetically to such an extent that two or more species result. This mode is encountered frequently in the origin of large adaptive complexes, so often cited to illustrate processes of island evolution (Carlquist, 1974). The genetic consequences of such splitting events are the division of the original gene pool into genetic subsets. The end result of this usually rapid process on islands are species that are morphologi-

cally quite distinct and adapted to divergent habitats, and that harbour low levels of genetic variation within each set of populations (i.e. in the Hawaiian silverswords, Witter & Carr, 1988; in *Dendroseris* D. Don, Asteraceae, in the Juan Fernández Islands, Crawford, Stuessy & Silva, 1987a). Exactly how speciation at the diploid level has progressed will affect the levels of genetic variation observed. An origin via peripheral isolates (Levin, 1993) will result in an unbalanced genetic spectrum, with more variation remaining in the parental taxon and much less in the newly derived one (Crawford, 2010). A more equal splitting of populations, such as a vicariant event (i.e. lava flow), will result in more equal genetic partitioning.

Each case must be examined carefully. For example, in Hawaiian *Bidens* L. (Asteraceae), there has been extensive radiation and speciation, but rather high isozyme variation is observed within each species (higher than in continental selfing species and comparable with many outcrossing continental species of the genus), and no genetic differentiation is seen among island species (Helenurm & Ganders, 1985). This suggests that speciation has occurred with divergence at only a few loci, and that isozymes neither control nor are linked to traits under divergent selection. These species are high polyploids and have a mixed mating system, however, which again emphasizes the complexity of factors that can influence observations with any marker. By contrast, in *Tetramolopium* (Asteraceae), also from the Hawaiian Islands, and mentioned above, there is low isozyme diversity within and divergence among the morphologically and ecologically diverse species (Lowrey & Crawford, 1985). In both of these insular lineages, it appears that substantial genetic variation exists for loci involved with adaptive divergence and speciation.

Anagenesis, however, involves the survival and proliferation of an immigrant population over many generations without splitting events (Stuessy, Crawford & Marticorena, 1990). Through mutation and recombination, genetic variation continues to accumulate over millions of years until the overall level of genetic diversity may approximate or even surpass that of the source (parental) populations (Stuessy *et al.*, 2006). Therefore, the end result of this process may be relatively high levels of genetic variation in endemic island species. Anagenesis is more probable in islands of low elevation and low habitat heterogeneity (Stuessy *et al.*, 2006).

HYBRIDIZATION

Another factor that can contribute to higher levels of genetic variation within populations is interspecific hybridization. In some oceanic archipelagos, such as the Juan Fernández Islands, hybridization is rela-

tively uncommon (Pacheco, Stuessy & Crawford, 1991; Stuessy *et al.*, 1998b). In other archipelagos, however, such as in Hawaii (Carr, 2003b; Friar, Cruse-Sanders & McGlaughlin, 2007) or the Canary Islands (Francisco-Ortega, Jansen & Santos-Guerra, 1996), hybridization has been frequently documented between endemic species. The closer the genetic similarity between the island taxa in question, the more easily they might be expected to hybridize. However, the greater the genetic difference between the species that are hybridizing, the greater the degree of likely genetic mixture in the hybrid populations. However, different molecular markers could give different pictures of gene flow between species, with neutral markers more easily exchanged than loci that underlie traits adaptive in particular habitats, e.g. under selection (Yatabe *et al.*, 2007; Kane *et al.*, 2009).

HUMAN DISTURBANCE

Most significant on oceanic islands, and well known to most biologists (i.e. Heywood, 2011), is the human impact on the environment during historical (and sometimes prehistoric) time. A good survey of major impacts on native vegetation in islands from humans is available in Caujapé-Castells *et al.* (2010: fig. 2). It should be emphasized, however, that, despite the obvious and well-documented negative impact of humans on the population number and size of endemic island plant species, less attention has been given to the negative *genetic* impact from such activities.

The most serious and direct impact on the population number and size in island ecosystems comes from the cutting of forests. These are cleared to build houses, to prepare land for domesticated crops and to yield pasture to raise cattle, sheep and goats. The harvested wood has also been used for construction as well as the refitting of ships that visited the islands, and as firewood for ships during the steamer period.

Fire has also been a major factor in the destruction of native forests on islands. Some have been burned intentionally to allow the development of pastures or to allow the cultivation of food plants, or just for a whim, such as that started in Valle Inglés on Masatierra (Juan Fernández Islands) by men heading to the California gold fields in 1849 (Woodward, 1969). Some fires start accidentally, such as that which occurred on Masafuera in 1992 when 70 ha burned (Barria, 1996), apparently caused by a fisherman's cooking fire spreading into the native vegetation [I. Leiva (San Juan Bautista, Robinson Crusoe Island, Chile), pers. comm.].

Another serious disturbance of the native and endemic vegetation of oceanic islands has originated from pressures associated with introduced plants and animals, again with an impact on population

number and size of endemic plant species. Many plants were brought to island ecosystems as cultivars for food or ornament, and many others were introduced inadvertently together with baggage, foodstuffs, feed for livestock, etc. Numerous studies have chronicled the devastation caused by weedy invasive species in Hawaii (Smith, 1985; Cuddihy & Stone, 1990), the Galapagos Islands (Lawesson, 1990), the Juan Fernández Islands (Wester, 1991; Matthei, Marticorena & Stuessy, 1993; Swenson *et al.*, 1997; Greimler *et al.*, 2002) and world-wide (Kueffer *et al.*, 2010). Similar pressures have arisen from introduced domesticated animals. One example comes from Juan Fernández, where *Solanum fernandezianum* Phil. was nearly extinct, but, when cattle were removed from a valley, this species came back in large numbers [G. Anderson (University of Connecticut, Storrs, CT), pers. comm.].

EXAMPLES OF INTERPRETATIONS OF PATTERNS OF GENETIC VARIATION

To emphasize the difficulties with the interpretation of causes of the observed genetic variation in plants of oceanic islands, we provide examples from the literature that illustrate different conditions and contexts. The important point, and the principal message of this article, is that many factors are potentially responsible for regulating the levels of genetic variation within and among populations of island species. For invasive species that have been recently introduced to an island, the main controlling factors are the biological characteristics that allow the successful establishment of a reproducing population, the breeding system and the initial founder effect. Endemic species require other perspectives.

EXAMPLE DEALING WITH A FOUNDER EFFECT

The first example deals with low levels of genetic variation in islands that are indeed a result of a founder effect, but in an introduced, rather than endemic, species. *Rubus alceifolius* Poir. (Rosaceae) is a wide-ranging species throughout south-eastern Asia (Thailand to Sumatra), which has also been introduced to Australia and to Madagascar and some smaller Indian Ocean islands (Mayotte, La Réunion, Mauritius). Amsellem *et al.* (2000) examined levels of genetic variability using amplified fragment length polymorphism (AFLP) markers with four primer pairs in 224 individuals of this species, plus an additional 30 individuals of other species of *Rubus* L. The analysis of genetic variation was by a simple matching algorithm, which provided an index of the breadth of genetic variability within the home region and each of the islands.

In its native range, *R. alceifolius* reveals considerable genetic variation within populations and among populations in the same general region. In the native region in south-eastern Thailand, six populations and 58 individuals; Vietnam, five populations and 31 individuals; Sumatra, three populations and 14 individuals), considerable genetic variability (divergence) was seen. The similarity values among the individuals in these regions are 0.77, 0.73 and 0.93, respectively. However, there was less genetic variability in populations that had been recently introduced to the islands, especially to the smaller islands. On the large continental island of Madagascar (19 individuals analysed from eight locations), moderate genetic variability prevailed (0.83 similarity values among individuals), somewhat higher than in south-eastern Asia. By contrast, the populations sampled from the smaller islands of Mayotte (eight individuals from uncertain localities), La Réunion (75 individuals from 67 documented locations) and Mauritius (seven individuals from two localities) showed high similarity values (0.99, 0.99 and 0.98, respectively). Each contained only a single genotype, and it is likely that all derived originally from part of the same clone. This is a clear indication of low levels of genetic variability probably resulting from a founder effect, perhaps even during historical time.

EXAMPLE DEALING WITH THE PHYSICAL DIMENSIONS OF ISLANDS

Changes that transpire in the island landscape, resulting from subsidence and erosion, will have a significant impact on the number and sizes of populations of endemic species. Common alterations are the broadening of valleys, causing them to become lower and drier, plus the lowering and drying of mountain slopes. During this process, the total land surface area is greatly reduced, which also affects the ecological zonation and attendant vegetation types across the island. An excellent example of this phenomenon is Lord Howe, which, at 6 Myr, is already a very senescent island. Recent population genetic studies on the two remaining endemic species of palms, *Howea belmoreana* (C. Moore & F. Muell.) Becc. and *H. forsteriana* (F. Muell.) Becc. (Savolainen *et al.*, 2006), have suggested that these two might have evolved sympatrically, because of their present close association in a small area. An alternative interpretation, however, is that these two species may have evolved allopatrically when the island was much younger (Stuessy, 2006), the close geographical association now observed resulting from compaction of the remaining flora as the island subsided and eroded.

A useful example of the important effect of the size and age of islands on the levels of genetic diversity

is provided by studies on populations of *Santalum austrocaledonicum* Vieill. in the New Caledonian archipelago (Bottin *et al.*, 2005). Four hundred and thirty-one individuals in 17 populations were analysed for eight polymorphic microsatellite loci. These populations were distributed into three different islands/regions: Grand Terre (168 individuals sampled from six populations; 16 350 km²); Ile des Pins (61 individuals sampled from two populations; 152 km²); and the Loyalty Islands, a group of three smaller islands, consisting of Lifou (93 individuals sampled from three populations; 1196 km²), Maré (61 individuals sampled from three populations; 650 km²) and Ouvéa (48 individuals sampled from three populations; 132 km²). Levels of genetic diversity, as measured by the observed heterozygosity and mean number of alleles, are as follows: Grand Terre (0.69, 16), Ile des Pins (0.74, 10.25), Lifou (0.40, 4.5), Ouvéa (0.39, 3.63) and Mare (0.16, 2). Because not all sampled populations were the same size, correlations were performed to assess the impact of population size on the observed genetic diversity, but no positive correlation was found. The New Caledonian archipelago is old, with Grand Terre with an age of approximately 37 Myr (Pillon, 2012) having been formed earlier (perhaps up to 80 Mya), but re-emerging during the late Eocene. The Loyalty Islands are much younger, having earlier been totally submerged and then uplifted again only at *c.* 1.8 Mya (Picard, 1999). Ile des Pins, now separated to the south-east of Grand Terre, was probably connected during the last glaciations some 9000–14 000 years ago (Stevenson, Dodson & Prosser, 2001), and hence may reflect the more ancient pattern of higher genetic diversity, even though these populations are now on a recently separated and much smaller island. In the Loyalty Islands, Lifou and Ouvéa show levels of observed heterozygosity of 0.40, but this is much lower (0.16) on Maré. The mean number of alleles also follows a similar pattern, with Grand Terre with 16, Ile des Pins with 10.25, Lifou with 4.5, Ouvéa with 3.63 and Maré with only two. From this example, island age and size are most probably fundamental in helping to regulate the levels of genetic diversity. All other factors being equal, an older island and a larger island should harbour populations with more diversity than younger and smaller islands (MacArthur & Wilson, 1967).

EXAMPLE DEALING WITH THE BIOLOGICAL CHARACTERISTICS OF ENDEMIC SPECIES

The biological characteristic of population size in relation to genetic diversity is illustrated with *Pittosporum beecheyi* Tuyama and *P. chichijimense* Nakai, tree species endemic to the Bonin Islands, Japan (Ito, Soejima & Ono, 1997). The low level of genetic diver-

sity (as assessed with isozymes) documented in these two island endemics is believed to be caused by the small population sizes, especially in comparison with the endemic congener, *P. boninense* Koidz., which is estimated to have > 10 000 individuals on the same islands.

Breeding systems can also have an impact on the levels of genetic diversity in populations of endemic island plant species. In general, the available data from isozymes and DNA sequences show lower levels of genetic variation within inbreeding populations in comparison with outcrossing ones (Charlesworth, 2003). Among endemic island taxa, Weller, Sakai & Straub (1996), based on isozyme analyses in *Schiedea* (Caryophyllaceae), showed lower levels of genetic identities within self-compatible species in relation to outcrossing ones. Another example that examines this point in endemic oceanic island taxa is *Tolpis* Adans. (Asteraceae; Crawford *et al.*, 2006). Nearly all species of the genus are self-incompatible or the system is 'leaky' and plants can produce some self-seed ('pseudo-self-fertile'; Levin, 1996); only *T. coronopifolia* (Desf.) Biv. and *T. barbata* (L.) Gaertn. are uniformly self-compatible and have high selfing seed set. Results from isozyme analysis show that the two highly selfing species have lower genetic diversity than the primarily outcrossing species. A clear reduction in the levels of genetic diversity in self-compatible species endemic to oceanic islands, however, has not been uniformly reported. In fact, this has clearly *not* been the case in general with the Canary Islands or the Juan Fernández Islands (Francisco-Ortega *et al.*, 2000; Crawford *et al.*, 2001). In both of these surveys, there is no positive correlation between high genetic diversity and outcrossing species, as might have been expected. This lack of correspondence may be a result of other factors that vary within the island setting, especially the evolution of wind pollination, reduction in suitable habitat, etc.

EXAMPLE DEALING WITH DIFFERENT MODES OF SPECIATION

The general types of speciation in plants of oceanic islands are somewhat more limited than in continental regions. Conspicuously rare are modes of speciation that involve chromosomal change; chromosomal stasis normally occurs in island lineages (Carr, 1998; Stuessy & Crawford, 1998). This perforce largely excludes evolution via allo- or autopolyploidy and also rapid speciation by means of chromosome dysploidy (Lewis, 1962). Homoploid speciation on islands has been documented, although only in a few cases (i.e. in *Scaevola* L., Goodeniaceae, in Hawaii, Howarth & Baum, 2005; *Argyranthemum* Webb, Asteraceae, in the Canary Islands, Fjellheim *et al.*, 2009).

The two major modes of speciation in islands are through cladogenesis, often accompanied by adaptive radiation, and anagenesis (Stuessy *et al.*, 1990). The former may result in a complex of closely related species, each adapted to different island environments and each having specific morphological adaptations. Anagenesis, or phyletic speciation, involves an immigrant species arriving on an oceanic island and, over time, accruing different morphological and/or genetic features, such that a new species designation seems warranted. The genetic consequences of speciation via cladogenesis or anagenesis in islands are very different. In the former, as a result of dispersal into different environments and strong selection, rapid change occurs in morphology that is not usually accompanied by genetic alterations that are measurable with commonly employed neutral molecular markers. Therefore, the levels of neutral genetic variation within and among populations of each derivative species remain low (Crawford, Whitkus & Stuessy, 1987b; Baldwin *et al.*, 1998). However, Savolainen *et al.* (2006) demonstrated that two island species can be highly similar at most neutral loci, but highly differentiated at several loci. This pattern suggests that the several outlier loci may be under selection or linked to loci under divergent selection. With anagenesis, the immigrant population changes over time and accumulates genetic variation (as assayed via molecular methods) through mutation and recombination. The end result is a single new species that harbours considerable molecular genetic diversity, even as much as found in the progenitor populations of the source area (Stuessy *et al.*, 2006; Stuessy, 2007).

Specific examples of the levels of genetic diversity that may be encountered in oceanic islands involve *Dystaenia* Kitag. (Apiaceae) and *Acer* L. (Sapindaceae) in Ullung Island, Korea, a small island of only 1.8 Myr (Kim, 1985). *Dystaenia* is a genus of only two species, with *D. ibukiensis* (Y.Yabe) Kitag. occurring in Japan and *D. takesimana* (Nakai) Kitag. endemic to Ullung Island, which lies in the Eastern (Japanese) Sea 150 km east of Korea. Analyses with AFLP markers have shown *D. takesimana* to have equal (or even slightly higher) levels of genetic diversity than the progenitor species in Japan (Pfosser *et al.*, 2005). With AFLP studies in *Acer*, two progenitor-derivative species pairs have been analysed: *A. okamotoanum* Nakai from Ullung Island and its progenitor species *A. mono* Maxim. from Japan and Korea (Takayama, Sun & Stuessy, 2012a), and *A. takesimense* Nakai and its progenitor species *A. pseudosieboldianum* Kom. from Korea (Takayama, Sun & Stuessy, 2012b). *Acer okamotoanum* showed slightly lower levels of genetic diversity in terms of allelic richness and heterozygosity than its continental progenitor. *Acer takesimense*

harbours slightly lower genetic diversity and less than half the number of private and rare alleles than *A. pseudosieboldianum*. In all cases of anagenesis analysed so far, no geographical patterning of the observed genetic variation has been seen among populations of the endemic island species.

EXAMPLE DEALING WITH HYBRIDIZATION

The occurrence of interspecific hybridization in oceanic islands, particularly between endemic species, varies depending on the archipelago and organismal group. The genetic differences among congeneric endemic species are usually not great, such that few genetic mechanisms exist to keep species isolated. Artificial garden crosses can easily be made between species of the same genus and even between genera (Carr & Kyhos, 1986; Crawford *et al.*, 1987b; Motley & Carr, 1998; Carr, 2003b). The issue is whether or not species in the wild have the opportunity to come into crossing contact. Obviously, human activities can promote hybridization in the island setting (i.e. in the Canary Islands, van Hengstum *et al.*, 2012). In the Juan Fernández Islands, present hybridization is rare within the endemic flora, with only two cases having been documented (in *Gunnera* L., Gunneraceae, Pacheco *et al.*, 1991; in *Margyricarpus* Ruiz & Pav., Rosaceae, Crawford *et al.*, 1993). In the Hawaiian Islands and the Canary Islands, however, numerous naturally occurring hybrids have been documented (Francisco-Ortega *et al.*, 1996; Carr, 2003b). Friar *et al.* (2007) used neutral microsatellite loci to infer gene flow between two species of *Dubautia* (members of the silversword alliance), but the species remain distinct morphologically despite apparent gene flow. These authors suggest that strong selection is maintaining the two species. Thus, neutral markers may indicate hybridization, but the process may have little or no impact on evolution.

An example of interspecific hybridization that has affected levels of genetic variation involves *Argyranthemum* (Asteraceae) in the Canary Islands. This genus contains 23 species that are restricted to the Macaronesian Islands (Francisco-Ortega *et al.*, 1996), with most confined to the Canary Islands. Plastid DNA restriction site studies have been performed on these species, and the patterns of molecular variation have been analysed to understand relationships as well as to infer possible hybridization events. All evidence suggests that hybridization has played an important role in the evolution of species within the genus, with naturally occurring hybrid swarms having been documented (Borgen, 1976; Brochmann, 1984). Hybridization is also suspected of causing high levels of genetic variation

within some species [i.e. *A. adactum* (Link) Humphries]. This species harbours two separate molecular groups, differing by 21 restriction site changes, even though the morphology is constant and unifying. The point is that, in groups in which hybridization is known to occur, this may well be an important factor influencing the levels of genetic variation seen within and among populations.

EXAMPLE DEALING WITH HUMAN DISTURBANCE AND IMPACT

It almost goes without saying that humans have had a strong influence on the ecosystems of oceanic islands. A good example of the impact of human-related activity on population number and size with respect to genetic variation comes from an AFLP study (including two plastid microsatellites) on populations of *Scalesia affinis* Hook.f. (Asteraceae) in the Galapagos Islands (Nielsen, 2004). Seven populations of this endemic species were examined with AFLP four primer combinations, resulting in 157 polymorphic markers suitable for scoring. Populations on the island of Isabela were distinctly different from those on Santa Cruz and Floreana islands. As expected, smaller populations harboured less genetic diversity than larger populations. The small population on Santa Cruz, for example, had the lowest value of AFLP diversity (0.185) in contrast with the other populations that ranged from 0.200 to 0.248. Some of the populations have become smaller only recently. The author revisited populations (the samples for her recent study were taken in 1998 and 2000) that were earlier inventoried in 1974, and a conspicuous reduction in population sizes was apparent, particularly in the populations on Santa Cruz and western Floreana. Nielsen (2004) suggested that domestic animal grazing, especially donkeys, caused a loss of plants within these populations.

PERSPECTIVE FOR THE INTERPRETATION OF PATTERNS OF GENETIC VARIATION

The main purpose of this article has been to emphasize that the interpretation of patterns of genetic variation within endemic species of oceanic islands is not a simple matter. Focus in the past has been heavily biased towards invoking the founder effect to explain low levels of neutral genetic variation in endemic species. Although the founder effect most certainly must have been a factor in reducing genetic variation through drift in the surviving immigrant population, we suggest that this impact has long been obscured as speciation has ensued and genetic changes have taken place over many generations (Stuessy *et al.*, 2012). We predict that the age of

genomics (see above) will eventually allow the dissection of the genetics of adaptive divergence and will be able to go beyond marker diversity in understanding the role of founder effects in radiation on islands. The recent study by Kolbe *et al.* (2012) is an attempt to resolve this question, although it deals with only incipient phases of population divergence and not with speciation.

To interpret the patterns of genetic diversity within and among populations on oceanic islands requires an examination of several possible factors. Over geological time, the physical environment of an island can change dramatically, brought about by volcanism, erosion and subsidence, all of which may have an impact on specific and genetic diversity (Stuessy, 2007; Whittaker, Triantis & Ladle, 2008). Different modes of speciation within an island can also influence the levels of genetic variation in each endemic taxon (Stuessy, 2007). The biological characteristics of the species themselves will also play a role in influencing the levels of genetic variation observed. Finally, human activities of many different types have combined to reduce the population number and size of many endemic species, in some cases resulting in extinction. Therefore, the successful interpretation of the observed levels of genetic diversity in populations of endemic species of oceanic islands requires a broad understanding of the organisms and their oceanic environment.

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