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REVIEW

Genetics, Evolution, and Conservation of Island Plants

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Abstract Islands are ideal model systems for testing ecological and evolutionary theory. This article reviews and synthesizes the findings of 24 studies of population genetics of island plants to gain insight into ecological and evolutionary processes on these unique, insular habitats. The studies reviewed found evidence for limited gene flow among islands and high genetic structure, but few tested for isolation by distance or among models of gene flow. Few studies compared diversity on islands with mainland populations or tested for bottlenecks, and the small number that did produced split results. Studies of rare species generally found that multiple islands would need to be protected to preserve genetic diversity. This review shows that surprisingly little work has been done to test theory using studies of population genetics on islands, and further work on testing among models of gene flow and examining population bottlenecks would be especially useful.

Keywords Conservation genetics · Evolution · Founder effect · Genetic bottleneck · Gene flow · Isolation by distance · Rare species · Island biogeography · Phylogeography

Islands as Models for Evolutionary Processes

Islands have long been important systems in ecology and evolutionary biology. Darwin's work on finches on the Galapagos Islands demonstrated adaptive radiation of these birds to new habitats and food types, becoming a foundational case of the action of evolution (Weiner 1994), and MacArthur and Wilson (1967) developed one of the seminal models of community diversity using islands as model systems. Islands have several characteristics which have made them so useful for biological studies.

First and foremost, islands are by their very nature isolated, which restricts the movement of organisms. This fact has profound implications for the processes of life on these unique habitats at every level of biological organization, and affords ideal opportunities to examine spatial patterns of dispersal and migration. Furthermore, islands and coastal habitats are extremely dynamic. We can watch islands form as volcanoes erupt, and we can observe beaches erode away and reform in new locations after a single severe storm. The fact that islands are so dynamic is conducive to rapid changes in population and evolutionary dynamics that can be observed in real time. Finally, islands often occur as groups or chains of many or even thousands of features such as atolls, cays, or archipelagos, thus providing replicated units that are, as with replicated experiments, particularly powerful for determining causes of biological patterns. Thus the insular, dynamic and repeated nature of islands makes them ideal for studying many biological processes.

These attributes of islands also make them ideal for studies of population genetics. Since the inception of the field, population geneticists have used molecular markers to examine such phenomena as rates of gene flow, degree of genetic isolation, the extent of founder effects, and the rate of evolution. By conducting population genetic studies on islands, it is possible to test predictions drawn from population genetic theory, providing empirical evidence which helps to validate and refine these models. In turn, population genetic data obtained from islands can provide

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useful information on both current and historical biological processes such as the movement of individuals, often with a higher degree of confidence than can be obtained from populations in a more continuous distribution in mainland areas. Population genetic data from islands is thus highly useful both for testing theory and for uncovering processes occurring over space and time, which is also important for informed conservation and restoration programs.

Despite the suitability of islands for addressing population genetic questions and the fact that islands have been used both directly and metaphorically in genetic theory, a relatively small number of plant population genetic studies on true islands have been performed. But the studies that have been done are informative and shed light on population and evolutionary processes. The purpose of this article is to review studies of plant population genetics that have occurred on oceanic islands and on coastal dunes and mangroves that occur at least in part on true islands and to use these studies to address several fundamental questions of population genetic theory and to inform management and conservation.

Predictions of Population Genetic Theory

Early in the history of population genetics, it was widely debated whether gene flow could be sufficiently restricted to cause genetic differences among local populations (genetic structure), or if gene flow was strong enough that all populations were highly genetically similar (panmictic). This was one of the central debates between two of the founders of population genetics and the modern evolutionary synthesis, R. A. Fisher and Sewell Wright. Fisher predicted high rates of gene flow and homogenous populations, while Wright expected differences among populations and the maintenance of genetic structure (Provine 1989). The degree to which populations are distinct is of fundamental importance for many processes, not the least of which relates to the efficacy of selection, the extent to which populations can adapt to local conditions, and the probability of sympatric speciation. At the heart of this debate is a conflict of views on both the degree and homogenizing effects of gene flow. While much theoretical work has been done by Fisher, Wright and many others to predict both of these attributes of gene flow, it has been for the empiricists to determine how much gene flow actually occurs, how rapidly genes are exchanged among populations, what factors influence these rates, and how much of an effect gene flow has in reducing differences among natural populations.

In a similar vein to the general debate on the degree and effects of gene flow, there has been widespread disagreement among population biologists on the genetic consequences of founding events. When a species arrives in a new area or undergoes a demographic reduction in population size, some genetic variation may be lost, an event known as a bottleneck (Nei et al. 1975; Barton and Charlesworth 1984). If this occurs, then the bottlenecked population could be less well able to evolve in response to environmental changes, since the loss of genetic variation would hinder the response of the population to selection (Falconer and MacKay 1996). Some theoretical and empirical studies seem to suggest that founder effects and bottlenecks can be both strong and frequent, which can be particularly damaging and worrisome for rare and threatened species (Avise and Hamrick 1996). On the other hand, some organisms such as many invasive or introduced species seem either not to have gone through a genetic bottleneck or not to have suffered much loss of fitness or evolutionary potential as a result (Hollingsworth and Bailey 2000; Richards et al. 2008; Ross and Shoemaker 2008; Suraez et al. 2008). Studies on islands are particularly well suited to addressing these issues and debates in population genetics.

Consequences of Isolation: Population Genetic Theory and Islands

Population genetic theory can be used to make specific predictions about genetic patterns expected on islands (Table 1). These hypotheses all presume that the insular nature of islands influences the movement of individuals and therefore genes within and among populations. Thus population genetic studies would be expected to show restricted gene flow among islands (H1), with gene flow decreasing with increased distance (H2). This restricted gene flow should then result in significant genetic structure, with more genetic variation among than within islands (H3) and a difference in genetic composition among islands (H4). Because the populations on islands are likely to be founded from mainland or other island sources, this should result in a population bottleneck due to a founder event (H5), causing a loss of genetic diversity (H6). Further, diversity should be lower the smaller and more distant the island (H7). While the insular nature of islands is expected to be important for all of these processes, particular islands need also be viewed in the unique geographical and historical contexts in which they occur. Thus gene flow should be affected not only by the isolation of islands but also by such landscape and seascape features as currents, mountain ranges and other disjunctions (H8). The changes in these features over time and the formation and disappearance of the islands themselves should leave a distinct genetic signature (H9), and the current population

Table 1 Shown are hypotheses about genetic parameters and patterns on islands drawn from population genetic theory

Gene flow
H1: Gene flow should be restricted among islands
H2: Gene flow should decrease with increasing distance (Isolation by distance)
Genetic structure
H3: More genetic variation among than within islands
H4: Populations on different islands are not panmictic
Founder effects
H5: Islands should show evidence of population bottlenecks
Genetic diversity
H6: Lower diversity on islands than mainland
H7: Lower diversity on islands that are smaller and further
Geography
H8: Gene flow should be affected by currents and other geographic features
History
H9: Historical processes such as glaciations or mountain formations should leave a genetic signature
H10: Genetic information can be used to infer these historical processes

genetic data should be useful to infer or confirm these historical processes (H10).

The Studies: A Microcosm of Population Genetics

In this article, I review 24 studies, taken from 20 publications, of plant population genetics on oceanic islands, including mangrove and coastal dune species that occur at least in part on true islands (Table 2). The studies were drawn from a literature search of the database of the Institute for Scientific Information (http://isiknowledge.com) using the search terms ‘plant,’ ‘population,’ ‘genetic,’ ‘island,’ ‘coast,’ and ‘dune.’ I excluded any studies that were not done on true islands or on coastal species occurring at least in part on islands or that did not use genetic markers. In any study that included more than one species, each species is given a separate identification number and is referred to throughout this article as a case (Table 2).

One interesting aspect of these studies is that they appear to be in many ways representative of the field of population genetics as a whole. The studies were conducted on species ranging from extremely rare and narrow endemics to widespread, invasive and weedy species (Table 2). They employed a range of molecular markers, including allozymes, AFPLs and RAPDs, microsatellites, and mitochondrial and chloroplast DNA sequences (Table 3). The studies also had a variety of objectives, including describing population structure, estimating rates of gene flow, determining clonal size and spread, inferring phylogenetic history, and conserving rare species (Table 2). These are many of the same objectives found in population genetic studies in general, including those not restricted to islands. Thus, these studies are somewhat of a microcosm of population genetics, and can therefore also be useful for drawing conclusions about the field as a whole.

While much of the information gained in these studies can be used to test theory and some were done for this reason, many were conducted explicitly with conservation aims in mind. Half (12 of 24) cases had some conservation intention (Table 2). Of these, three were done on invasive exotic species and the rest were on rare, threatened, or endangered species. This emphasis on rare species was a common theme among the studies, with 14 of the cases on species with narrow distributions. In fact, some of the studies included species that represent extreme cases of rarity. For example, Kim et al. (2005) sampled individuals of the shrub *Sonchus gandogeri* on the Canary Islands. Only two populations are known to exist on a single island, and the 44 individuals sampled represent almost every individual in the species currently alive. Thus, there was a strong emphasis on conservation genetics, especially of rare species, among these studies.

The studies varied in the molecular makers used and in sampling scheme, reflecting the variation in the different intentions of the cases (Table 3). Of the 24 cases, eight used allozymes, 16 used some nuclear genetic markers such as AFLPs, RFLPs, ISSRs, or microsatellites, and two used DNA from mitochondria and/or chloroplasts. One study (Ohsako and Matsuoka 2008) used sequence variation at a single coding gene (Adh).

There was a great deal of variation in the types of sampling schemes employed (Table 3). While most of the cases (20) took place within a single broad geographic region, four of the studies included multiple regions or continents. Eleven of the cases were on a single island or location. The average number of islands sampled was 3.3, with one study sampling 14 islands. Many of the studies included populations sampled along the coast. The number

Table 2 Studies of population genetics on islands and coastal dunes

ID	Reference	Purpose	Species	Status	Distrib
1	Batista et al. 2004	GS, CG, GF, IBD	*Myrica rivas-martinezii*	N	R
2	Batista et al. 2004	GS, CG	*Sideritis discolor*	N	R
3	Bushakra et al. 1999	GD, CS	*Lynonthamnus floribundus*	N	R
4	Castillo-Cárdenas et al. 2005	GS, GF, IBD	*Pelliciera rhizophorae*	N	R
5	Chung et al. 2004	GD, PH, CI, IBD	*Cunninghamia konishii*	N	R
6	Chung et al. 2004	GD, PH, CI, GF	*Cunninghamia lanceloata*	N	I
7	Clausing et al. 2000	PH	*Cakile maritima*	N	I
8	Clausing et al. 2000	PH	*Eryngium maritimum*	N	R
9	Dlugosch and Parker 2007	GS, GF	*Hypericum canariense*	E	W
10	Erickson et al. 2004	DG, FE	*Myrica cerifera*	N	I
11	Franks et al. 2004	GS, CG, CS	*Uniola paniculata*	N	I
12	Holzapfel et al. 2002	GS, LG, CG, IBD	*Dactylanthus taylorii*	N	R
13	Juan et al. 2004	GS, GF, CG, FE	*Medicago citrine*	N	R
14	Kim et al. 2005	GS, CG, GF	*Sonchus gandogeri*	N	R
15	Kingston et al. 2004	GS, CG, IBD	*Angiopteris chauliodonta*	N	R
16	Lönn and Prentice 2002	GS, DG	*Gypsophila fastigiata*	N	R
17	Maki and Morita 1998	GS, CI, GF	*Aster spathulifolius*	N	R
18	Maki 2001	GS, CG, FE, GF	*Aster miyagii*	N	R
19	Maki et al. 2003	GS, CG, GF	*Suzukia luchuensis*	N	R
20	Nettel and Dodd 2007	GF, PH	*Avicennia germinans*	N	W
21	Ohsako and Matsuoka 2008	GS	*Calystegia soldanella*	N	W
22	Subudhi et al. 2005	GS, CG, GF, IBD	*Uniola paniculata*	N	I
23	Suehs et al. 2004	GS, CG, CS	*Carpobrotus edulis*	E	W
24	Suehs et al. 2004	GS, CG, CS	*Carpobrotus acinaciformis*	E	W

ID Study identification number, *Reference* reference information, *Purpose* purpose of the study, *Species* focal species, *Status* status as a native or exotic, *Distrib* distribution, *GS* genetic structure, *CG* conservation genetics, *CS* clonal structure, *CI* comparing islands with mainland, *PH* phylogeography, *GF* gene flow, *GD* genetic diversity, *DG* demographic genetics, *LG* landscape genetics, *FE* founder event, *IBD* isolation by distance, *N* native, *E* exotic, *R* narrow, *I* intermediate, *W* widespread

of populations sampled varied from one to 33, with an average of 13. Some studies, such as Clausing et al. (2000), sampled only one individual per population, while most sampled more intensively within populations. The number of individuals sampled averaged 167.5 and ranged from 16 to 960.

Gene Flow and Genetic Structure

Population genetic theory predicts that gene flow among islands is likely to be limited, resulting in significant genetic structure (Table 1). Nineteen of the 24 cases examined genetic structure and/or gene flow (Table 2). Of the nine cases that quantified or examined gene flow, all found that gene flow was at least somewhat restricted among islands or populations (Table 4). Based on genetic differences among subpopulations, it is possible to estimate gene flow as Nm, or the number of migrating individuals per generation (Hartl and Clark 2007). Theory shows that a single migrating individual per generation can be enough to offset the effects of drift in small subpopulations and to maintain genetic uniformity among subpopulations (Conner and Hartl 2004).

Of the studies of gene flow on islands that estimated Nm, the average was less than one individual per generation (Nm=0.72), indicating gene flow that is low enough that subpopulations could diverge genetically. Several other studies did not provide quantitative estimates but did find evidence that gene flow was restricted or limited among populations or islands (Table 4). In a typical example, Maki et al. (2003) examined the genetics of the herbaceous island endemic *Suzukia luchuensis* in Japan and Taiwan. They found low genetic diversity on all islands sampled, strong genetic structure and differentiation among islands, and high gene flow within but low gene flow between islands.

Of the seven cases testing for isolation by distance (IBD) among islands, only one (Subudhi et al. 2005) found strong support for this hypothesis. In this study, Subudhi et al.

Table 3 Sampling design and molecular markers

ID	Regions	Islands	Pops	Individuals	Markers
1	1	3	3	47	RAPD
2	1	1	3	82	RAPD
3	1	1	8	29	RAPD
4	1	1	6	57	AFLP
5	1	1	11	146	AFLP
6	1	0[a]	10	54	AFLP
7	3	2	25	25	RAPD, ISSR
8	3	5	16	16	RAPD, ISSR
9	1	6	33	294	ITS, AFLP
10	1	1	3	670	Allozymes, microsatellites
11	1	14	20	960	Allozymes
12	1	2	17	146	RAPD
13	4	8	9	84	AFLP
14	1	1	2	44	AFLP
15	1	1	6	25	RAPD
16	1	1	16	NG	Allozymes
17	1	6	13	NG	Allozymes
18	1	3	18	466	Allozymes
19	1	4	9	225	Allozymes
20	3	5	33	382	ITS, cpDNA, AFLPs, microsatellites
21	1	3	19	91	Sequence variation in Adh gene
22	1	8	19	~325	AFLP
23	1	1	1	268	Allozymes
24	1	1	1	265	Allozymes
AVG	1.4	3.3	13	167.5	

[a] This is a mainland species in an island–mainland comparison

ID study case ID (shown from Table 2), *Regions* the number of broad geographic regions, *Islands* the number of islands, *Pops* the number of populations, *Markers* the types of molecular genetic markers used, *AVG* averages (given in the final row), *NG* information was not given in the study

(2005) examined the dune grass *Uniola paniculata* in the southeastern US using RAPD markers and found an increase in genetic differentiation with increased geographic distance. In a previous study of the same species using allozymes, Franks et al. (2004) found only weak support for the IBD hypothesis. The contrasting conclusions of these studies could have been due to differences in the genetic markers used or to differences in the populations sampled. The other studies testing for IBD did not support this hypothesis. For example, Castillo-Cárdenas et al. (2005) examined the tropical mangrove tree *Pelliciera rhizophorae* on the Columbian pacific coast and found strong genetic structure but no evidence for isolation by distance. Thus, there does not appear to be a strong support for the IBD hypothesis among these studies, but because most of the studies were not conducted with the objective of explicitly testing this hypothesis or among models of gene flow, such as the island or stepping stone models (Hartl and Clark 2007) in mind, it is not possible to conclude from this limited data set whether more distant islands are more likely to be genetically distinct. Additional studies directly testing the IBD hypothesis and among different models of gene flow would thus be highly illuminating.

Genetic structure, or the degree to which different populations are genetically distinct rather than homogeneous, is generally measured by the parameters F_{ST} or G_{ST} (single or multi-locus estimators, respectively) or θ (an unbiased estimator) of among versus within population differentiation. Of the 11 cases giving estimates of genetic structure, ten found evidence for significant population structure, with an average of 0.34 (Table 4). This level of genetic structure is much greater than zero (the expected level if all of the populations are genetically similar), and is also greater than previously found for plant species in general irrespective of their occurrence on islands (Hamrick and Godt 1996). Population structure can also be examined using a hierarchal analysis of molecular variation (AMOVA), which can further partition genetic variation into within and among individual, population, and regional components. The 11 studies using AMOVA found an average of 38.7% of variation among populations. Because many of the studies sampled more than one population per island, this already high amount of among population variation likely underestimates the degree of differentiation among islands. Thus as expected, island species seem particularly likely to show genetic differentiation and population structure. Although the exact levels of

Table 4 Gene flow and genetic structure

ID	Gene flow	IBD	Diversity	FST	Var among pops
1	very limited	No	$H_O=0.8$	0.487*	48.70%
2	NG	NG	$H_O=1.4$	0.149*	14.90%
3	NG	NG	NG	NG	NG
4	Nm=0.3–2.1	No	$H_E=0.2$	NG	26.50%
5	NG	No	$H_E=0.18$	NG	25%
6	Nm=1.65	NG	$H_E=0.29$	NG	12%
7	NG	NG	NG	NG	NG
8	NG	NG	NG	NG	NG
9	NG	NG	NG	NG	30%
10	NG	NG	$H_E=0.82$	NG	NG
11	NG	Weak	$H_E=0.15$	0.3*	NG
12	NG	No	NG	NG	NG
13	Restricted	NG	NG	0.2*	20%
14	Nm=0.29	NG	$H_O=0.38$	0.15*	NG
15	NG	No	$H_O=0.27$	0.43*	NG
16	NG	NG	$H_O=0.3\text{-}0.5$	NG	NG
17	Nm=0.26	NG	$H_O=0.97$	0.491*	NG
18	Nm=0.27	NG	$H_O=0.14$	0.477*	83%
19	Nm=0.04	NG	$H_O=0.23$	0.863*	85%
20	NG	NG	$H_O=0.87$	0.38*	33%
21	NG	NG	NG	0.176*	NG
22	Limited	Yes	NG	NG	47.80%
23	NG	NG	$H_O=0.33$	NG	NG
24	NG	NG	$H_O=0.65$	0.001	NG
AVG	Nm=0.72			0.342	38.72%

Shown is the case ID (from Table 2), estimates of gene flow, tests for isolation by distance, estimates of diversity as observed (H_O), or expected (H_E) heterozygosity, estimates of FST, GST or theta, and the percent of variation among populations from an analysis of molecular variation

IBD isolation by distance, *AMOVA* analysis of molecular variation, *NG* indicates that this information was not given in the study

*$p<0.05$, significant population structure is indicated by a value of FST

gene flow and genetic structure will obviously depend on the species, breeding system, size and degree of isolation of the populations and other factors, it is clear from this research that plants occurring on islands generally do show restricted gene flow and significant population structure.

Diversity

In population genetics, estimates of genetic diversity is made in a number of ways, including the percent of polymorphic loci, the number of alleles per locus, and the average observed (H_O) or expected (H_E) heterozygosity. Parameters such as percent polymorphic loci and alleles per locus are often strongly affected by which particular loci are chosen. These loci, rather than being a random sample of the genome, are often picked exactly because they are variable, making meaningful comparisons among studies of these parameters difficult. In contrast, heterozygosity is a more consistent measure and incorporates both total allelic diversity as well as the distribution of alleles among individuals, which is affected by such factors as inbreeding and assortative mating (Conner and Hartl 2004). I thus limit discussion of genetic diversity in this review to those studies providing estimates of H_O or H_E. It is important to note that for dominant markers such as RFLPs and AFLPs, heterozygotes are not distinguishable from homozygotes, so heterozygosity must be inferred, although this calculation is straightforward as long as the alleles are in Hardy-Weinburg equilibrium. For co-dominant markers such as allozymes or microsatellite, heterozygotes can be observed directly. Heterozygosity can vary from zero (no heterozygotes) to one (all heterozygotes).

Many of the cases (16 of 24) provided estimates of genetic diversity (Table 4). There was a wide range in these parameters with, for example H_E ranging from 0.15 to 0.82. While some studies showed limited diversity, many found relatively high levels of diversity, often higher even than expected based on species of similar breeding and life history characteristics not found on islands. For example, Batista et al. (2004) found higher than predicted diversity for two endangered island endemics.

While many of the studies measured diversity, very few examined causes of variation in diversity or tested diversity hypotheses. In one exception, Lönn and Prentice (2002) looked at diversity and demography in the perennial herb *Gypsophila fastigiata*. They found that there was lower diversity in peripheral than in central populations, indicating that some diversity was lost in the marginal populations. Future studies on causes of variation in patterns of diversity would clearly be useful.

Founder Effects

The likelihood that a species has experienced a population bottleneck due to a founder event should be particularly high for species occurring on islands. If an island is colonized by a small number of individuals from the mainland or other islands, and gene flow continues to be restricted among islands, then we expect that populations on islands would show a loss of diversity and other genetic signatures of a bottleneck. While this hypothesis is particularly suitable for testing on plants occurring on islands, only three of the 24 cases reviewed here have explicitly tested for a population bottleneck. Two of these: Juan et al. (2004) and Maki (2001), found evidence for a founder event or bottleneck while Erickson et al. (2004) did not. Juan et al. (2004) examined the genetics of all ten known populations of the endangered endemic *Medicago citrine* on islets of the Balearic archipelago and the Spanish coast. They base their conclusion that bottlenecks have occurred in this species on the very high amount of genetic structure among islands and the fact that Ibiza appears the most genetically diverse, with populations on other islands containing only a subset of this diversity and thus likely founded from by a small number of colonists arriving from the central population. Similarly, Maki (2001) also studied a rare species, in this case *Aster miyagii*, an herbaceous plant from the Ryukyu Islands in Japan. For this species, there was high genetic structure among islands. The southernmost island had low diversity and contained a subset of alleles on other islands, consistent with a founder event and subsequent bottleneck on this island. Erickson et al. (2004) examined population genetics in the shrub *Myrica cerifera* on a barrier island on the mid-Atlantic coast of the USA. Data from allozymes showed high levels of gene flow from outside populations via seed dispersal and no evidence for a bottleneck. The fact that there was not a bottleneck in this population while there was in the other two studies may have to do with geography. The barrier island studied by Erickson et al. (2004) is much closer to the mainland and other islands than the Ryukyu Islands or the Balearic archipelago are to mainland sources.

It is not possible to determine the prevalence of founder effects on islands because only three of these studies explicitly tested for a bottleneck and gave conflicting results. Although the preponderance of evidence for high genetic structure among islands in other studies (see section above) would indicate that bottlenecks are likely, many of the studies have also found relatively high levels of diversity, and genetic structure may be a result of restricted gene flow but not necessarily from a small number of founding events of only a few individuals. Thus, there is very limited information than can be used to examine the likelihood of founder effects on island species, and the data that do exist are equivocal. Testing for population bottlenecks and founder events on island species would thus be a highly useful objective for further studies.

History and Geography

Several of these studies have examined the extent to which the unique historical and geographical context in which the particular species under investigation occur have influenced population genetic processes, and in turn whether population genetic information can shed light on such historical processes. Six of the cases studied phylogeography or landscape genetics (Table 2). Two of these studies, representing 4 cases, (Chung et al. (2004) and Clausing et al. (2000)) were comparisons of two different species. Chung et al. (2004) found lower diversity in an island species (*Cunninghamia konishii*) occurring on Taiwan than in a closely related mainland species (*Cunninghamia lanceloata*) occurring on mainland China. They also found that the island species was likely derived from the mainland with probably several separate introductions, and that historical glaciations likely forced populations of *C. konishii* into refugia.

Similarly, Clausing et al. (2000) found that phylogeographic patterns in sea rocket (*Cakile maritima*) and sea holly (*Eryngium maritimum*) also appeared to have been influenced by previous glaciations events. Both Holzapfel et al. (2002) studying the endangered holoparasite *Dactylanthus taylorii* and Nettel and Dodd (2007) examining the mangrove *Avicennia germinans* found that such features as the directions of currents and the locations of potential frosts influenced genetic patterns in these species. Thus geographic history and current features seem to have a clear influence on population genetic processes based on the relatively small number of studies of island plants addressing these questions. Understanding broader scale geography and the effects of geographic features should thus play a key role in designing conservation strategies for species on islands. These results also indicate that population genetic studies of island species can continue to reveal a great deal of information on the geographic and geological history of the regions examined.

Clonal Structure

Many plants, in addition to sexual reproduction, can also reproduce clonally by spreading through rhizomes or other structures. While the ability of a plant to produce clonally is often obvious, the extent of clonal versus sexual reproduction in natural populations is often more cryptic, especially because clonal offshoots may frequently become physically separated from the parent. Genetic markers offer a very useful tool for uncovering the extent of clonal reproduction. In some cases, studies using genetic markers have found vast expanses of a single genotype, indicating extensive clonal growth in species like aspens (Mitton and Grant 1996). While there have not previously been theoretical predictions for the extent of clonal growth specifically on islands, it is possible that the potential for clonal growth offers species an advantage especially in small or isolated populations, causing island species to be more likely clonal or to have greater clonal spread or structure than species occurring on the mainland. The ability to reproduce clonally would clearly seem to be advantageous if an individual arrived on an island too far from any potential pollen donors. Thus, there could potentially be more clonal species, or clonal growth could be more extensive, on islands than on the mainland.

While none of the studies here compared clonal structure between island and mainland species or populations, three of these studies (four cases) did examine clonal structure on species occurring on islands. Suehs et al. (2004) examined invasion dynamics of two alien *Carpobrotus* species on a Mediterranean island. They found that both species (*C. edulis* and *C. acinaciformis*) have above average genetic and clonal diversities, indicating limited clonal size and spread. They also found that *C. acinaciformis* relies more on clonal reproduction than on sexual recruitment and that clonal identity did not vary with distance in *C. edulis*. Franks et al. (2004) examined clonal structure in the coastal dune grass *Uniola paniculata*. They found that despite the potential for clonal spread in this species and the fact that few seedlings are observed in the field, the high clonal diversity found in this species indicates that clones appear to be small and highly local, and much of the recruitment was apparently from seed. Bushakra et al. (1999) examined the extent of clonality and genetic diversity in the Santa Cruz Island ironwood, *Lyonothamnus floribundus*. This study showed that this species has very extensive clonal growth, with large groves of thousands of stems genetically identical, though separate groves were genetically distinct. The extent of clonality thus clearly varies greatly among species, and the hypothesis that clonality aids colonization and establishment on islands has yet to be adequately tested.

Conclusions

The studies here reviewed can provide a number of conclusions about ecological and evolutionary processes on islands. First, there is clear evidence for a high degree of genetic structure and differentiation among islands, indicating that gene flow can be quite limited among these insular habitats. This validates the idea that dispersal among islands is restricted, with important implications for ecological and demographic processes as well as for evolution. Islands are especially likely to be “speciation laboratories” and to facilitate the development of novel adaptations and new species. This finding also has strong relevance for conservation, indicating that multiple islands must be the targets of conservation efforts if genetic variation is to be maintained.

Despite this finding of limited gene flow and strong genetic structure, there is little evidence for isolation by distance among islands. But because very few studies have tested this hypothesis, more work needs to be done to be able to draw strong conclusions about this or any model of gene flow. Similarly, few studies have examined population bottlenecks on islands, and those that have produced conflicting results. More research on bottlenecks and founder events on islands are needed to resolve this inconsistency.

The studies reviewed here also indicate that geography and history clearly influence genetic patterns of species on islands. Population genetic and phylogeographic studies of island species can continue to provide useful information to help uncover both current and historical ecological and evolutionary processes. Finally, the extent of clonal reproduction varies among island species, and the hypothesis that clonal reproduction benefits island species still needs to be tested.

Studies of the genetics of species on islands can clearly add to our understanding of evolutionary and ecological processes and provide information critical for the conservation of rare and threatened species. Islands are ideally suited for and offer a tremendous opportunity to test some of the most important and yet unresolved hypotheses of population genetic and evolutionary theory. We are best able to take advantage of this unique opportunity if future genetic studies of island species are conducted with theory in mind and, for example, are designed explicitly to test among models of gene flow, to test for the extent of population bottlenecks, or to examine factors influencing the amount and distribution of genetic diversity. Such carefully designed, hypothesis-driven studies would be the most likely to expand and deepen our understanding of ecology and evolution.

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