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INVITED REVIEW

Evolution on oceanic islands: molecular phylogenetic approaches to understanding pattern and process

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Abstract

By their very nature oceanic island ecosystems offer great opportunities for the study of evolution and have for a long time been recognized as natural laboratories for studying evolution owing to their discrete geographical nature and diversity of species and habitats. The development of molecular genetic methods for phylogenetic reconstruction has been a significant advance for evolutionary biologists, providing a tool for answering questions about the diversity among the flora and fauna on such islands. These questions relate to both the origin and causes of species diversity both within an archipelago and on individual islands. Within a phylogenetic framework one can answer fundamental questions such as whether ecologically and/or morphologically similar species on different islands are the result of island colonization or convergent evolution. Testing hypotheses about ages of the individual species groups or entire community assemblages is also possible within a phylogenetic framework. Evolutionary biologists and ecologists are increasingly turning to molecular phylogenetics for studying oceanic island plant and animal communities and it is important to review what has been attempted and achieved so far, with some cautionary notes about interpreting phylogeographical pattern on oceanic islands.

Keywords: colonization, diversification, ecology, evolution, islands, phylogeny, speciation

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Introduction

Islands have become synonymous with the study of evolution since the famous association between Darwin's theory of evolution by natural selection and the finches of the Galápagos Islands (Darwin 1859). In 1836 Darwin returned from his five year voyage around the world with a wealth of floral and faunal material, including skins from finches collected in the Galápagos Islands. These were passed to the ornithologist John Gould for analysis who described nine new species within four genera (Gould 1837), and the group has become one of the best known cases of adaptive radiation. Such island systems are attractive environments for studying evolution for a number of reasons: (i) they present discrete geographical entities within defined oceanic boundaries; (ii) gene flow between individual islands is reduced by oceanic barriers; (iii) their often small geographical size has made the cataloguing of flora and fauna easier than continental systems; (iv) despite their small geographical size they can contain a diversity of habitats and; (v) they are often geologically dynamic with historical and contemporary volcanic and erosional activity. In combination the above factors have manifested themselves in typically high levels of endemism within oceanic island systems, presenting a microcosm of the evolutionary process.

After several centuries of work describing and cataloguing species it is obvious that islands do harbour a great diversity of organisms, however, understanding their origins is not so obvious. For example, despite having become a textbook example of adaptive radiation the question of the origin of Darwin's finches has until recently remained open (Sato *et al*. 2001). This problem of understanding origins can only be addressed with an accurate reconstruction of the phylogenetic relationships within a group of species. Phylogenetic information will also help to determine the processes that have led to species richness within island ecosystems. Such species diversity can be the result of a number of factors; (i) the diversification of a founding

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population into an array of species differentially adapted to diverse environmental niches (adaptive radiation); (ii) multiple successful colonizations to an island from neighbouring islands or a continental land mass; (iii) the diversification of a founding population into a number of species caused by vicariant events such as lava flows and erosional events and; (iv) increased speciation through bottleneck and founder flush events (Templeton 1980; Carson & Templeton 1984). The diversity observed within any species group can be the product of any or all of these factors.

The ability to reconstruct the phylogenetic histories of taxa has been dramatically improved by the now fairly routine task of acquiring DNA sequence data from taxa. Also there have been significant developments for the phylogenetic analysis of this data. For these reasons recent years have seen an increasing number of molecular phylogenetic analyses of floral and faunal groups on islands, primarily the Canary Islands, Hawaiian Islands, Galápagos Islands, and the Caribbean Islands. What follows is not intended to be an extensive review of all such studies, but a critique of successes so far in terms of gaining an understanding of, and answering questions about, the origins of species diversity on islands. For details of methods of phylogenetic analysis employed in individual studies readers are directed to those papers and the wealth of literature on phylogenetic analysis of molecular data.

Adaptive radiations on islands

Givnish (1998a) defines the term adaptive radiation as 'the rise of a diversity of ecological roles and attendant adaptations in different species within a lineage', a phenomenon most apparent on oceanic islands (but see Givnish 1998a for earlier definitions). To effectively study an adaptive radiation in a rigorous, noncircular way requires a phylogeny that has been derived independently of the traits involved in that radiation (Givnish 1998a). To this end several recent studies of diverse oceanic island plant and animal groups have demonstrated that DNA sequence (or restriction site) data provides a powerful tool for studying species assemblages that appear to be the product of adaptive radiation.

Darwin's finches

Current classification has put Darwin's finches of the Galápagos Islands into three groups: (i) the ground finches, so named because they typically feed on seeds on the ground. This group is comprised of six species within the genus *Geospiza*; (ii) the tree finches which spend most of their time in foliage and vegetation. This group is comprised of 6 species within the genera *Cactospiza*, *Camarhynchus*, and *Platyspiza*, and; (iii) the warbler finches which resemble warblers in their small size and slender beaks. This group is comprised of two monospecific genera, *Certhidea* and *Pinaroloxias*. Phylogenetic analyses of mitochondrial DNA (mtDNA) cytochrome b (cytb) and control region (CR) genes and two nuclear copies of mtDNA genes (numts) by Sato *et al.* (1999; 2001) have demonstrated that this group is the result of a single colonization from the South American continent. Of 28 representatives of the main tribes of the family Fringillidae, the grassquit *Tiaris obscura* was revealed to be the nearest relative to the Galápagos finches. Sato *et al.* (2001) estimate from DNA sequence divergence levels that diversification within the *Tiaris* group began about 2–3 Ma (Million years ago) and this was soon followed by the separation of the ancestor of Darwin's finches. Within Darwin's finches, the warbler finch of the Galápagos islands is the result of the first diversification event, and is apparently the oldest species within the group. The second warbler finch from the Cocos Islands is more closely related to the tree finches. Of the tree finches, the single vegetarian species is divergent from the others and the result of an early divergence event within the group.

Phylogenetic analysis of major histocompatability complex genes and simulation analyses have been used to estimate the minimum number of founding individuals for the colonizing ancestral species of Darwin's finches to have been no less than 30 individuals (Vincek *et al.* 1997). Darwin's finches are known to fly in flocks and Vincek *et al.* (1997) postulate that the colonization may have occurred in an El Niño year when flocks are largest. During this period there is a also a greater occurrence of vegetation mats originating from rivers on the continent that may have acted as resting places for a flock of finches colonizing the Galápagos from the continent.

Hawaiian silverswords

The Hawaiian silversword alliance has been regarded as the best example of adaptive radiation in plants (Raven *et al.* 1992). The alliance comprises 30 species within the genera *Argyroxiphium*, *Dubautia* and *Wilkesia*, and all are endemic to the Hawaiian Islands. Species are found in a variety of habitats from desert-like settings to rainforest environments, with a diversity of life-forms occurring within the group: (i) trees; (ii) shrubs; (iii) subshrubs; (iv) mat-plants; (v) monocarpic and polycarpic rosette plants (vi) vines.

Early anatomical work by Carlquist (1959) revealed vegetative and reproductive characteristics uniting the silversword alliance with the western American tarweed subtribe Madiinae, suggesting the silverswords arose from a tarweed ancestor. Phylogenetic analyses of both chloroplast DNA (cpDNA) restriction site data (Baldwin *et al.* 1991) and sequence data from the internal transcribed spacer (ITS) region of nuclear ribosomal DNA (rDNA)

(Baldwin 1992; 1996; Baldwin & Robichaux 1995; Baldwin & Sanderson 1998) have confirmed this relationship and have shown that the Hawaiian silverswords are indeed derived from within a paraphyletic group of species within the tarweed genera *Madia* & *Raillardiopsis*. Baldwin & Sanderson (1998) have been able to make a conservative estimate of the time of diversification of the Hawaiian silverswords using an external calibration point based on the fossil record and palaeoclimatic data. Nearly all species of the continental tarweed group that gave rise to the silversword alliance occur in the summer-dry California Floristic Province. The vast majority of species are restricted to this region which began to change from a summer-wet to summer-dry climate approximately 15 Ma. Because the silversword alliance is nested within the California tarweed phylogeny their most recent common ancestor (MRCA) could not have arisen before the diversification of the tarweeds, which in turn must postdate the onset of the summer-dry climate of the California Floristic Province. Thus, by calibrating their phylogeny with an age of 15 Myr (million years) as a conservative estimate of the maximum age for the MRCA of the tarweeds, Baldwin & Sanderson (1998) estimated an age of 5.2 ± 0.8 Myr for the MRCA of the silversword alliance, which is about the time of origin of the oldest extant Hawaiian island, Kaua'i. The data do not preclude an earlier arrival of the MRCA of the silversword alliance, but if that were the case then all but one species that occurred on now submerged atolls must have gone extinct without colonizing and leaving descendants on younger islands.

The radiation of species within the Hawaiian silversword alliance appears to have occurred more recently and rapidly than diversification of the continental tarweed sister lineage (Baldwin 1997). Reconstructions of the ancestral morphological and dispersal characteristics onto the molecular phylogenies suggest that the ancestor of the Hawaiian silversword alliance was a herbaceous radiate plant with pappose disk fruits and characteristics conducive to external bird dispersal (Baldwin *et al*. 1998). Recent phylogenetic analyses by Barrier *et al*. (1999) may provide a mechanistic explanation for the adaptive radiation of the silversword alliance. They have obtained DNA sequence for the orthologs of two *Arabadopsis* floral homeotic genes, APTELA1 and APTELA3/TM6 from members of the silversword alliance and the tarweeds. Species of the silversword alliance are tetraploid in contrast to the diploid state of the closely related *Madia*/*Raillardiopsis* lineages, and both homeotic genes are present in two copies in the Hawaiian species but only one copy in the tarweeds. The results of the Barrier *et al*. (1999) phylogenetic analyses suggest the silverswords are an allopolyploid group descended from a hybrid between members of extant tarweed lineages. They conclude that a variety of genetic factors associated with allopolyploidy may have been critically important in the adaptive radiation of the Hawaiian silverswords. A hybrid constitution of the Hawaiian founder may have promoted the adaptive radiation of the silversword alliance, particularly given the ecological and morphological diversity of the tarweed lineages implicated in the hybrid MRCA. The presence of two divergent genomes would give the MRCA of the silverswords more genetic variation to respond to selection, and any chromosome pairing between the two hybrid genomes could increase the diversity of genetic segregants and resulting phenotypes.

Nesotes beetles of the Canary Islands

The Canary Island *Nesotes* form one of the more speciose coleopteran genera in the archipelago. Current taxonomy recognizes 19 species, one of which is divided into three subspecies. Several of these species occur on more than one island and the species of an individual island can occupy a range of habitats. For example, on Tenerife there are species associated with subalpine scrub (*N. altivagans*), pine forest (*N. elliptipennis*), laurel forest (*N. conformis*), shrubland areas (*N. transversus*), and xeric coastal areas (*N. helleri, N. fusculus*). Phylogenetic analyses of sequence data from the cytochrome oxidase II gene (COII) of mtDNA have revealed a complex colonization and speciation history (Rees *et al*. 2001a). Adaptive radiation has clearly featured in the evolution of this group and this is perhaps best exemplified by detailed examination of the species of Gran Canaria, the only island clearly identified as having a monophyletic assemblage of *Nesotes* species.

The five *Nesotes* species of Gran Canaria are descended from a single Gran Canarian ancestor (Rees *et al*. 2001a) and inhabit a range of niches; xeric coastal areas (*N. lindbergi* and *N. fusculus*), open areas and pine forests (*N. quadratus* and *N. piliger*) and laurel forest (*N. conformis*). Detailed sampling across the distributions of the Gran Canarian species and phylogenetic analyses of mtDNA COII gene sequences has revealed this group to be most probably derived from a MRCA ancestor resembling the extant species *N. quadratus* (Fig. 1). *Nesotes quadratus* has the broadest distribution of the Gran Canarian species inhabiting open and pine forest areas, and the diversification into xeric, rainforest and high altitude habitats appears to have been both recent and rapid (Fig. 1). Phylogenetic analyses of DNA sequence data suggest there has been two colonizations of the xeric coastal habitat (*N. lindbergi* and *N. fusculus*), two colonizations of the laurel forest (*N. conformis*) and one of the higher altitudes (*N. piliger*). Rees *et al*. (2001b) view this group as being in an early stage of diversification/speciation, with different morphotypes in different habitats. Other islands within the Canarian archipelago such as Tenerife may have undergone similar phenomena but with subsequent extinction and recolonization masking this.

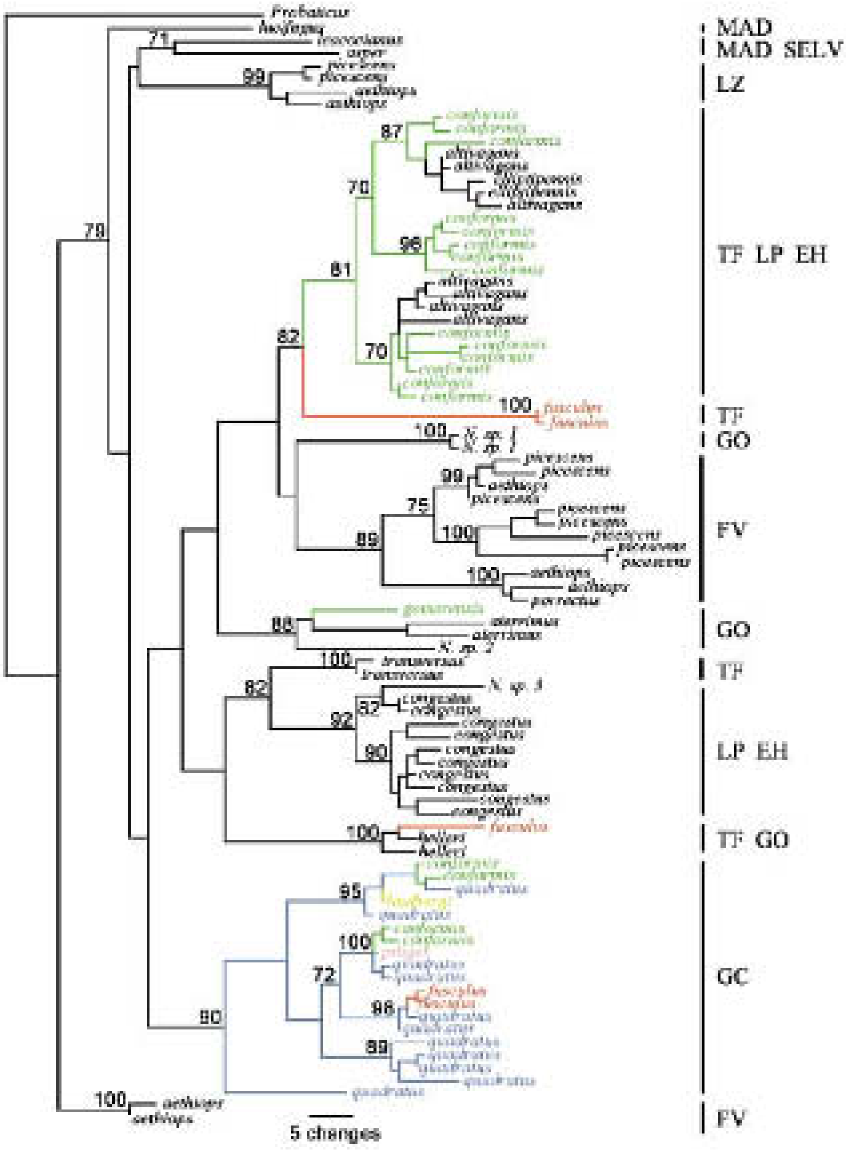

Fig. 1 A maximum parsimony tree for Macaronesian *Nesotes* beetles using mtDNA COII sequence data. Bootstrap values indicate nodes gaining more than 70% support with character weighting following two rounds of successive character reweighting. Composition of clades by island is indicated by the codes MAD (Madeira), SELV (Salvages), TF (Tenerife), LP (La Palma), EH (El Hierro), GO (La Gomera), GC (Gran Canaria), FV (Fuerteventura) and LZ (Lanzarote). The clade of Gran Canarian species has been colour coded to highlight the conclusions of Rees *et al*. (2001b) that the ancestral species on this island resembled the extant species *N. quadratus* (blue) and diversified into the laurel morphotype *N. conformis* (green), high altitude morphotype *N. piliger* (pink), and xeric coastal species *N. fusculus* (red) and *N. lindbergi* (yellow). The species *N. fusculus* (red) and *N. conformis* (green, including the morphologically similar *N. gomerensis*) occurring on other islands are clearly the result of convergent evolution (modified from Rees *et al*. 2001a).

Other features of the Canary Islands *Nesotes* phylogeny also suggest that much of the diversity within the group is the result of adaptive radiation. Several species have been recognized on the basis of traditional taxonomy as occurring on multiple islands. For example, *N. fusculus* is found in xeric coastal environments and has been described on Gran Canaria, Tenerife, and La Gomera. However, it is clear from the mtDNA phylogeny that this is a paraphyletic group, and that the '*fusculus*' phenotype has evolved independently in the xeric coastal environment on each of the three islands (Fig. 1). Similarly *N. conformis* has been described from the laurel forests of Gran Canaria, Tenerife, La Palma and El Hierro. Phylogenetic analyses clearly indicate the paraphyly of this group (Fig. 1). The '*conformis*' phenotype has evolved twice on Gran Canaria and once in the western islands. Phylogenetic analyses with more detailed geographical sampling (Rees *et al*. 2001c) have been used to infer an origin in Tenerife for the '*conformis*' morphotype, with subsequent colonization to La Palma and El Hierro. A morphometric analysis (unpublished data) has demonstrated the extreme convergence among the morphologies of the Gran Canarian and western island *N. conformis*. Additional to this, another laurel forest species, *N. gomerensis* of La Gomera has been considered closely related to *N. conformis*, but phylogenetic analyses reveal it to be of independent origin (Fig. 1).

Anolis lizards of the Greater Antilles

Anolis lizards feature prominently in the Caribbean fauna with 140 of the 400 species occurring there (Jackman *et al*. 1999). Within the Greater Antilles (Cuba, Hispaniola, Jamaica, and Puerto Rico) each island is inhabited by six different ecomorphs (species specialized to use particular structural microhabitats), with the exception of Jamaica with four and Puerto Rico with five. The presence of the same set of ecomorphs (crown-giant, grass-bush, trunk, trunk-crown, trunk-ground, and twig) on each island suggests that either each evolved once and then colonized other islands, or that each ecomorph evolved independently on each island. Losos *et al*. (1998) have used DNA sequence data from a region of the mtDNA to reconstruct phylogenetic relationships within the *Anolis* lizards of the Greater Antilles. Their results indicate that, with only two exceptions, members of the same ecomorph class from different islands are not related. Rather, the species assemblages on each island are the result of the repeated evolution of ecomorphs suggesting that adaptation is responsible. A similar situation appears to exist for spiders of the genus *Tetragnatha* of Hawaii. Gillespie *et al*. (1997) have used DNA sequence data from the 12S and COI genes of mtDNA to reconstruct phylogenetic relationships and their results indicate that different ecomorphs have evolved independently on different Hawaiian islands.

There are only two cases of the same *Anolis* ecomorph evolving twice on an island, and Losos *et al*. (1998) suggest that interspecific competition, known to be intense among anoles, may drive their adaptive radiation. From the observation of extensive adaptive radiation within the Greater Antillean anoles and studies of adaptation to structural habitat, Losos *et al*. (1997) formulated *a priori* predictions about how introduced populations should adapt to new structural habitats. In a long-term experiment populations of the lizard *A. sagrei* were introduced to small islands from a nearby source and their degree of morphological differentiation measured after a 10–14 year period. The direction of morphological differentiation was consistent with expectations based on the evolutionary diversification of *Anolis*, supporting the contention that environment determines the evolution of morphology. While the genetic basis of this differentiation is uncertain, Losos *et al*. (1997) contend that the parallel between differentiation in experimental populations and the differentiation of the diverse Caribbean *Anolis* fauna suggests similar processes acting at the micro and macroevolutionary time scale.

Hawaiian Drosophila

The *Drosophila* of the Hawaiian Islands are represented by more than 800 species that have evolved after an initial colonization more than 30 Ma involving one or maybe two original founders (Kambysellis & Craddock 1997). They have radiated into a wide variety of habitats spanning a range of altitudes and ecological niches in both wet and dry montane forests. Ecological divergence of the breeding niche involves not just the type of plant used for oviposition but also the part of the plant. Their evolution has been the subject of much interest with work having centred around the role of sexual selection (Carson 1978; 1986; Kaneshiro 1983; 1989) and founder events (Carson 1971; Carson & Templeton 1984). However, recently a molecular phylogenetic approach (Kambysellis *et al*. 1995; Kambysellis & Craddock 1997) has been taken to understand the adaptive radiation of this group in terms of ecological, morphological, developmental, physiological and behavioural aspects of female reproduction. Kambysellis & Craddock (1997) have analysed 39, primarily picture winged, Hawaiian drosophilid taxa using a 1 kilobase (kb) fragment of the *Yp1* yolk protein gene. In addition, to assess deeper relationships, they included a phylogeny of 15 more divergent Hawaiian drosophilids supplied by Rob DeSalle based on fragments of four mitochondrial and four nuclear genes. By tracing the evolution of ecological and reproductive characters onto a molecular phylogeny their results suggest that female reproductive strategies broadly correlate with ecological divergence in host plant and larval substrate. It appears that the most primitive Hawaiian drosophilids were fungus-breeders and ecological shifts occurred to decaying leaves, stems and fruit, bark, and finally to tree fluxes. Kambysellis & Craddock (1997) conclude that the evolution of the Hawaiian *Drosophila* appears to be the result of natural selection exerted by the breeding substrate together with sexual selection on male behaviour and morphology.

Multiple colonization and species diversity

Two assumptions, or null hypotheses, are often unstated but implicit with regard to island organisms. The first is that a given species group within an archipelago is the product of a single colonization event from a continent (or neighbouring archipelago). If this is false then the species group within an archipelago will be paraphyletic, and if it is true the species group will be monophyletic (Fig. 2a and b). However, if there has been back colonization from the archipelago to a continent this will also result in a paraphyletic island assemblage (Fig. 2c). Although apparently uncommon, this has been observed within the plant genus *Aeonium* in the Canary Islands that has colonized North Africa (Mes & Hart 1996; Jorgensen & Frydenberg 1999), and within chameleons. A recent phylogenetic analysis of chameleons using both molecular and morphological data (Raxworthy *et al*. 2002) supports an origin for the group in Madagascar with three dispersal events to Africa and a single dispersal to both India and the Seychelles. The second assumption is that for a given species group within an archipelago, the species assemblage of an individual island within the archipelago is the product of a single colonization event. This suggests within island diversification (either adaptive or nonadaptive) to be the mechanism of species diversity and has important

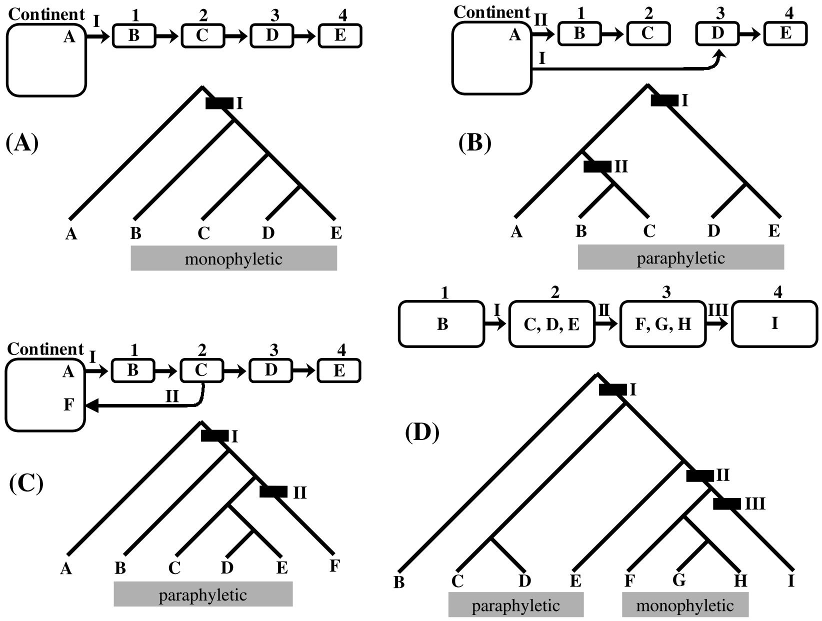

Fig. 2 Interpreting monophyly and paraphyly in terms of colonization history. (A) A scenario of a single colonization (denoted I on the island map and phylogeny) from the continent followed by sequential colonization from island 1–2 to 3–4. This sequence of colonization events gives rise to a single taxon on the continent and each island (taxa A-E). Such a colonization history will result in a monophyletic grouping of the island taxa in a molecular phylogenetic analysis of the group. (B) A scenario of a double colonization (denoted I and II) from the continent. Colonization I gives rise to taxa D and E on islands 3 and 4, colonization II gives rise to taxa B and C on islands 1 and 2. Such a colonization history will result in a paraphyletic grouping of the island taxa in a molecular phylogenetic analysis of the group. (C) A scenario of single colonization (denoted I) from the continent and back colonization (denoted II) to the continent. Such a colonization history will result in a paraphyletic grouping of the island taxa in a molecular phylogenetic analysis of the group. (D) A scenario of single colonization events (denoted I, II and III) from island 1–2 to 3–4. Colonization I gives rise to taxa C, D and E, and the lineage leading to taxon E is involved in colonization event II to island 3 resulting in paraphyly for the taxa of island 2. Colonization event III to island 4 occurs before the diversification of taxa F, G and H resulting in monophyly for the taxa of island 3.

implications for the study of ecology and evolution. If this assumption is false then for an individual island the species group will be paraphyletic. However, if it is true then the species assemblage of an individual island may be either monophyletic or paraphyletic (Fig. 2d). Both assumptions require special attention for testing and interpretation within a phylogenetic framework.

The first assumption of monophyly for a species group within an archipelago can only be effectively tested by the inclusion of all closely related species from continental areas and neighbouring archipelagos. When there are congeners outside the archipelago their relationship to the island species must be considered. Sampling of continental congeners for molecular phylogenetic analysis has revealed multiple colonizations for *Lavatera* (Malvaceae) to the Canary Islands (Ray 1995), *Hedera* (Araliaceae) to Macaronesia (Vargas *et al.* 1999), the *Asteriscus* (Asteraceae) and *Sonchus* (Asteraceae) alliances to Macaronesia (Kim *et al.* 1996a; 1996b; Francisco-Ortega *et al.* 1999), the yellow warbler (*Dendroica petechia*) to the West Indies archipelago (Klein & Brown 1994), warblers to Madagascar (Cibois *et al.* 1999), *Tarentola* geckos to Macaronesia (Nogales *et al.* 1998; Carranza *et al.* 2000) and *Calathus* (Coleoptera: Carabidae) to the Canary Islands and Madeira (Emerson *et al.* 2000a). Understandably as the number of continental congeners increases the task of including all representatives becomes more difficult, if not impossible. When faced with such a large number one should at least seek to sample broadly across the known taxonomic divisions. Sampling purely on the basis of geographical proximity may not account for historical continental geographical distributions that have subsequently changed due to climatic events (Emerson *et al.* 2000a; Hewitt 2000). When sampling of continental congeneric species is limited one should treat conclusions of monophyly for a species assemblage on an archipelago with caution, particularly if large intra-archipelago genetic divergences are involved (Fig. 3). This is perhaps highlighted by recent molecular phylogenetic studies of *Tarentola* geckos (Nogales *et al.* 1998; Carranza *et al.* 2000) that identified two colonization events from Africa to the Canary Islands. Extended sampling of North African *Tarentola* species has further reduced the unity of the Canary Island *Tarentola* by identifying a third colonization (Carranza *et al.* 2002).

The second assumption that a species assemblage on an individual island for a species group within an

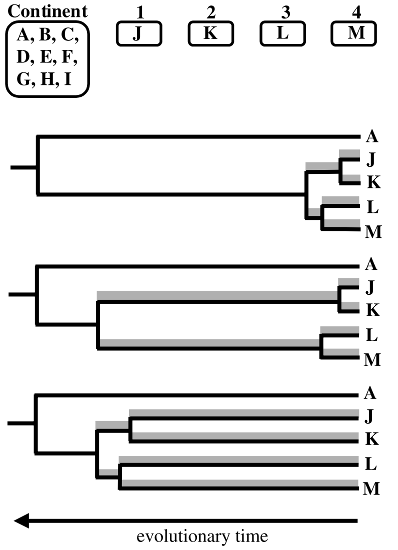

Fig. 3 Inferences of monophyly for island taxa should be treated with caution when sampling of continental congenerics is limited, particularly when intra-archipelago divergences are high. Consider the hypothetical scenario of four islands (1–4) each with a single endemic taxon (J–M) and nine continental relatives (A–I), of which only one (A) has been sampled for a phylogenetic analysis of the island group. Three possible phylogenies are shown and for each one branches are highlighted in grey where it is possible for the remaining continental taxa to be connected resulting in paraphyly of the island group.

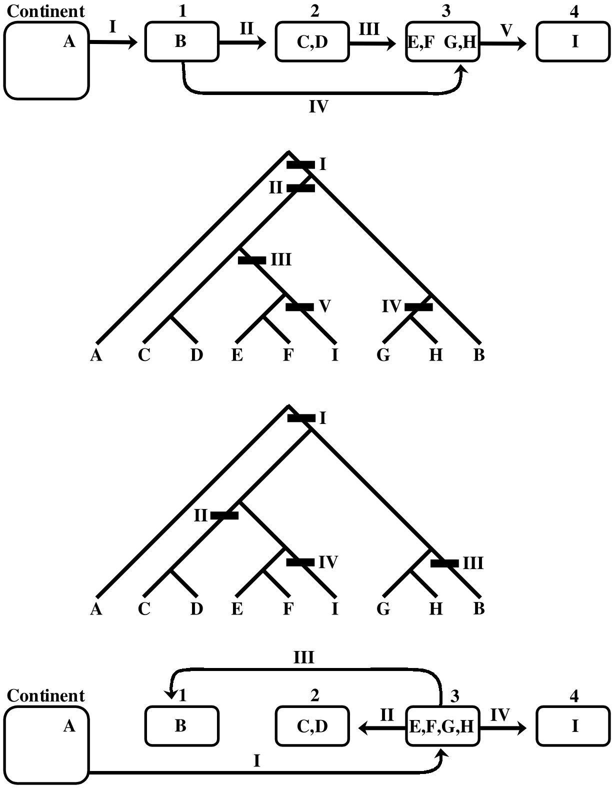

Fig. 4 Reconstructing colonization pathways from phylogenetic data can lead to erroneous conclusions about the evolutionary history of an island group. Consider the hypothetical colonization scenario at the top of the figure where the fauna of island 3 is the result of two colonization events, taxa G and H resulting from colonization event III and taxa E and F resulting from colonization event IV. Such a colonization history will result in the phylogeny with colonization events I to V mapped on. However, working in reverse and inferring the colonization history from the phylogeny could result in an altogether different inference requiring less colonization events (I–IV in the lower phylogeny) and resulting in the conclusion that the fauna of island 3 is the result of a single colonization event (I).

archipelago is the product of a single colonization is difficult to disprove because both monophyly and paraphyly are consistent with this (Fig. 2c). Consider the illustrative example of Fig. 4. The true speciation history for the archipelago involves a double colonization for island 3 and a total of 5 colonization events across the archipelago. However, phylogenetic analysis of the species group could lead to a phylogeographical interpretation of only 4 colonization events and a single colonization of island 3. Such an interpretation would lead one to conclude that the 4 species of island 3 evolved *in situ* following a single colonization event.

Often, as is the case in the *Nesotes*, island monophyly is not clearly refuted by the results of molecular phylogenetic analyses and in such cases the parametric bootstrap or other tests of *a priori* hypotheses can be used (Emerson *et al.* 2000a; Rees *et al.* 2001a) to test null hypotheses of island monophyly. Complicated molecular phylogenetic results involving paraphyletic island assemblages also make the inference of colonization pathways difficult. In such cases the availability of morphological information on ancestral character states may provide a means of assessing which island faunas are derived from a single colonization event and help to refine hypotheses of colonization pathways.

Hybridization and introgression between two independently colonizing lineages may act to produce a phylogenetic signal indicating the single colonization of an island, a potential problem that has been noted for yellow warblers in the West Indies archipelago (Klein & Brown 1994). Additionally the retention of ancestral genetic polymorphism may also confound issues of island monophyly and infer a complicated colonization history, as has been suggested to have occurred within a species complex of *Nesotes* on the western Canary Islands (Rees *et al.* 2001c). Issues of introgression and incomplete lineage sorting can best be dealt with by a multiple marker molecular phylogenetic approach.

Molecular evolution and the timing and sequence of colonization

As noted above, complicated molecular phylogenetic results involving paraphyletic island assemblages make

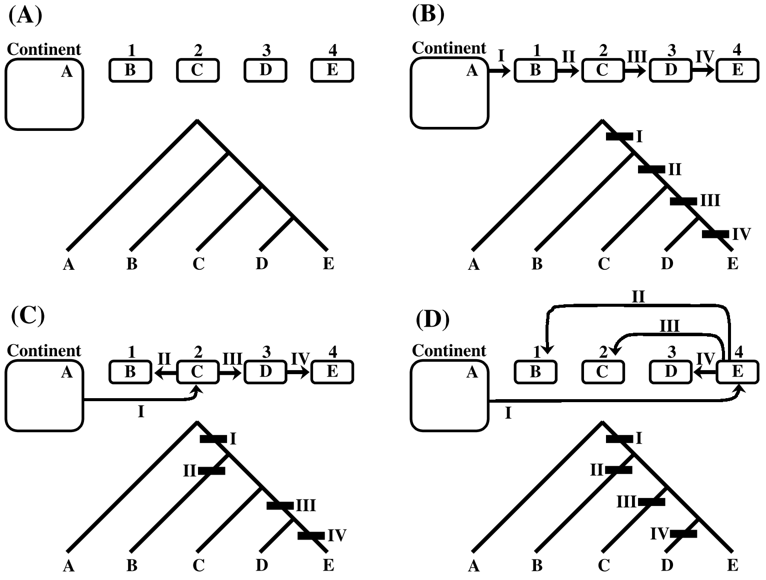

Fig. 5 Reconstructing the sequence of colonization events from a phylogeny for a group of oceanic island organisms requires consideration of multiple hypotheses. (A) The distribution of four island taxa (B, C, D, E), each endemic to a single island (1, 2, 3, 4), their continental relative (A), and a phylogeny for the group. (B) The simplest interpretation of the phylogeny is of a stepping stone colonization history. Colonization events I–IV are mapped onto the tree. The phylogeny and geographical distribution of taxa are also consistent with more complex colonization histories deviating from a simple stepping stone model, examples of which are shown in (C) and (D).

the inference of colonization pathways difficult. The simplest model of colonization within an archipelago is that of stepping stone colonization, and evidence for this within various Canary Island groups has recently been reviewed by Juan *et al.* (2000). Intuitively this model is perhaps a good working null hypothesis, but the acceptance of it from a molecular phylogenetic analysis can be complicated, and even a seemingly clear example is open to alternative interpretations (Fig. 5). Thorpe *et al.* (1994) have proposed two ways of interpreting a tree in terms of colonization sequence. One method uses tree topology and geography under the premise that an island will be colonized by a neighbouring island rather than a more distant one. The other method infers the direction of colonization using information from tree topology and branch length. This method relies on the proposal that there is accelerated molecular divergence caused by a founding event, thus allowing discrimination between colonist and ancestor. Both methods describe a single colonization pathway when applied to phylogenetic analyses of a number of mtDNA gene regions for the Canary Island lizard *Gallotia galloti* (Thorpe *et al.* 1994). However, the applicability of these methods will be limited by violations of the assumptions of nearest island colonization and founder effects only occurring after colonization.

Inferring the ages of molecular divergence events and island colonization often requires the use of a molecular clock calibration derived from other molecular studies (e.g. Juan *et al.* 1995; 1996; Francisco-Ortega *et al.* 1996; Rassmann 1997; Kim *et al.* 1998; Emerson *et al.* 1999; Marshall & Baker 1999; Carranza *et al.* 2000; Sequeira *et al.* 2000; Sato *et al.* 2001). Although useful this is not altogether satisfactory, and under certain conditions it may be possible to use an intrinsic clock calibration. When information on the ages of islands is available it may be possible to use these to calibrate divergence ages and infer colonization sequence from a molecular phylogeny. Emerson *et al.* (2000b; 2000c) have used sequence data from the mtDNA COI and COII gene regions to reconstruct phylogenetic relationships within the species *Brachyderes rugatus* (Coleoptera: Curculionidae) and within the *Tarphius canariensis* species complex (Coleoptera: Colydiidae) on the Canary Islands. For both groups the direction and approximate ages of colonization events were estimated using a combination of phylogeographical pattern, geological data and estimated divergence times using geological age data to calibrate one of the internal nodes. Wright *et al.* (2000) have used the ITS region of nuclear rDNA to reconstruct phylogenetic relationships of *Metrosideros* subgen. *Metrosideros* (Myrtaceae). This group is represented by 26 species of woody tree throughout the islands of the Pacific basin. Wright *et al.* (2000) have used phylogeographical pattern, geological data, the fossil record and estimated divergence times using geological data to calibrate an internal node to infer the colonization history of the group. They suggest a mid/late tertiary origin for the group, with an origin in New Zealand and at least four major dispersal events, the most recent in the Pleistocene.

Baldwin & Sanderson (1998) have pointed out that it will be more reliable to use an 'external' calibration where possible, and have used North American palaeoclimatic and fossil data to calibrate the age of the Hawaiian silversword alliance. The concern of Baldwin & Sanderson (1998) is that when using an internal calibration within the tree, any error in the placement of an islands age will be magnified in age calculations of deeper events within the tree. Thacker & Hadfield (2000) have used sequence data from the 16s ribosomal gene of mtDNA to reconstruct

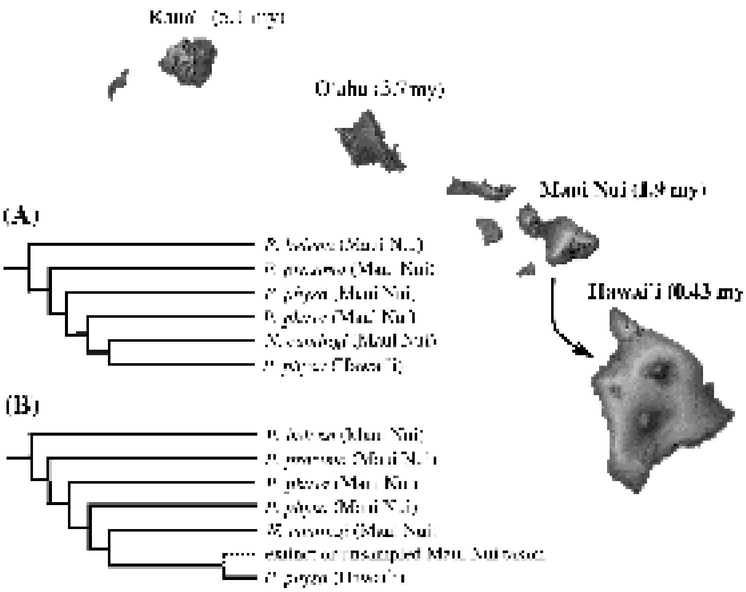

Fig. 6 Lineage extinction or incomplete sampling of extant taxa are important considerations when estimating the ages of colonization events from a molecular phylogeny. (A) Within the Hawaiian tree snails (Achatinellidae) a deep divergence between *N. cumingi* and *P. physa* suggests a high rate of molecular evolution and recent radiation. (B) Such a calibration point is likely to be misleading if one takes into account extinct and unsampled taxa. See Emerson *et al.* (2000b) for a more detailed discussion of this.

phylogenetic relationships among extant Hawaiian tree snails (Achatinellinae), and derived several estimates of molecular divergence rate using geological data. An estimate of 14% per Myr was derived from the assumption that Hawaii was colonized from Maui by the ancestor of *Partulina physa* and *Newcombia cumingi* (Fig. 6). This leads to conclusions of a very recent diversification (less than 2 Myr) within this group. Given the dramatic population reductions and species extinctions within tree snails due to introduced predators (Thacker & Hadfield 2000), an unsampled or extinct sister species to *P. physa* can not be ruled out as an explanation for the high observed molecular divergences (Fig. 6). Both lineage extinction and sampling error have been shown to be important considerations for inferring divergence times from a phylogeny (Emerson *et al.* 2000b).

A more convincing argument for accelerated molecular evolution comes from a recent phylogeographical analysis of the land snail genus *Mandarina*, endemic to the Bonin Islands (Chiba 1999). The uplift of the Bonin Islands started in the Pleistocene and they are estimated to have appeared above sea level before the middle Pleistocene. Chiba (1999) has used sequence data from the 12S and 16S ribosomal genes of mtDNA to reconstruct the phylogenetic relationships of the 12 morphologically and ecologically diverse (arboreal, semiarboreal, terrestrial, dry, and wet habitats) species. Phylogenetic results show that radiation and divergence of arboreal, semiarboreal, and terrestrial species have occurred repeatedly. By using an external calibration date for the MRCA of the species group of 1.8 Myr (the age of island emergence) Chiba (1999) estimates a rate of sequence evolution of 10% per Myr for the ribosomal genes, 20 times higher than the standard rate in other animals (Lynch 1993).

The flora of Macaronesia: relict survivors or recently successful?

Many plant genera from Macaronesia (Canary Islands, Madeira, Azores, Selvagens, and Cape Verde Islands) have been considered relict survivors from the Tertiary period. This hypothesis of a relict origin for many elements of the Macaronesian flora can be traced back to the end of the last century (Engler 1879) and has continued to win favour with more modern biogeographers (e.g. Wulf 1943; Lems 1960; Ciferri 1962; Meusel 1965; Takhtajan 1969; Bramwell 1972; 1976; Humphries 1976; Sunding 1979; Cronk 1992). Evidence for a relict origin comes from fossil data suggesting that many groups now found in the laurel forests and sclerophyllous zones of Macaronesia were apparently lost from the flora of Europe at the end of the Tertiary and in the Pleistocene due to climate change. The woody habit of many Macaronesian plants has also been viewed as an ancestral trait that identifies them as a relict fauna. However, the case for support for either relictual or recent origin depends on how one interprets data such as taxonomy, morphology, cytology and palaeobotany, as has been noted for the *Bencomia* alliance (Helfgott *et al.* 2000).

Recent phylogenetic analyses of a number of Macaronesian plant groups have been able to test the general hypothesis of a relict origin, and the nature and origin of the woody habit (Table 1). The *Bencomia* alliance (Rosaceae) comprises eight species of small tree in three genera; *Bencomia (*4 species), *Dendriopoterium (*2 species) and *Marcetella* (2 species), found in the Canary Islands and Madeira. Their radiation into eight species appears to have been relatively recent as they are virtually identical in their ITS sequences. The phylogenetic analyses of Helfgott *et al.* (2000) also show that the species closely related to the alliance are

Table 1 Plant groups used in molecular phylogenetic studies to test the hypothesis of a relict origin for woody species in Macaronesia

Plant group	Species in Macaronesia	Phylogenetic marker	Woody relict?	References
Bencomia alliance	8	nuclear ITS (DNA sequence)	No	Helfgott *et al*. (2000)
Echium	27	chloroplast intron and spacers, ITS (DNA sequence)	No	Böhle *et al*. (1996), Kim *et al*. (1996a;1996b)
Sonchus alliance	30	nuclear ITS (DNA sequence)	No	Mes & Hart (1996)
Aeonium	38	chloroplast DNA (RFLP), nuclear ITS (DNA sequence)	No	Jorgensen & Frydenberg (1999)
Argyranthemum	23	chloroplast DNA (RFLP), nuclear ITS (DNA sequence)	No	Francisco-Ortega *et al*. (1996), Francisco-Ortega *et al*. (1997)
Ixanthus	1	nuclear matK and ITS (DNA sequence)	No	Thiv *et al*. (1999)
Pericallis	15	nuclear ITS (DNA sequence)	No	Panero *et al*. (1999)

either herbs, small shrubs, or suffrutescent perennials and that the arborescent habit in the *Bencomia* is an insular derived trait. All but two species of *Echium* in Macaronesia are woody perennials, while those of the continent are predominantly annual to perennial herbs. A molecular phylogenetic analysis of Böhle *et al*. (1996) shows that *Echium* in Macaronesia are clearly not of relict origin. Results indicate that the island species are derived from a single herbaceous island colonist, and that their diversification is recent relative to the continental species. Similarly to the phylogenetic interpretations for the *Bencomia* alliance and *Echium*, recent phylogenetic analyses (Mes & Hart 1996; Jorgensen & Frydenberg 1999) confirm the woody Macaronesian species of *Aeonium* to be derived within the group that has recently diversified, offering no support for the hypothesis of a relict origin. Also within the endemic Macaronesian genus *Argyranthemum* (Asteraceae) phylogenetic analyses (Francisco-Ortega *et al*. 1996; 1997) of the origin and antiquity of this woody group have refuted a possible relict nature. The groups appears to have an origin in the Mediterranean with an estimated divergence time of between 1.5 and 3 million years between *Argyranthemum* and its continental relatives.

Phylogenetic analyses of the subfamily Sonchinae (Asteraceae) (Kim *et al*. 1996a; 1996b) define a Macaronesian clade that includes the 19 woody members and one herbaceous member of the genus *Sonchus*, one species of *Prenanthes* (*P. pendula*) and the genera *Babcockia*, *Taeckholmia*, *Sventenia* and *Lactucosonchus*. While the age of the MRCA of the woody species may date back to the Late Tertiary, the phylogenetic position of related continental taxa indicates that this woody *Sonchus* alliance is not part of a relict woody fauna but derived from a single herbaceous coloniser from the continent. Similarly to the *Sonchus* alliance a long history for the Canary Islands laurel forest endemic *Ixanthus viscosus* (Gentianaceae) can also not be ruled out, but phylogenetic analysis suggests a derived rather than relict origin for woodiness in this species (Thiv *et al*. 1999). The genus *Pericallis* (Asteraceae) is endemic to Macaronesia with six woody species and nine herbaceous species. A phylogenetic analysis of the 15 species (Panero *et al*. 1999) indicates a strong sister group relationship between *Pericallis* and the New World herbaceous genus *Packera*, and character mapping yields a most parsimonious interpretation of growth form to be the evolution of woodiness twice within group from a herbaceous MRCA of the *Pericallis*.

The phylogenetic results of Panero *et al*. (1999) point to a strong biogeographical link between Macaronesia and the New World. Distributions of other plant groups also conform to this pattern (see Panero *et al*. 1999), and the Madeiran endemic species of *Sedum* is placed within a clade of Mexican taxa from a cpDNA restriction site of the Crassulaceae (Van Ham & Hart 1998). Panero *et al*. (1999) view this biogeographical connection to be the result of dispersal rather than the vicariant break-up of a North American-Eurasian-African floral connection. Fossil and phylogenetic evidence make it seem unlikely that *Pericallis* was part of the northern hemisphere boreotropical flora of evergreen rain and laurel forests of the Tertiary that were later replaced by broad-leaved deciduous taxa.

The emerging pattern for the flora of the Macaronesian islands is one of a recent, as opposed to relict origin. A recent chloroplast DNA restriction site phylogeny of the genus *Androcymbium* (Colchicaceae) has identified the two Canary island species to be monophyletic and related to North African/Iberian species, with the colonization of the archipelago possibly occurring in the early Pliocene (Caujapé-Castells *et al*. 1999). Francisco-Ortega *et al*. (2001) have undertaken a phylogenetic analysis including the two genera of the subtribe Gonosperminae (Asteraceae) in Macaronesia, and other species groups from the Macaronesian region and the continent that have been suggested to be related. Although the data lacks strong support for monophyly, sequence data from the ITS region of nuclear rDNA indicates a recent origin for a Canarian species group with a Eurasian origin for the MRCA. Similarly a chloroplast DNA restriction site analysis of the endemic Macaronesian genus *Sideritis* (Lamiaceae) (Barber *et al.* 2000) has confirmed the monophyly and recent diversification of this group of 24 species. However, until further sampling of continental species is undertaken it remains unclear how recently the group may have colonized from the continent.

Rather than relictual origin it is apparent that the high frequency of woodiness, 70% among Macaronesian endemics (Francisco-Ortega *et al.* 1997), is better explained by insular island evolution from an ancestral herbaceous condition (Carlquist 1965; 1974; 1995). Mechanisms suggested to favour this process include competition mediated selection for higher stature, response to the uniformity of insular climates, or selection for longevity in an environment depauperate of pollinators (Carlquist 1974; Böhle *et al.* 1996; Givnish 1998b). Although no compelling support for relict floral elements in Macaronesia have come to light, further phylogenetic studies of Macaronesian laurel forest groups also occurring in the Mediterranean and considered remnants of the boreotropical flora, such as *Clethra*, *Ocotea*, and *Persea* (Bramwell 1972), may yet provide evidence for this.

Phylogeny, ecology and evolution

Island biogeography

Molecular phylogenies are powerful tools for both the generation and testing of specific ecological and evolutionary hypotheses. Particular to island systems is the equilibrium theory of island biogeography (MacArthur & Wilson 1967) that describes species area relationships as a function of island size, immigration rate and extinction rate. However, on islands that generate most of their species *in situ* species area relationships should be driven by higher speciation rates in larger areas. Losos & Schluter (2000) have been able to quantitatively test this theory using a phylogeny for 53 species of *Anolis* lizards (48 from the Caribbean) constructed from mtDNA sequence data for the nicotinamide adenine dinucleotide (NADH) dehydrogenase subunit 2 gene (ND2) and five transfer-RNA (tRNA) genes (Jackman *et al.* 1999). The results of Losos & Schluter (2000) support an evolutionary theory of island biogeography with the rate of species proliferation increasing with island area above a threshold island size. Their results suggest that an evolutionary theory of diversity is quite probably of general use and will be of interest to investigate in other island organism systems.

In the Lesser Antilles 10 islands contain two species of *Anolis*, and on nine of these the two species are substantially different in size. In contrast, on 16 of the 17 islands inhabited by only one species, the size is intermediate. Two processes can be invoked to account for this, either (i) character displacement in which similar sized species evolve in different directions in sympatry, or (ii) size assortment in which only different sized species can successfully colonize the same island together. By analysing size patterns in a phylogenetic context (based on immunological, electrophoretic, karyological, and morphological data) Losos (1990) was able to distinguish between these two processes and concluded that size assortment by competitive exclusion was largely responsible for body size differences between coexisting species. Morphological variation suggestive of character displacement occurs among lizards of the genus *Cnemidophorous* on islands in the sea of Cortez and on the surrounding mainland. A recent molecular phylogenetic approach using sequence data from the mtDNA cytb gene has been used to infer the evolution of body size changes within this group (Radtkey *et al.* 1997). Their results suggest that both character displacement and size assortment are implicated in the observed size variation on islands and the mainland. Other molecular phylogenetic analyses of island organisms suggest that size displacement may account for sympatric species of different size skink (Macroscincus and Mabuya) on the Cape Verde Islands (Carranza *et al.* 2001), but it offers little explanatory power for size variation among chaffinches in the Macaronesian region (Marshall & Baker 1999).

Morphology and selection

Recent molecular phylogeographical studies of reptilian island communities have sought to delimit the causes of morphological variation observed within and between islands. The hypotheses to be tested are: (i) that morphological variation observed simply reflects dispersal history or; (ii) it is it the result of environmental selective pressures. Partial Mantel tests can be used to test the origin of a morphological variable against both hypotheses. Each morphological character (coded as a similarity matrix among individuals) can be tested simultaneously against the phylogeny (represented as a genetic distance matrix) or natural selection variables (represented as matrices of environmental variation). In a study of the Canary Island lizard *Gallotia galloti* Thorpe (1995) found 30% of morphological characters to be significantly associated with a DNA phylogeny constructed from mtDNA cytb, COI and 12s rRNA. Body-dimension variation was found to be most usually associated with climatic conditions or biodiversity, colour-pattern variation with phylogeny or climate, and variation in scalation was found to be associated with biodiversity or phylogeny. In a subsequent study of populations of *G. galloti* on Tenerife using mtDNA cytb sequence data Thorpe *et al.* (1996) have used Mantel tests to test among competing hypotheses of the geological causes of phylogeographical pattern. Their results suggest that different molecular lineages are a consequence of secondary expansion of predifferentiated populations on a pair of precursor islands. Malhotra & Thorpe (2000) found no congruence of phylogeographical pattern (mtDNA cytb) with body shape and scalation for the lizard *Anolis oculatus* on the Caribbean island of Dominica, suggesting a minor role for vicariance in generating morphological divergence. A significant correlation of colour pattern with phylogeny was found, but when correcting for phylogeny a relationship between colour pattern and vegetation is also apparent.

Evolutionary consequences of ecological specialization

A recent molecular phylogenetic analysis of the pantropical plant genus *Dalechampia* (Euphorbiaceae) has added support against the once commonly held viewpoint that extreme ecological specialization is irreversible and thus limits the potential to adapt to new conditions. Continental species of *Dalechampia* possess blossoms offering a nonnutritive pollinator reward in the form of a resin used by specific bee species for nest construction. The island of Madagascar does not appear to have been colonized by the resin collecting bee group and consequently flowers are visited by a variety of pollen feeding insects (Armbruster *et al*. 1993). Armbruster *et al*. (1993) could not distinguish between a derived or ancestral condition for the generalized pollination system of Madagascan species based on a morphological phylogeny but a molecular phylogenetic analysis using nuclear ribosomal and chloroplast DNA sequence data (Armbruster & Baldwin 1998) clearly points to a reversal from a specialized to generalized pollination system.

Phylogenetic studies of island organisms provide an opportunity to not only explore the evolutionary consequences of ecological specialization but also the development of it. In a morphological analysis of Hawaiian carabid beetles Liebherr 1997) found that differentiation among marginal isolates may have played a role in species formation among Hawaiian carabid beetles. Results of a molecular phylogenetic analysis (mtDNA COI and COII sequences) of the carabid genus *Calathus* on the Canary Islands (Emerson *et al*. 1999) suggest that the seven species on La Gomera evolved by marginal isolation or niche specialization from a generalist ancestor. In addition to this *C. spretus* on the neighbouring island of El Hierro appears to have undergone ecological release from a recent colonization event to the island involving the ecologically restricted La Gomeran species *C. gomerensis*.

Taxon cycling

The term 'taxon cycle' was coined by E. O. Wilson (1961) in reference to a phenomenon of cyclic patterns of species diversification, extinction, and secondary diversification. Central to this idea is the shift of species from marginal (ecologically or geographically restricted) to interior (ecologically or geographically broad) habitats. In an island environment this can be visualized as colonization by a species followed by range expansion and population differentiation. Subsequent extinction among local populations may lead to global island extinction, or a new phase of range expansion leading to a renewal of the cycle.

Ricklefs & Cox (1972) have suggested that the avifauna of the West Indian Islands conform to a model of taxon cycling. They assigned relative ages to taxa on the basis of geographical distribution and taxonomic differentiation, and then went on to demonstrate that, as populations get older, they become more restricted in their distribution and suffer an increased probability of extinction. It is through recent molecular phylogeographical appraisals of elements of the West Indian avifauna (Seutin *et al*. 1993; 1994; Bermingham *et al*. 1996; Ricklefs & Bermingham 1997; Lovette *et al*. 1998; 1999) that the time dimension of the taxon cycle can be measured quantitatively. Ricklefs & Bermingham (1998) have analysed these phylogenies and have been able to confirm, among independently evolving populations, that older populations tend to have restricted geographical and ecological distributions. Their analyses of phylogeny, ecology and geography lead Ricklefs & Bermingham (1998) to suggest that taxon cycles in the Lesser Antillean avifauna are not driven by extrinsic factors (e.g. climate) but are intrinsically mediated, possibly through evolutionary lags in the dynamics of host parasite responses.

In a phylogenetic analysis of weevils of the genus *Galapaganus* on the Galápagos Islands using sequence data from the mtDNA COI gene, Sequeira *et al*. (2000) have postulated a history of taxon cycling within the group, with basal species occurring in arid coastal regions and derived species occurring in upland mesic habitats. Panero *et al*. (1999) have also suggested a role for taxon cycling in the evolution of *Pericallis* (Asteraceae) in Macaronesia. Among the *Anolis* lizards of the Lesser Antilles hypotheses of both character displacement and taxon cycling have been implicated in the evolution of the group (Miles & Dunham 1996).

Conclusions

Advances in both the acquisition and analysis of DNA sequence data for reconstructing the phylogenetic relationships of organisms has been accompanied by an increasingly phylogenetic approach to studying evolution and ecology on oceanic islands. Island organisms are often subject to a myriad of adaptational pressures, manifesting themselves through high levels of morphological diversity. Any study seeking to understand the origin of such a group of organisms requires phylogenetic characters independent from the influences of natural selection. Molecular data can essentially provide an almost limitless supply of such character information.

Perhaps of primary interest is gaining an understanding of the origin(s) of a particular group of taxa on an archipelago, and the colonization sequence among islands, indicating the number of times each has been colonized and the relative ages of colonization events. It is apparent from studies to date that while set guidelines can be employed for constructing phylogenies from molecular data, the interpretation of these as colonization pathways can be problematic because of factors such as extinction, incomplete sampling, incomplete lineage sorting and hybridization. Even without these considerations the colonization sequence underlying a clearly resolved phylogeny can be misinterpreted (Figs 4 and 5). In this respect researchers are compelled to consider these factors with respect to their island study group, as some may be more relevant than others (e.g. incomplete lineage sorting when genetic divergences are low, extinction when it has been documented through human activity, hybridization when it has been observed).

Given the extent of morphological convergence that has been documented on islands (e.g. Losos *et al*. 1998), and often high levels of intraspecific genetic divergences observed, careful consideration of sampling representatively across the geographical distribution of each species is also particularly important for the accurate assessment of species relationships and colonization sequences. Careful sampling without over-reliance on existing taxonomic concepts is important for phylogenetic studies of island plants (Baldwin *et al*. 1998) and recent analyses of the Canary Island beetle fauna have also drawn attention to the importance of sampling (e.g. Juan *et al*. 1996; Emerson *et al*. 2000b; 2000c; Rees *et al*. 2001a; 2001b; 2001c).

Beyond establishing the colonization histories of individual groups, molecular phylogenetic analyses of island organisms are enabling biologists to get at the heart of some key ecological and evolutionary theories such as the equilibrium theory of island biogeography and the taxon cycle hypothesis. Incorporating a historical component to studies of body size change and phenotypic trait variation is also enabling researchers to distinguish between both character displacement and size assortment, and adaptational and historical causes of morphological variation. Molecular phylogenetics has provided a clear refutation of the once popular belief of the relict nature of the Canary Island flora, and as the number of individual studies on each archipelago increases it may be possible to gain an understanding of the evolutionary history of community build-up. Much has been achieved in less than a decade and island biologists can expect to see continued progress in coming years.

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