Anagenetic evolution in island plants

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ABSTRACT

Aim Plants in islands have often evolved through adaptive radiation, providing the classical model of evolution of closely related species each with strikingly different morphological and ecological features and with low levels of genetic divergence. We emphasize the importance of an alternative (anagenetic) model of evolution, whereby a single island endemic evolves from a progenitor and slowly builds up genetic variation through time.

Location Continental and oceanic islands.

Methods We surveyed 2640 endemic angiosperm species in 13 island systems of the world, both oceanic and continental, for anagenetic and cladogenetic patterns of speciation. Genetic data were evaluated from a progenitor and derivative species pair in Ullung Island, Korea, and Japan.

Results We show that the anagenetic model of evolution is much more important in oceanic islands than previously believed, accounting for levels of endemic specific diversity from 7% in the Hawaiian Islands to 88% in Ullung Island, Korea, with a mean for all islands of 25%. Examination of an anagenetically derived endemic species in Ullung Island reveals genetic (amplified fragment length polymorphism) variation equal or nearly equal to that of its continental progenitor.

Main conclusions We hypothesize that, during anagenetic speciation, initial founder populations proliferate, and then accumulate genetic variation slowly through time by mutation and recombination in a relatively uniform environment, with drift and/or selection yielding genetic and morphological divergence sufficient for the recognition of new species. Low-elevation islands with low habitat heterogeneity are highly correlated with high levels of anagenetic evolution, allowing prediction of levels of the two models of evolution from these data alone. Both anagenetic and adaptive radiation models of speciation are needed to explain the observed levels of specific and genetic diversity in oceanic islands.

Keywords Amplified fragment length polymorphism, anagenesis, cladogenesis, endemic plants, genetic differentiation, habitat heterogeneity, island biogeography, island evolution, speciation.
may be low (DeJoose & Wendel, 1992; Frankham, 1997; Baldwin et al., 1998; Crawford & Stuessy, 1998; Emerson, 2002). Well-known examples include the lobelioids and silverswords in Hawaii (Givnish et al., 1995; Carlquist et al., 2003).

A contrasting mode of evolution is one in which a founder population arrives on an island and simply diverges through time without further specific differentiation. This anagenetic speciation (also known as simple geographic or phyletic speciation) has been suggested as an important mode of evolution in the endemic vascular plants of the Juan Fernandez Islands (Stuessy et al., 1990), but the pattern has not been studied in other oceanic archipelagos and is less well understood regarding its genetic consequences than is the classical model of adaptive radiation. The term anagenetic speciation has been selected for convenience in communication. It is realized that the source populations could also be undergoing change, especially if the environment were to be changing rapidly, for example as a result of Pleistocene events. If speciation were to occur in the continental region, therefore, one might label this simply cladogenesis, involving the production of two new species, one on the islands and one on the continent. We do not object to this point of view, but it is likely that in most cases the ecology of the newly formed islands will be changing faster and more dramatically than that of the continental source area, and, therefore, speciation may be occurring in the islands more often or faster than in the source region. We recognize these definitional problems, but they should not obscure the main point of this paper, which is to focus on what is occurring during speciation on the islands after colonization. We regard the term anagenetic speciation as useful to contrast with speciation during adaptive radiation, which clearly involves the splitting of lineages (or cladistic divergence) in a more dramatic fashion.

This report surveys the angiosperm floras of 13 island systems, of both oceanic volcanic (Canary, Cape Verde, Galapagos, Hawaii, Juan Fernandez, Madeira, Ogasawara, St Helen, Tristan da Cunha, Ullung) and continental (Chatham, Falklands, Taiwan) origins, revealing that anagenetic speciation conservatively explains 25% of the total endemic species diversity. We seek correlations with physical and environmental parameters that might explain observed levels of the two patterns of speciation within each island or archipelago. We also offer a hypothesis, based on available data, for genetic consequences of the anagenetic speciation model.

**METHODS**

A data base of 2640 endemic species for the island survey was prepared from published floras for 13 island systems plus additional literature: Canary Islands, Wildpret de la Torre & Del Arco Aguilar (1987), Coello et al. (1992), Hansen & Sunding (1993); Cape Verde Islands, Bernard-Griffiths et al. (1975), Boekschoten & Manuputy (1993), Brochmann et al. (1997); Chatham Islands, Wills-Johnson et al. (1996); Falkland Islands, Moore (1968), Lawrence et al. (1999); Galapagos Islands, Wiggins & Porter (1971), Hamann (1981), Perry (1984); Hawaiian Islands, Wagner & Funk (1995), Wagner et al. (1999); Juan Fernandez Islands, Skottsberg (1953), Stuessy et al. (1984), Marticorena et al. (1998), Greimler et al. (2002); Madeira, Press & Short (1994), Hughes & Malmqvist (2005); Ogasawara Islands, Ono & Okutomi (1983), Takayama et al. (2005); St. Helena, Cronk (2000); Taiwan, Huang (1994), Huang et al. (2004); Tristan da Cunha Islands, Wace & Holdgate (1958), Wace (1961), Miller (1964), Gass (1967), Groves (1981), McDougall & Ollier (1982), Roux et al. (1992); Ullung Island, Kim (1988), Sun & Stuessy (1998).

Data on natural vegetation types, ages of islands, and other environmental parameters were taken from the literature cited above. Comparing vegetation heterogeneity among archipelagos is difficult because different systems of classification of vegetation are in use. We extracted from the literature the number of vegetation types of comparable hierarchical level from each island/archipelago. To reduce problems of comparability we then grouped the number of vegetation types into classes: class 1 (1–4 vegetation types); 2 (5–8); 3 (9–12); 4 (13–16); 5 (17–20); and 6 (>20).

The most effective way of knowing whether a species has evolved anagenetically or cladogenetically is by in-depth studies of each group, including comparisons with continental progenitors. Such a detailed level of understanding is not available comprehensively for any island system. For the purposes of this study, therefore, we have taken a simple (conservative) approach to estimating levels of anagenetic speciation. Single endemic species on an island or archipelago are assumed to have evolved by anagenetic speciation. This does not account for possible loss of species as a result of extinction. This is an important point, as it is likely that Pacific oceanic (and other) islands have undergone considerable reduction in both surface area and ecological habitat breadth during their ontogeny, and specific and genetic diversities have surely been lost (Stuessy et al., 2005). Hence, some single endemic species may be merely the surviving member of a once larger endemic group. Unfortunately, without fossil evidence, which is rarely available from plants on islands, it is simply impossible to determine levels of extinction in particular groups. Two or more endemic species in a genus within an island or archipelago are regarded as reflecting cladogenesis, if the assumption is made that they both have descended from the same continental introduction. This ignores possible inter-island anagenesis, and therefore our approach doubtless underestimates this mode. Endemic monotypic genera have also been treated as reflecting anagenesis, even though it may be the case that some of these related genera may represent radiating lines from one original ancestor to the islands.

In addition to the above analysis, we present analyses of genetic variation in populations of *Dystaenia* (Apiaceae) from Ullung Island and Japan based on amplified fragment length polymorphism (AFLP; Vos et al., 1995) data (Ploos ter al., 2005). A few technical comments are therefore in order. It is now well accepted that AFLPs can provide a sensitive measure of overall genetic variation within and among plant
populations (e.g. Tremetsberger et al., 2003; Muellner et al., 2005). Six populations of *Dystaenia takesimana* (Nakai) Kitag. (Ullung Island) and six of *Dystaenia ibukiensis* (Yabe) Kitagawa (Japan) were sampled, involving a total of 126 individuals. These were chosen to reflect the geographic spread of populations within each species. Total genomic DNA was extracted from silica-dried leaves following the CTAB protocol (Doyle & Doyle, 1987), with slight modifications, followed by standard AFLP protocols (Vos et al., 1995; Tremetsberger et al., 2004). An initial screening of selective primer combinations yielded three that gave clear and reproducible bands: EcoRI-AC/MSel-CAG, EcoRI-ACC/MSel-CTG, and EcoRI-AGG/MSel-CAT. The fluorescence-labelled selective amplification products were separated on a 5% polyacrylamide gel with an internal size standard on an automated ABI 377 sequencer. The data were imported into Genographer (Version 1.6.0, http://hordeum.oscs.montana.edu/genographer) for scoring of the fragments; the results were exported as a presence/absence matrix for further analysis. The Shannon index was calculated as $H_{sh} = -\sum (p_j \ln p_j)$, where $p_j$ is the relative frequency of the $j$th fragment. Tests for significance of correlations were calculated with SPSS 8.0 (SPSS, Inc., Chicago, IL, USA). Analyses of molecular variance (AMOVA) and the coefficient of genetic differentiation ($F_{ST}$) were calculated with Arlequin 2.0 (Schneider et al., 2000). R package 4.0 d6 (Casgrain & Legendre, 2001) was used to perform Mantel tests for each species (10,000 permutations), comparing the genetic matrix of inter-individual Jaccard distances with a matrix of geographic distances between individuals in kilometres.

**RESULTS AND DISCUSSION**

Table 1 shows levels of anagenetic vs. cladogenetic speciation in 2640 endemic species of 10 oceanic islands and archipelagos and three continental islands taken from published floras. The highest level of anagenetic speciation is for Ullung Island, Korea, at 88%. At the other extreme are the Hawaiian Islands, at 7%. The average value for oceanic archipelagos is 22%, and for continental islands it is 31%. Overall, anagenetic speciation accounts for approximately one-quarter of all endemic plant species on these islands.

It is important to emphasize that these values may underestimate the level of anagenetic speciation in some archipelagos. For example, the most detailed assessment of cladogenetic and anagenetic speciation, based on more than 25 years of evolutionary studies on many island taxa, is for the endemic flora of the Juan Fernandez archipelago (Stuessy et al., 1990). In this study, anagenesis was estimated as 71%, which is much higher than the figure given here (36%, Table 1), and presumably closer to the actual percentage. Another island where it is possible to give an estimate of anagenesis based on evolutionary studies is Ullung Island, where the difference is less. The figure given here is 88% (Table 1), whereas our previous estimate based on evolutionary studies was 100% (Sun & Stuessy, 1998; Pfosser et al., 2002). For other archipelagos with larger endemic floras, however, no detailed summaries are currently possible. The other archipelago that has received much recent, especially molecular, attention is the Canary Islands. Even there, however, only a portion of the endemic taxa has been examined with modern techniques (Santos, 1998), and the genetic data are therefore insufficient for a complete summary of modes of speciation.

The different levels of anagenetic speciation in different island systems allow a search for correlations with physical environmental factors (Table 1). No significant correlations exist with the number of islands in archipelagos, their size, age, or distance from major source areas, these being traditional factors used to explain total species diversity (i.e. endemic and native taxa) on oceanic islands (MacArthur & Wilson, 1967). Likewise, no significant correlation exists with latitude (not included in Table 1). Only two factors, elevation and habitat.

**Table 1** Features of island systems, numbers of endemic species, and levels of anagenetic vs. cladogenetic speciation

<table>
<thead>
<tr>
<th>Island system</th>
<th>Number of islands</th>
<th>Size (km²)</th>
<th>Distance from mainland (km)</th>
<th>Age (Myr)</th>
<th>Elevation (m)</th>
<th>Vegetation heterogeneity</th>
<th>No. endemic species</th>
<th>Anagenetic speciation (%)</th>
<th>Cladogenetic speciation (%)</th>
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<tbody>
<tr>
<td>Oceanic</td>
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<tr>
<td>Hawaii (H)</td>
<td>8</td>
<td>16,885</td>
<td>3660</td>
<td>5</td>
<td>4250</td>
<td>6</td>
<td>828</td>
<td>7</td>
<td>93</td>
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<td>Canary (C)</td>
<td>7</td>
<td>7601</td>
<td>100</td>
<td>5</td>
<td>3710</td>
<td>6</td>
<td>429</td>
<td>16</td>
<td>84</td>
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<td>Tristan da Cuhna (T)</td>
<td>4</td>
<td>208</td>
<td>2580</td>
<td>18</td>
<td>2060</td>
<td>3</td>
<td>27</td>
<td>33</td>
<td>67</td>
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<tr>
<td>Juan Fernandez (J)</td>
<td>3</td>
<td>100</td>
<td>600</td>
<td>4</td>
<td>1319</td>
<td>5</td>
<td>97</td>
<td>36</td>
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<td>12</td>
<td>4033</td>
<td>570</td>
<td>10</td>
<td>2829</td>
<td>2</td>
<td>68</td>
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<td>16</td>
<td>7847</td>
<td>930</td>
<td>5</td>
<td>1707</td>
<td>4</td>
<td>133</td>
<td>43</td>
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<td>792</td>
<td>630</td>
<td>14</td>
<td>1862</td>
<td>3</td>
<td>96</td>
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<td>52</td>
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<td>Ogasawara (O)</td>
<td>12</td>
<td>99</td>
<td>800</td>
<td>Tertiary</td>
<td>916</td>
<td>3</td>
<td>118</td>
<td>53</td>
<td>47</td>
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<td>St. Helena (S)</td>
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<td>123</td>
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<td>15</td>
<td>826</td>
<td>2</td>
<td>36</td>
<td>53</td>
<td>47</td>
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<td>Ullung (U)</td>
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<td>73</td>
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<td>2</td>
<td>984</td>
<td>2</td>
<td>33</td>
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<tr>
<td>Taiwan (TW)</td>
<td>1</td>
<td>35,800</td>
<td>130</td>
<td>5</td>
<td>3950</td>
<td>3</td>
<td>724</td>
<td>29</td>
<td>71</td>
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<td>Chatham (CH)</td>
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<td>963</td>
<td>668</td>
<td>80</td>
<td>294</td>
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<td>37</td>
<td>62</td>
<td>38</td>
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<tr>
<td>Falkland (F)</td>
<td>2</td>
<td>8500</td>
<td>410</td>
<td>Tertiary</td>
<td>705</td>
<td>2</td>
<td>14</td>
<td>71</td>
<td>29</td>
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(vegetation) heterogeneity, correlate significantly with this pattern (Fig. 1a, Pearson two-sided, \( r = 0.84, P < 0.01 \); Fig. 1b, Pearson two-sided, \( r = 0.77, P < 0.01 \)). Higher islands generally have greater habitat diversity, and this stimulates cladogenesis and adaptive radiation (e.g. in Hawaii). Lower islands with more uniform environments yield higher levels of anagenetic speciation (e.g. in Ullung Island). Hobohm (2000) has shown a positive correlation of species diversity in the Macaronesian Islands with elevation and number of vegetation zones.

The genetic consequences of anagenetic speciation are also of interest. In the model of adaptive radiation, the original immigrant gene pool becomes divided as a result of ecological isolation, and the resultant genetic variation within and among populations is low (Johnson et al., 2000). Even if a founder-flush model is advocated (Rundle et al., 1998), the resultant genetic variation within endemic lineages stays reduced. Genetic AFLP comparisons of a progenitor-derivative species pair between Japan and Ullung Island, which shows the highest level of anagenesis (88%; Table 1), suggest another pattern. A comparison (Fig. 2) between six populations of *D. takesimana* (Apiaceae; endemic to Ullung Island) and six of *D. ibukiensis* (scattered throughout Japan) fails to show a reduction in genetic variation (Pfosser et al., 2005) within the island endemic (number and per cent of polymorphic fragments, 117.33, 96.17% vs. 103.67, 86.73%, and Shannon index 33.13 vs. 29.13, respectively). Furthermore, the island populations all behave as one large island population with no geographic partitioning of genetic variation (\( F_{ST} = 0.014 \); Mantel test with genetic and geographic distances, \( R_M = 0.042, P = 0.15 \)). Based on the AFLP data, each of the two populational systems is clearly monophyletic, excluding multiple introductions for the island endemic. This generic system was selected because the two taxa are morphologically distinct (Sun et al., 1997), they have the same breeding systems (outcrossing, Pfosser et al., 2005), they are the only two species in the genus, hence eliminating complicating factors such as hybridization among congeners, and a deletion in the *trnL-F* intron and spacer regions in the island taxon strongly suggests that it was derived from the Japanese species, rather than vice versa (Pfosser et al., 2005).

Examples of single progenitor-derivative species pairs that do not fit this genetic pattern, based on allozyme data, include (1) *Rhaphithamnus* (Verbenaceae), whereby the Chilean continental *R. spinosus* has much more allozymic variation than the endemic *R. venustus* of Masatierra Island in the Juan Fernandez archipelago (Crawford et al., 1993); and (2) *Gossypium* (Malvaceae), whereby the Galapagos endemic *G. klotschianum* has less allozymic variation than the progenitor *G. davidsonii* from Baja California (Wendel & Percival, 1990). In these cases, however, it may be that the reduction of population number and size over several million years (Cox, 1983; Stuessy et al., 1984) as a result of natural and human impacts has led to the pattern of reduced genetic variation now seen (Stuessy et al., 2005). There is also a recent report (Woo et al., 2002) of reduced allozymic variation in the Ullung Island endemic *Hepatica maxima* in comparison with its Korean peninsula congener *H. asiatica*. We have examined

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**Figure 1** Correlation of anagenetic speciation (%) in endemic angiosperms of island systems with (a) highest elevation and (b) habitat (vegetation) heterogeneity. For acronyms see Table 1.

**Figure 2** Genetic (Shannon) diversity among populations of *Dystaenia takesimana* (1–6) and *Dystaenia ibukiensis* (7–12) calculated as \( H_{SK} = - \sum (p_i \ln p_i) \), where \( p_i \) is the relative frequency of the \( j \)th fragment. Data from Pfosser et al. (in press).
this species pair with DNA sequences and AFLP data, however (Pfosser et al., in press, unpubl. data), and see a similarly high level of genetic variation in the island endemic to that shown in Dystaenia. More work on H. maxima and its progenitor will be needed to resolve this discrepancy.

The equal or higher level of genetic variation seen in species derived through anagenetic speciation suggests a mechanism for their origin. After an initial founder event, the established immigrant population will have greatly reduced genetic variation. In a favourable uniform environment, populations will proliferate. Over generations, genetic variation will accumulate through mutation and recombination (Lande, 1992) in the isolated island populations as a result of changes in allelic frequencies through drift and/or selection (if the island habitat is significantly different from that of the continent). Lack of eco-geographic partitioning of genetic variation within the island keeps genetic levels high. The result is eventually a new species, divergent in genetic and morphological composition from its progenitor, but harbouring equal or nearly equal levels of genetic variation.

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REFERENCES


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