

RANGE CONTRACTION AND EXTINCTION VULNERABILITY: WHAT IS NATURAL?

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Abstract

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The potential of species to generate new taxa or go extinct may be a consequence of their evolutionary history. Here, parameters involved in the natural contraction of species ranges, in particular whether distributional change is affected by the scale at which populations differentiate, are examined. It is argued that, for taxa in which local differentiation is impossible, the primary opportunity for taxonomic divergence will only occur subsequent to colonisation of a new habitat, at which time taxa are also likely to expand their geographic and ecological range. In such a scenario, the most ancestral species will be relictual, with the narrowest ranges and greatest vulnerability to extinction. For taxa in which local population subdivision is possible subsequent to colonisation of a land mass, subdivided taxa become progressively more restricted in geographic and ecological range. In this second scenario the more derived species will be confined to ever-decreasing ranges, their probability of extinction coincidentally enhanced. Representatives of various lineages from the Hawaiian Islands are used to test these concepts. First, for spiders in the genus *Tetragnatha*, the phylogeny of two clades that differ in vagility is compared. As predicted, more derived species have broader ranges in the more vagile clade. In the more sedentary clade, the more derived species appear to be more restricted. For flies in the genus *Drosophila*, and plants in the Hawaiian silversword alliance, genus *Dubautia* on Kauai, known molecular data sets were used to examine the history of species in terms of population size. Applying recent theory based on coalescence, it is shown that the *Drosophila* lineage has been expanding its range through its history, as expected from a group that requires colonisation of a new land mass to form new species. On the other hand, the *Dubautia* lineage has suffered range contraction through its history, which is also as predicted because the group differentiates extensively within the same mountain mass. The results provide a method with which to predict how species will respond to conservation action. This reasoning suggests that species that are confined to small ranges as a result solely of their phylogenetic legacy are unlikely to be vulnerable to immediate extinction. However, species that have been confined to small ranges as a result of recent ecological modification, such as alien invasion, are highly vulnerable to extinction.

Introduction

Anthropogenic disturbance, either direct or indirect, is causing species to decline much more rapidly than they can be replaced. No area in the United States has such a high proportion of endemic species nor suffers the impact from as many new species annually as Hawaii. As a consequence, the Hawaiian archipelago represents a microcosm for global issues and concerns for the generation and loss of biodiversity. Here, distributional range is used as an indicator of vulnerability to extinction. Natural parameters that may dictate changes in the distributional range of species are considered. Anthropogenic factors responsible for accelerating species range contraction and demise are then examined.

The natural propensity of species to go extinct

can be examined by considering the following two questions:

1. Do patterns of geographic and ecological range expansion and contraction have a phylogenetic component?
2. To what extent does the scale at which population subdivision occurs, affect patterns of distributional change.

Previous studies have suggested that the evolutionary course leading to extinction is at least somewhat deterministic and predictable (Ricklefs, 1990): Species tend to undergo regular changes in geographic and ecological range over evolutionary time, although the nature of the relationship remains unclear. Elucidation of the mechanisms of such a relationship could provide an answer to a critical question in the analysis of biodiversity: Which species are

naturally prone to extinction, and which might serve as a crucible for evolution and future speciation?

The most widely recognised patterns of geographic change during taxonomic diversification are those in which there is a progressive, largely irreversible shift towards habitat specialisation during speciation episodes (Darlington, 1957, 1959, 1971; Wilson, 1961; Erwin, 1985). Wilson's (1959, 1961) 'taxon cycle' was used to describe such changes in the distributional pattern of Melanesian ants. He suggested that widespread, dispersive populations give rise to many more restricted and specialised species. The related 'taxon pulse' hypothesis of Erwin (1979) provides a general explanation of patterns of lineage radiation and extinction in carabid beetles. Regular changes in ecological and geographical distribution have now been recognised in many island systems (e.g., Cox and Ricklefs, 1977; Ricklefs, 1990). A number of studies have attempted to test these regular changes in distribution, but have failed to produce conclusive results (e.g., Johnston, 1975; Ricklefs and Cox, 1972, 1978; Pregill and Olsen, 1981; Jones et al., 1987; Liebherr and Hajek, 1990). Part of the problem may be the difficulty in recognising and defining stages within a cycle of distributional change versus merely documenting patterns (Pregill and Olson, 1981). In addition, it is often unclear as to the scale on which the cycle should operate. Failure to detect a cycle may indicate that insufficient time has elapsed for a pattern to develop. Alternatively, the cycle may have run its course, and the pattern of distributions it generated may have been obliterated by subsequent extinctions and interactions.

The recent development of phylogenetic analysis allows the prediction and testing of different biogeographical, ecological, and behavioral phenomena against an evolutionary framework (see Harvey and Pagel, 1991; Maddison and Maddison, 1992 for recent reviews). Such analyses therefore present an opportunity to measure the role of evolution in dictating changes in geographic and ecological range. Liebherr and Hajek (1990) used a cladistic approach to test the reality and generality of regular changes in distributions through the phylogeny of a lineage. They examined eight groups of New World carabid beetles and compared cyclic changes in habitat preference to patterns of data generated randomly under a null hypothesis. Their results did not support the predicted unidirectional shifts towards specialisation in habitat occupation.

The abundant evidence for ecological release and range expansion during the initial establishment of species in new habitats, and subsequent increase in range fragmentation and restriction (MacArthur et al., 1972), indicates that cycles of distributional change are real phenomena for some, and perhaps most, species (Ricklefs, 1990). Hence, tendencies towards extinction have an evolutionary component that is potentially predictable. The reason for the lack of evidence for such directional shifts in ecological and geographic range when tested using phylogenetic methodology may be a consequence of different mechanisms and levels through which a regular cycle in distributional range could potentially be achieved:

Conditions eliciting different patterns of distributional change

1. Colonisation

Populations frequently initiate a cycle of distributional change upon colonisation of a novel habitat or an unoccupied set of niches, during which they undergo ecological release, and expand their range, adopting a more generalised habit (e.g., Cox and Ricklefs, 1977; Otto and Svenson, 1982). During this period of release, divergence can occur rapidly (Carson, 1968, 1982; Carson and Templeton, 1984).

2. Adaptation

Over time, a population tends to adapt to local environmental conditions and/or be competitively displaced from part of its original range by new colonists. Concomitantly, the population may become fragmented, and its distributional range may be reduced. However, the evolutionary context of population fragmentation and change in distributional range is likely to depend on the extent of interdemographic gene flow and/or local selection:

a Minimal local differentiation. When a population of colonists is vagile with weak habitat associations, then very little local differentiation is likely to occur (Slatkin, 1985, 1987). The population would be constrained from differentiating on a local scale, a situation reflected in Figure 1A. Over time, range fragmentation and competition from heterospecifics would restrict the range of the colonists, increasing their vulnerability to extinction. But individuals could go on to colonise new environments as they became available. A regular change in geographic and/or ecological distribution would be evident if differentiation occurred subsequent to

colonisation. The youngest species would have the most widespread ecological and geographic distribution, while the oldest would have the most fragmented and/or restricted distribution.

- b *Considerable local differentiation.* If the population of colonists were more sedentary and/or had a stronger tendency to be associated with specific habitat types, then fragmented populations may differentiate due to local selection or genetic drift (Wright, 1951), and each isolate may become specialised to local conditions

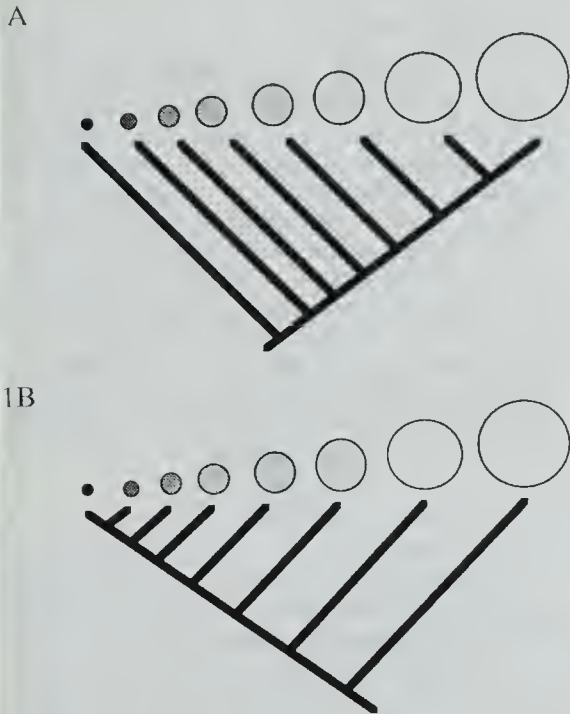


Figure 1. Hypothetical relationships between distribution and phylogeny of a lineage. The size of the circles reflects the geographic area occupied. Different patterns of shading indicate differentiation between taxa. (1A) The range of species is restricted over time since speciation (relictual contraction). Differentiation between taxa occurs subsequent to colonisation of a new habitat. At the same time, taxa also undergo geographic and ecological range expansion. Consequently, the most primitive taxa are the most restricted, the most widespread being derived. (1B) The range of species is restricted with each speciation event (adaptive contraction). Differentiation between taxa occurs within an area subsequent to colonisation. As taxa adapt to local conditions, they become more restricted in geographic and ecological range. Consequently, the most widespread taxa are the most primitive; most restricted derived.

(Rosenzweig, 1978, 1990; Wood, 1980; Bush and Howard, 1986; Wood and Keese, 1990). This situation is reflected in Figure 1B. Speciation would occur coincidentally with fragmentation of the initial population, and extinction probability would increase with each new taxon formed.

These different scenarios all suggest that phylogenetic affinity could play an important role in dictating geographic range, and hence vulnerability to extinction. However, the evolutionary causes and distributional consequences differ for each situation. Therefore, there may be contrasting patterns of phylogeny underlying similar present-day patterns of geographic and ecological range. Previous studies have shown that for more vagile taxa, where speciation would most likely be dictated by geographical separation, the most ancestral species appear to be the most specialised and have the smallest ranges, while the most derived species are more generalised and/or widespread (Mindell et al., 1989; Moran, 1988; Carson and Kaneshiro, 1976). Alternatively, in less vagile species, or those exhibiting a propensity towards fine scale ecological isolation, it is possible for divergence to occur between contiguous habitats. Examples of less vagile/ecologically specialised groups might include cave-dwelling spiders (Cesaroni et al., 1981), some beetles (Ball, 1985; Erwin, 1985; Howden, 1985) and ants (Wilson, 1961) and perhaps also some vertebrates (e.g., salamanders, Larson et al., 1981). In each of these cases, the derived species appear to be the more specialised and restricted.

Speciation (Gillespie, 1991 a, b, 1992a, 1993; Gillespie and Croom, 1995; Gillespie et al., 1994) and extinction (Gillespie, 1992b; Gillespie and Reimer, 1993) have recently been examined in a radiation of spiders in the long-jawed orb-weaving genus *Tetragnatha* in the Hawaiian Islands. The tetragnathid radiation spans a tremendous spectrum of morphologies, ecological affinities, and behaviors. One entire clade of 16 species ('spiny-leg' clade) has abandoned web building, with the concomitant adoption of a vagile, cursorial predatory strategy. A second clade ('elongate' clade) consists entirely of sedentary web-building species. In this study the Hawaiian *Tetragnatha* are used to examine distributional changes through phylogeny. The tendency of lineages to expand or contract their range during their evolutionary history is then tested using the methodology developed by Nee and colleagues (Nee et al., 1992, 1994; Harvey et al., 1994) to investigate historical properties of a

clade using the geometric distribution of coalescent events in a reconstructed molecular phylogeny. If time is scaled by the expected interval between coalescences ($1/[n(n-1)/2]$, Kingman, 1982), then a linear relationship results between the number of lineages and scaled time (Nee et al., 1995). However, if, instead of being linear, the relationship is

1. convex, then the time between coalescences is greater than expected, consistent with a population/species that was expanding during this period in history;
2. concave, then the time between coalescences is less than expected, consistent with a population/species that was shrinking during this period in history.

This theory is used to examine range expansion/contraction of two lineages during their evolutionary history:

1. the *planitibia* clade of Hawaiian 'picture-winged' *Drosophila* (DeSalle, 1995); and
2. two Kauai clades of Hawaiian silverswords, genus *Dubautia* (Baldwin and Robichaux, 1995).

Methods

Hawaiian Tetragnatha

Preliminary analysis of phylogenetic relationships have been conducted for two clades of Hawaiian *Tetragnatha* that differ in vagility: The actively foraging spiny leg clade and the more sedentary web-building 'elongate' clade (Gillespie and Croom, 1995). Analysis of the 'spiny-leg' clade was conducted using fixed differences between allozyme loci for 5–30 individuals from 1–5 populations of the species in the 'spiny leg' clade. The allozymes GPDH, G3PDH, 6PGDH, IDH-1, IDH-2, ME, PGI and PGM were used (Richardson et al., 1986). For the 'elongate' clade phylogenetic relationships among species were examined using morphological information only (30 characters related to cheliceral armature, leg spination, color of the cephalothorax and abdomen and structure of the male palp) (Gillespie and Croom, 1995). Characters were analyzed using parsimony in PAUP (Swofford, 1993), and were scaled for equal character weighting regardless of the number of states.

Hawaiian 'picture-winged' *Drosophila*:

D. planitibia clade

Phylogenetic relationships have been established for the *planitibia* clade of Hawaiian 'picture-winged' *Drosophila* using mtDNA RFLPs (DeSalle, 1995). The *planitibia* clade comprises

the following taxa: *D. cyrtoloma* Hardy and Kaneshiro, *D. melanocephala* Hardy, *D. hanau-lae* Hardy, *D. neoperkinsi* Hardy and Kaneshiro, *D. obscuripes* Grimshaw, *D. nigribasis* Hardy, *D. oahuensis* Grimshaw and *D. neopicta* Hardy and Kaneshiro (alpha clade), and *D. silvestris* Perkins, *D. heteroneura* Perkins, *D. planitibia* Hardy, *D. differens* Hardy and Kaneshiro, *D. hemipeza* Hardy, and *D. neopicta* Hardy and Kaneshiro (beta clade). The distance between species was examined using a Kitch analysis (Phylip, Felsenstein, 1993), which is based on the assumption of constant evolutionary rates.

Hawaiian silverswords

Phylogenetic relationships have been established for the Hawaiian silverswords using ITS region sequences (Baldwin and Robichaux, 1995). For this study, two clades with representatives confined to Kauai (except where noted) were used: *D. latifolia* (A. Gray) Keck, *D. paleata* A. Gray, and *D. raillardioides* Hillebr. (one clade), and *D. imbricata* H. St. John and G. Carr, *D. knudsenii* Hillebr., *D. laevigata* A. Gray, *D. laxa* Hook and Arnott (Kauai, Oahu, Maui), *D. pauciflorula* H. St. John and G. Carr, *D. microcephala* Skotts., *D. plantaginea* Gaud. (Kauai, Oahu, Maui, Hawaii) (second clade). As with the *Drosophila*, The distance between species was examined using a Kitch analysis.

Results

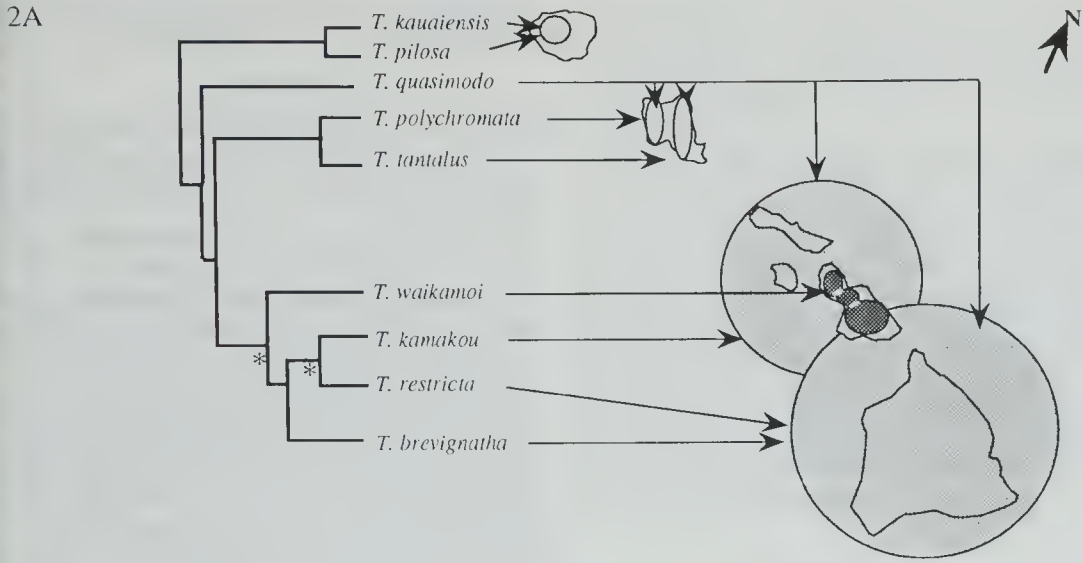
Hawaiian *Tetragnatha*

The 'spiny-leg' clade allozyme results yielded large genetic distances between species (considering polymorphic loci only, Nei's $D > 1$ between *T. pilosa* and both *T. brevignatha* and *T. restricta*). The pattern of relationships is shown in Figure 2A. The morphological characters for the 'elongate' clade gave two equally parsimonious trees, length 61 (CI 0.731, RI 0.775) (Fig. 2B shows strict consensus) (Gillespie and Croom, 1995).

Hawaiian 'picture-winged' *Drosophila*:

D. planitibia clade

Distances between nodes were transformed by multiplying inter-node intervals by $n(n-1)/2$ (Nee et al., 1995). The number of lineages were then plotted against the transformed distances. The result was a convex curve, indicating a decreasing rate of branching as the present time is approached (Fig. 3A). This suggests that population sizes have been expanding over the phylogenetic history of this clade.



2B

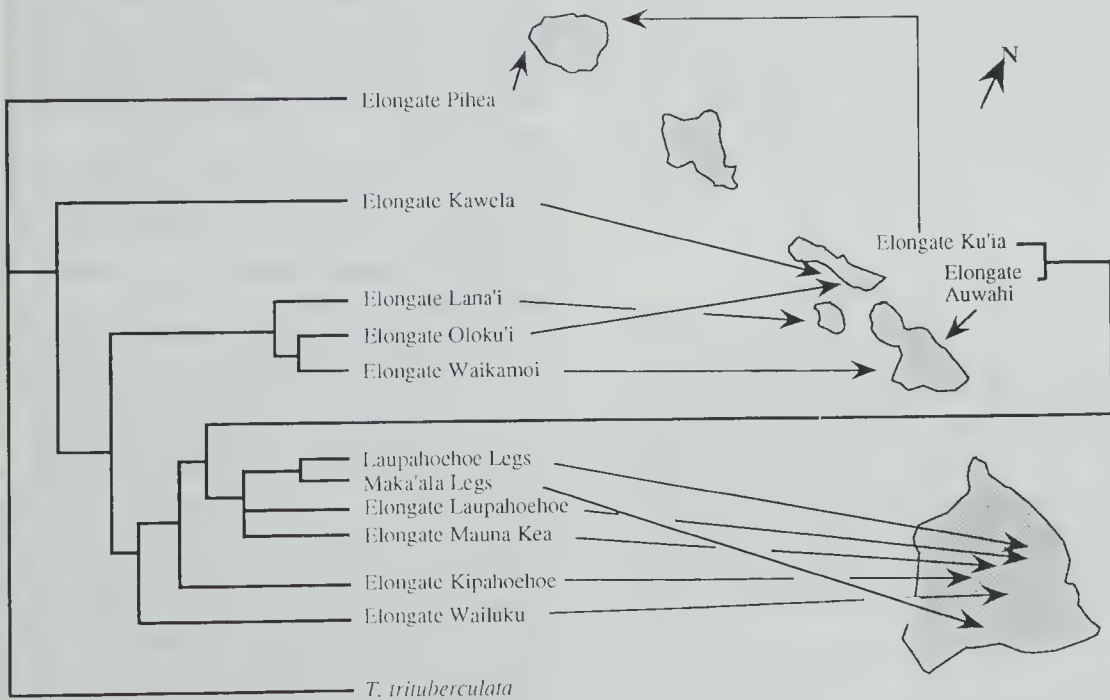


Figure 2A. Pattern of distributional change of the Hawaiian 'spiny leg' *Tetragnatha* through the Hawaiian archipelago based on allozyme data. 2B, Phylogeny of the 'elongate' clade of Hawaiian *Tetragnatha* based on morphological characters (from Gillespie and Croom, 1995). Because representatives of the 'elongate' clade have not yet received formal descriptors, a taxonomic unit was defined for the purpose of the analysis as a population exhibiting a distinct set of characters unique to a given island.

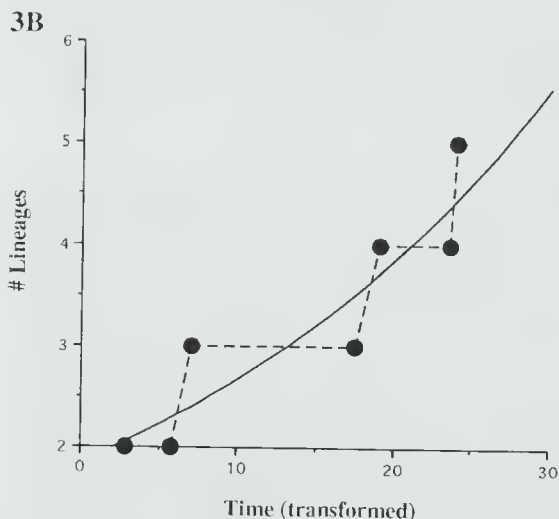
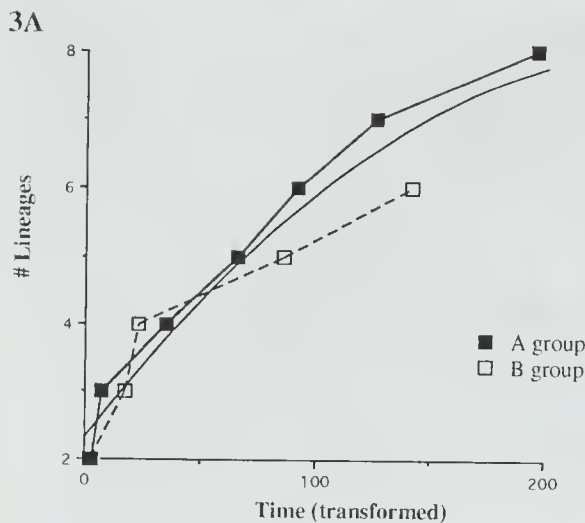


Figure 3A. *Drosophila: Planitibia* Lineage. The curve for the alpha group was not significant (uniform conditional test, Cox and Lewis, 1966: Kolmogorov test statistic, $D = 0.248$, $n = 7$, $0.10 < p < 0.15$), and can only be considered a tendency. However, the curve for the beta group was significant ($D = 0.438$, $n = 6$, $p < 0.01$). 3B. *Dubautia*: Two Lineages from Kauai. The uniform conditional test showed that the curve was significant (Kolmogorov test statistic, $D = 0.275$, $n = 9$, $p < 0.05$).

Hawaiian silverswords

As for the *Drosophila*, the number of lineages were plotted against transformed distances. The result was a concave curve, indicating an increasing rate of branching as the present time is approached (Fig. 3B). This suggests that

population sizes have been decreasing over the phylogenetic history of this clade.

Discussion

Natural factors affecting distributional range

For the 'spiny-leg' (vagile) species of Hawaiian *Tetragnatha*, the allozyme results showed that:

1. Taxa on any one island tend to be most closely related to taxa on other islands;
2. In general, the most derived taxa occur on the youngest island and have the broadest ecological and geographical range.

It might be argued that this effect is an artifact of the larger size of the youngest island. However, all species on the youngest island (Hawaii) range from 300 to >2000 my, and occur in dry — wet forest on all five volcanoes as well as on Maui, whereas on the older islands (Oahu and Kauai) single species are confined to narrow elevational and environmental ranges and are endemic to single volcanoes within each island. In *T. quasimodo*, a relatively ancestral species that is found throughout the islands, populations on the youngest islands have a much greater geographic and ecological range than those on the older islands, consistent with all the other species in the clade. The phylogeny of the 'elongate' clade of Hawaiian *Tetragnatha* suggests that:

1. certain groups have diversified within an island (cf Hawaii Island);
2. The most derived taxa occur on the youngest island; and
3. ranges are smaller for groups that have diversified within an island.

The molecular phylogenies of the Hawaiian *Drosophila* and silverswords revealed intriguing results, and showed the usefulness of this type of analysis for examining changes in distribution through the evolutionary history of a lineage. The *Drosophila* showed a pattern of increasing population size in the component species through the phylogeny of the lineage. This pattern is consistent with the model presented above: *Drosophila* tend to speciate between land masses only, likely because of substantial gene flow prohibiting species formation within islands. As a consequence, speciation will be associated with colonisation of a new land mass, and rapid expansion of the newly derived species, as indicated in Figure 3A. Similarly, for the Kauai silverswords, the large number of species with closest relatives on the same island suggests that local differentiation is possible. As a consequence, speciation

is associated with decreasing population sizes of the derived species as indicated in Fig. 3B.

Anthropogenic factors affecting distributional range

Many species are likely to be products of natural restriction, maintaining healthy and abundant populations within these limited ranges. However, many species are restricted as a direct consequence of anthropogenic restriction on an otherwise widespread population. Two examples from Hawaii are considered.

Tetragnatha albida Gillespie occurs in remnant dry forest of Auwahi, East Maui, a discrete dryland community on unweathered lava with little soil formation (Gillespie, 1994). Individuals build webs in the trees at night, and spend the day camouflaged against white lichen that covers many of the trees. Auwahi is recognised as the finest dryland forest in the Hawaiian Islands (Rock, 1913). However, despite its high diversity of dry forest tree species, many of these trees are not reproducing (Medeiros et al., 1986). More importantly for the unique spider fauna, the aggressive ant *Pheidole megacephala* (Fabricius) is found immediately below the range of *T. albida*, and appears to be expanding its range upwards (Medeiros, pers. comm.). Ants are the most notorious of all alien invertebrate predators because of their effect on the native Hawaiian biota (Perkins, 1913; Howarth, 1985; Howarth and Medeiros, 1989; Gillespie and Reimer, 1993), and are likely responsible for the extirpation of *T. albida* from much of its native range: *T. albida* is part of a phylogenetically derived lineage of Hawaiian *Tetragnatha*, and most likely its historical range was broad. The population would probably respond well to active management of alien species.

A second species of tetragnathid, *Doryonychus raptor* Simon, is almost entirely confined to small, remnant pockets of lowland forests directly below high waterfalls on the island of Kauai. *D. raptor* exhibits one of the most remarkable morphological features ever found in spiders (Simon, 1900, Gillespie, 1992b): The prolateral claws on the tarsi of leg pairs I and II of *D. raptor* are immensely elongated and the spider captures insects using only these claws to impale prey and draw them to the chelicerae in a single, rapid movement. The spider is phylogenetically ancient (Gillespie et al., 1994), and its small distributional range may reflect its evolutionary 'relictual' nature. However, within its small range, the species is abundant. Never-

theless, because many aggressive ants are broadly expanding their ranges in lowland habitats throughout the Hawaiian Islands, species such as *D. raptor* are extremely vulnerable to extirpation.

In conclusion, the identification of species with naturally restricted ranges can allow the adoption of suitable management practices for mitigating the impact of anthropogenic disturbance. Novel ecological interactions, such as competition and predation by alien species, are likely to affect extinction much more rapidly than changes that occur over evolutionary time. The form of a management plan, and the ability of a species to respond, will be affected by its natural distributional range, and, as is argued here, it is also likely to be a product of its phylogenetic legacy.

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