Colonizing species: a probe into evolution via the organism

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By concentrating upon the ecobehavioural components of the phenotype, colonizing species provide a probe into evolution via the organism. Genetic studies of colonists are being developed to reconcile contrasting approaches based upon the gene and the organism as units of natural selection, and to advance understanding of evolutionary transitions.

Colonizing species typically invade disturbed, ephemeral, and marginal habitats, where sporadic and unpredictable environmental selection leads to dramatic changes in the distribution and abundance of populations and species. These features will also be important at the boundaries of species distributions from which colonists are likely to be derived.

Ecologists frequently classify life-history characteristics of species into an r-K continuum whereby, under favourable conditions, population size increases exponentially at a rate determined only by its net reproductive rate, r (figure 1). Eventually, however, individuals interact with each other and compete for resources so that the increase in number slows to a point where the population size tends towards constancy at its carrying capacity, K (figure 1). Populations of colonizing species tend to increase exponentially under favourable conditions. They are, therefore, typical r species, which include many insects, especially pests, and weed plants. In less ephemeral and more benign habitats, numbers are assumed to vary less because the environment is more stable; this is a situation tending towards K-selection. Under these circumstances, the major factors affecting population size have been argued to be

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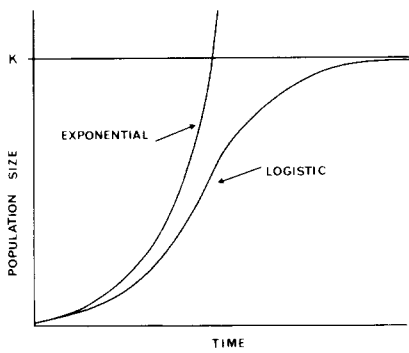
predators, parasites, and competitors, whereby rarer phenotypes are likely to be at a selective advantage [1]. Such frequency-dependent selection should be a powerful force in maintaining genetic diversity if populations are in some sort of equilibrium with their resources. But it is important to note that recent theoretical and experimental work is placing less emphasis on this model [2].

Colonizing species should therefore provide a probe into evolution in circumstances when some of the phenomena important under K-selection can be largely discounted. A simplicity in genetic analysis at the individual and population level should follow.

Changes during range-expansions

During a range-expansion, repeated exposure to climatic stress implies selection for increased tolerance to the stress. For example, the insect genus *Drosophila* is believed to have evolved in the humid tropics, and subsequently spread to the temperate zone [3] characterized by a seasonal pattern of cool wet ·winters and warm dry summers, where temperature ·extremes exceed those of the tropics. In agreement, species from non-tropical habitats have evolved substantially greater tolerance to climatic extremes, as measured in the laboratory by resistance to extremes of temperature and desiccation (figure 2). More generally, an analysis of the adaptations of the Australian flora shows that extremes of temperature are important biogeographically [4] because they correlate well with floral type. In addition, severe climatic selection can lead to quite dramatic changes in the distribution and abundance of species over short periods of time. Under such circumstances, competition between species—a dominant theme for many ecologists—can be regarded as unimportant [5]; this in itself highlights the importance of abiotic factors, in particular climate, in explaining the distribution and abundance of species.

Within species, selection for tolerance to environmental extremes should be most intense at the margins. Furthermore, climate, assessed directly or indirectly by some function of temperature, is likely to vary over the distribution of a widespread species, especially in temperate zones. It therefore follows that the phenotypes and genotyes of widespread species should track temperature in some way. This has been found at the phenotypic level for insect morphology, in particular body size. Indeed, there is good evidence for local differentiation due to the direct effects of climatic selection, although high levels of migration in some widespread species may cause some blurring.

At the genotypic level, allele frequencies of many electrophoretic polymorphisms (for example, alcohol dehydrogenase in *Drosophila melanogaster*) show correlations with temperature on a geographical basis. Using human data, two-thirds of 35 enzymes or proteins show significant associations with climate and hence—directly or indirectly—with temperature [6]. Such associations are predictable given the importance of temperature for all biological processes. However, an approach based upon single loci cannot provide a full understanding of the ecologically important characteristics of central, marginal, and colonizing populations. Indeed, while many elegant laboratory and field studies on enzyme variation have shown that selection acts at these loci [7], it does not follow that this variation is important in major evolutionary shifts involved in the occupation of new habitats differing ecologically from those of source populations. The enormous heterogeneity found at the breeding site (individual fruit) level in *D. melanogaster* (Table 1) for three polymorphic electrophoretic loci—which greatly exceeds that among adults collected at baited traps within populations—strongly argues against the direct involvement of this type of variation in

Figure 1 Population growth curves. The exponential growth in an environment of unlimited resources depends upon the net reproductive rate, r. In a limited environment, the logistic curve is more likely, where the population size approaches K, the carrying capacity.

northern Queensland to south-eastern Victoria (latitudes 17°S to 38°S) over a climatic range from tropical to temperate. It is a remarkably efficient pest of unripe fruit, and any one of about 150 hosts will suffice. Indeed, in a climatically favourable region, *D. tryoni* will almost certainly locate every orchard or even isolated tree where fruit is developing. The mean lethal time (LT_{50}) in hours for tolerance to cold and heat stress for adults of strains ranging from the tropics to the temperate zone (figure 3) indicates increasing tolerances towards the south. This is to be expected, because temperatures become more extreme away from the tropics. This result parallels that found among *Drosophila* species in figure 2, and analogous results have been found within *D. melanogaster* and its sibling species *D. simulans*. Combining these results with the above conclusion [4] that extremes of temperature play an important role in biogeography, and hence in the distribution (and abundance) of organisms, it follows that extremes of temperature (and desiccation) are important ecological phenotypes.

How are ecological phenotypes analysed genetically? In genetically well-known organisms, especially *Drosophila melanogaster*, genetic activity can be localized to chromosomes and regions of chromosomes based upon extreme strains from a population, or those derived by a selection procedure. Following such an analysis, the involvement of electrophoretic loci with an ecological phenotype should become apparent more directly than by using electrophoretic loci as the primary assessment. Ecological phenotypes—which tend to be quantitative—based upon the organism as the unit of selection should, therefore, form the basic data. Comparisons among populations, each based upon several strains, should then enable the genetic dissection of ecologically central, marginal, and colonizing populations. It means a phenotypic approach to ecological genetics on the interface of ecology and quan-
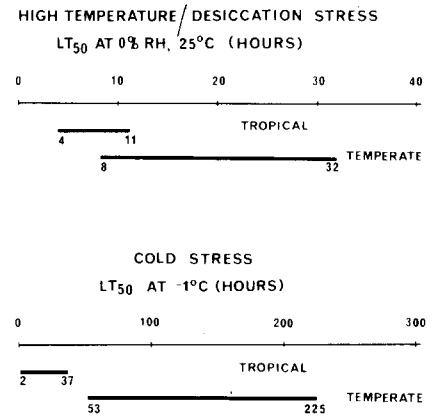

Figure 2 Range of LT_{50} values (number of hours at which 50% of flies died from stress) for nine tropical and 10 temperate-zone *Drosophila* species. For cold tolerance, there is no overlap across zones and for high temperature/ desiccation the overlap is minimal comprising only *Drosophila simulans* which is a cosmopolitan species distributed across both zones.

titative genetics [11], additional to the more usually considered genotypic interface of ecology and population genetics (Table 2). On the borderline between the two extremes are situations where ecological phenotypes are controlled by just one or two genes; for example, a population of *D. melanogaster* where a single locus accounted for most of the response to selection for reduced heat tolerance [12].

At the genotypic level, steadily accumulating evidence suggests that the major underlying genetic component of quantitative traits is a few (less than 10) nuclear genes that can be studied individually. In *D. melanogaster*, this conclusion comes from studies on the location of genes controlling quantitative morphological traits; from the irregular responses of quantitative traits to laboratory selection; and from the characteristics of variation within and among strains set up from single-inseminated females from natural populations. Even if a continuous distribution for a trait is found, it may still be consistent with a genetic architecture consisting mainly of a few genes. Assuming a few genes, colonization into a new ecological niche could occur quite rapidly. During a climate-induced population crash, only a few individuals survive, and these may be resistant to climatic stress. If resistant phenotypes are heterogeneous for genes for tolerance to climatic stress in marginal populations, then quite rapid responses to selection imposed by the stress could occur, provided that the selection intensity is sufficiently high.

A major difficulty in understanding changes during colonization is the very

evolutionary shifts including colonizing events [8]. The basic problem is that questions of ecological importance are frequently asked *a posteriori* in a statistical sense. While significant correlations are often obtained, fundamental biological interpretations are frequently elusive. The single locus (or chromosome) approach is often informative, but cannot provide the whole understanding of ecologically important characteristics because of multiple loci, linkage, and interactions between loci.

Ecological phenotypes
H. G. Andrewartha and L. C. Birch in a classic—but recently rather neglected—book [9] argue for the fundamental importance of habitat as determined by climate, or physical (abiotic) factors and resources, or biotic factors, in the determination of the distribution and abundance of animals. In contrast with the above genotypic approach, this approach based upon ecologically important characteristics or ecological phenotypes, is a logical starting point for understanding range-expansions of natural populations. A colonizing species, the Queensland fruit fly, *Dacus tryoni*, occurs from

TABLE 1 STANDARDIZED VARIANCES AT THREE ELECTROPHORETIC LOCI IN *DROSOPHILA MELANOGASTER* [8]. THE FLIES WERE COLLECTED FROM THE SAME OVERALL LOCALITY IN AN ORCHARD NEAR MELBOURNE, VICTORIA

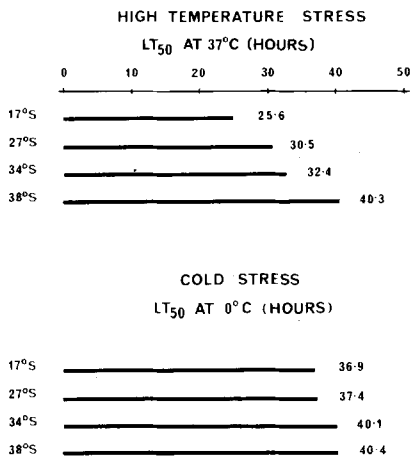| Locus	Triosephosphate isomerase	Glycerophosphate isomerase	Alcohol dehydrogenase
Among breeding sites (individual fallen ripe fruits)	0.046	0.039	0.030
Among adults (baited traps)	0.013	0.012	0.013

Figure 3   Climatic races in the Queensland fruit fly, *Dacus tryoni*, assessed by LT$_{50}$ values (number of hours at which 50% of flies died from stress) for four populations from Cairns (latitude 17°S), Brisbane (27°S), Sydney (34°S), and East Gippsland (38°S). [Drawn from data in [10]]

small number of cases where the actual introductions or range-expansions are documented. For example, population sizes at the time of the introduction and during the range-expansion immediately following are usually unknown, as are possible changes in ecological phenotypes and other components of the life-history of an organism. Electrophoretic data are often obtained, and gradients after the introduction certainly act as 'markers' of genetic change. Such a gradient occurs for the sorbitol dehydrogenase (*Sdh*) locus in the marine toad, *Bufo marinus*, introduced into Queensland, Australia, in 1935 (101 individuals), which has now spread over a substantial portion of the state (figure 4). Yet spread will almost certainly be limited by
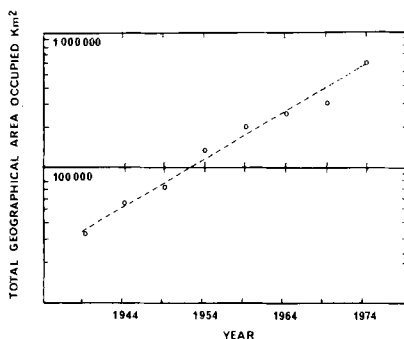

Figure 4   Range expansion of the marine toad, *Bufo marinus*, across the state of Queensland, Australia, following the primary introduction in 1935. The average annual growth rate is 8.1%. The line is drawn using a least-squares fit [13]. The total area of Queensland is 1.728 × 10^6 km^2.

temperature and moisture [13]; the southern distributional limit will probably be determined by cold climate whereas spread to the arid interior will probably be limited by insufficient breeding sites due to lack of water. However, temperature and moisture should not limit the present population expansion across the monsoonal northern portion of Australia. Detailed work on climate-related ecological phenotypes are therefore essential, as also deduced from recent studies on the northern limits to the spread of the wild rabbit in Australia [14].

Resource utilization
Resource utilization comprises a second major component of the ecological phenotype. Species of the genus *Drosophila* almost certainly entered the man-made fermented-fruit habitat of orchards and urban areas from more austere habitats comprising slowly decomposing leaves and plant parts in rainforests, and the plants themselves [3]. Such an austere existence may well have provided a step towards the exploitation of the fermentation mode of

existence in forest habitats, and ultimately range-expansions into man-made habitats.

After exposing adults to various concentrations of ethanol-water vapour mixtures, five *Drosophila* species collected in Australia can be ranked into three groups for ethanol resource-utilization thresholds:

(a) *D. melanogaster*   >

(b) *D. lativittata*
    D. nitidithorax   >

(c) *D. inornata*
    D. hibisci

Groups (a) and (b) species are attracted to fermented-fruit baits but not normally group (c) species, which utilize little or no ethanol. *D. melanogaster* (a) is a colonist, being common in urban and orchard habitats on a

world-wide basis, while group (b) species are spreading into orchard and urban habitats. *D. hibisci* utilizes flowers of endemic *Hibiscus*, and *D. inornata* is collected by sweeping foliage close to water in temperate-zone rainforests. Both of these group (c) species appear not to have major active alleles at the alcohol dehydrogenase (*Adh*) locus as assessed electrophoretically [15], and for simplicity can be called *Adh*-null (figure 5). In contrast, group (b) species are polymorphic for 'high activity' and *Adh*-null alleles, which means that rapid changes could occur during colonization into a fermented-fruit habitat compared with the more resource-specific *Adh*-null species. Even so, *D. inornata* utilizes very low levels of ethanol as a resource, and under climatically non-stressful situations is occasionally found on the edge of urban areas in southern Australia. During such colonizations, an active *Adh* allele could be favoured with consequent higher ethanol tolerance, so that spread into the fermented-fruit habitat could occur. Therefore a change from a rather austere, and

TABLE 2   APPROACHES TO ECOLOGICAL GENETICS

	Primary Traits considered	Primary unit	Approach
Ecology + quantitative genetics	Quantitative ecological phenotypes	Organism	Phenotypic
Ecology + population genetics	Gene (electrophoretic) + chromosomal variants	Gene	Genotypic

probably specialized, habitat towards generalism may be based initially upon one gene leading to an ecobehavioural change concerning resources utilized, and so opening up a previously unoccupied category of habitats. Regrettably, as in the examples cited earlier, this is an *a posteriori* hypothesis based upon ethanol tolerance as an ecological phenotype. A deeper understanding of this phenotype within and among species is needed, especially as the relationship between ethanol tolerance and the status of the *Adh* locus obtained from studies of populations of *D. melanogaster* is complex.

Environmental stresses and genetic variation
In this discussion ecological phenotypes have been described based upon different mortalities as the metric. In general, differences among phenotypes are maximized when stresses are severe.
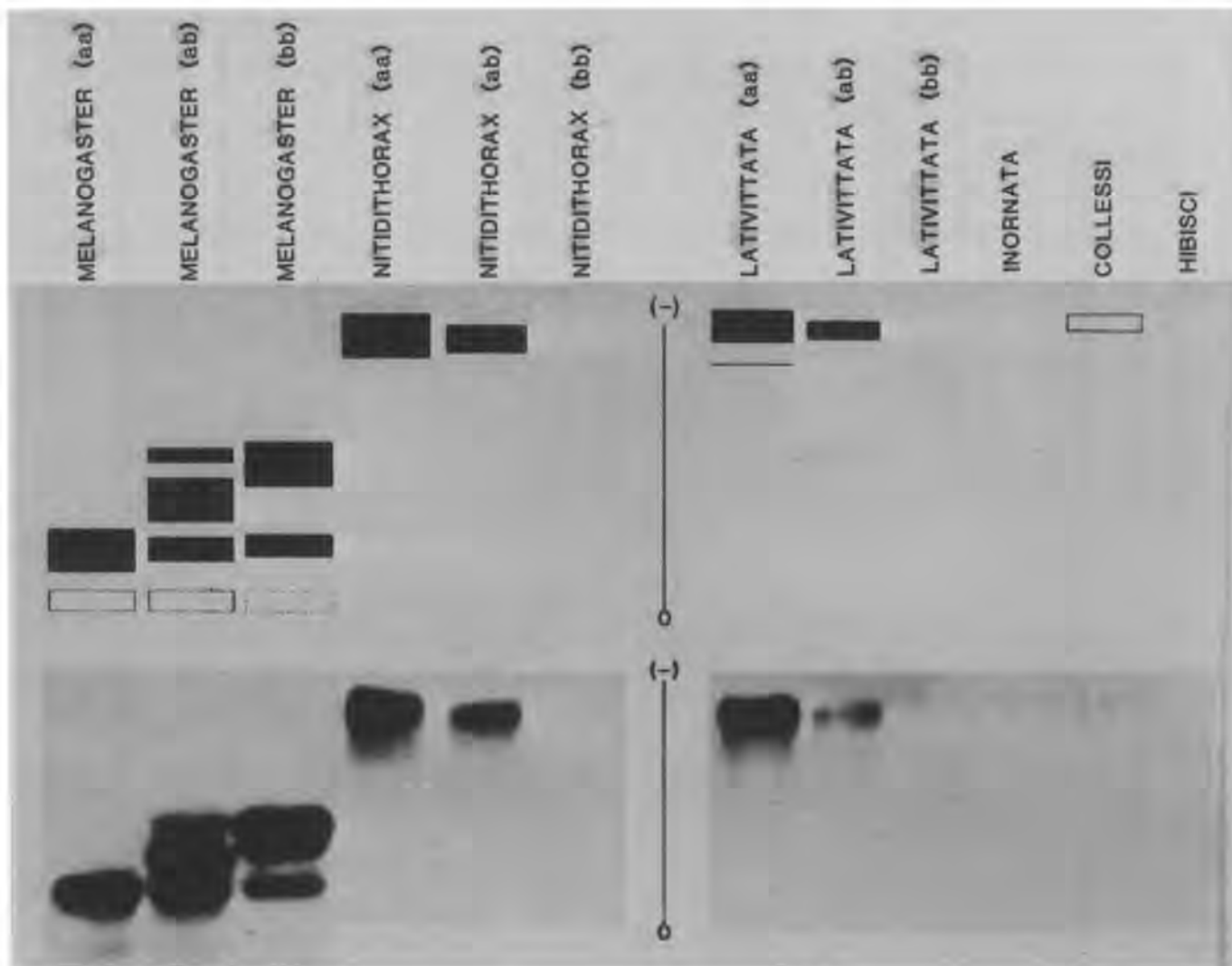
Figure 5 Electrophoretic variants of alcohol dehydrogenase (ADH) from various endemic Australian *Drosophila* species, and the cosmopolitan species *D. melanogaster*. Note that group (c) species *D. inornata* (and a close relative *D. collessi*) and *D. hibisci* are effectively *Adh*-null, while the group (b) species *D. lativittata* and *D. nitidithorax* are polymorphic for 'high-activity' and *Adh*-null alleles [15].

This applies to both physical stresses and to resource utilization measured by exposing flies to ethanol or acetic acid vapour. Under these conditions, the genetic basis of ecological phenotypes is mainly additive, but when death rates are not affected so drastically, the additive component tends to be lower and, furthermore, interactions between genotype and environment may be large. Therefore during colonization involving ecological change under conditions when selection pressures are intense, rapid genetic changes are likely because of large differences between phenotypes.

Clearly, rapid evolution depends upon the relevant genes being heterozygous in natural populations. However, phenotypic homogeneity tends to be found in marginal popula-

tions for ecological phenotypes because of continuous phenotypic selection for the extreme conditions. In contrast, marginal populations have a tendency to be more heterozygous for electrophoretic loci than do populations from more benign habitats, unless small population sizes are frequent. Accordingly, variability levels at electrophoretic loci cannot be regarded as a predictor of colonizing potential, even though there is often a statistical association between heterozygosity level, fitness, and environmental stress in outbred populations. The only real solution appears to be a direct knowledge of the specific genes directly underlying ecological phenotypes—an analytical procedure at present restricted to very few organisms, in particular *D. melanogaster*.

Evolutionary transitions
A genetic architecture of a quantitative trait dominated by a few genes is consistent with discontinuities in the fossil record, whereby long periods of stasis tend to be interrupted by short periods of rapid change. For example, in a sequence of East African fossil beds containing freshwater molluscs, long periods of morphological stability were interrupted by fossil beds in which relatively rapid changes in shell size took place for several lineages common enough for detailed analysis [16]. During these periods of rapid change, there is evidence for major lacustrian regressions when the fauna was probably isolated and stressed. This suggests synchronous environmental stresses affecting all lineages in parallel ways, corresponding to periods

of ecological stress. The analogy with the need for colonists to adapt to environmental stresses is clear; however, the time-scale is magnified. Even so, it can be argued both for colonization of new habitats on a measurable time scale and for evolutionary change, that adaptation to new habitats in the broadest sense is likely to show discontinuities whereby long periods of relative phenotypic stability are interspersed by genetic revolutions producing rapid phenotypic change [17].

Again, this is an *a posteriori* approach to evolutionary change, since the genes underlying ecological phenotypes involved in adaptation to new habitats have not been followed in the fossil record! Evolutionary trees have been constructed from electrophoretic loci, and over this very long time-span, there is a general correlation of evolutionary divergence measured morphologically, behaviourally, and electrophoretically. However, large shifts in the means of morphological and ecological traits within species, without major changes in electrophoretic loci, have been found in *D. melanogaster* [8]. Indeed, closely related species of Hawaiian *Drosophila* [18] may be almost indistinguishable electrophoretically (and also chromosomally) compared with obvious divergences of quantitative morphological and behavioural traits for which major genes are often locatable [19]. Discontinuities with electrophoretic variation observed at the speciation level for quantitative traits, however, become ultimately damped down in evolutionary trees. This is consistent with the indirect effects of natural selection on most electrophoretic loci in natural populations, compared with ecological phenotypes.

Discussion and conclusions

Within the genus *Drosophila*, colonizing species tend to be physiologically tough and relatively easy to culture in the laboratory, compared with non-colonist species which tend to be specialised, physiologically sensitive, and more difficult to culture. When considering the distribution of *Drosophila* species in Australia, non-colonist species occur mainly in undisturbed rainforests where physiological tolerance is

at a lower premium than for the colonists of urban and orchard habitats. The very small overlap between the *Drosophila* faunas of the two habitat categories is, therefore, to be expected. A greater understanding of these two faunas is now beginning to come from a comparison of the ecological phenotypes of their component species. At the genetic level, studies are rudimentary but a probe into the genetic basis of ecological traits of colonizing species such as *D. melanogaster* seems an appropriate initial step.

While this article mainly considers *Drosophila*, it is important to extrapolate to additional organisms where genetic analyses are possible and ecological phenotypes can be defined, e.g. the fruit-fly genus *Dacus*. A comparison of the house mouse, *Mus musculus*, with its various relatives is another possibility, given its economic significance as a pest in urban and agricultural regions.

By way of a summary, the probe into evolution proposed by concentrating upon colonizing species is based firmly on the organism as the unit of selection [20]. The organism can be considered as a behavioural phenotype, ecological phenotype, metabolic phenotype, electrophoretic phenotype, biochemical phenotype, physiological phenotype, morphological phenotype, and so forth, according to emphasis. All are important in understanding colonizing events, but in adapting to new habitats in the broadest sense, ecobehavioural components of the phenotype dominate. This contrasts with an alternative—and commonly considered—probe via the gene as the unit of natural selection. An ultimate aim is convergence in approaches, as occurs in evolutionary time. One outstanding current problem in obtaining convergence is to reconcile electrophoretic—and more generally molecular—variation with ecobehavioural variation (Table 2). Because of the ecological extremes to which colonizing populations are subjected, phenotypic and genotypic differences are magnified and hence simpler to study, compared with more favourable situations. Colonizing species may therefore provide the necessary probe to reconcile the contrasting approaches to

evolution based upon the gene and the organism as the unit of natural selection.

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